Biogeography and ecology of beetles in a tropical archipelago:
A case study from Kepulauan Seribu Marine National Park

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by

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I, Shinta Puspitasari, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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Abstract

Beetles comprise not only the most diverse group of insects, but also contribute significantly to vital ecological functions. A quantitative formula to determine the optimal level of investment in the beneficial beetle conservation is still not available. I aim to establish specific attention to beetles and their role in tropical island ecosystems in small archipelago in Indonesia. The study aims to give further insights into beetle diversity patterns on islands in the Kepulauan Seribu Marine National Park and on Java, and how island isolation and area affect assemblage composition. My research also provides insights into the effects of anthropogenic activities on beetle diversity on these islands.

A first important result is the substantial number of highly abundant island species and a high number of unique island species found in the study areas, indicating islands as potentially important for the global conservation of genetic resources. My results also highlight the highly varied results relating to the use of two different types of traps, pitfall traps and FITs, for sampling beetles. It underscores the need for complementary trapping strategies using multiple methods for beetle community surveys in tropical islands. When testing the equilibrium theory of island biogeography using beetle assemblages, the overall results of this study chiefly support the classic theory of island biogeography. My works also highlight the impacts of anthropogenic activities. The positive effects of such human activities on the overall species richness of beetles are clearly reflected in my result. More island beetle species encountered chiefly in settlement areas than forest species. However, when comparing the type of forest habitat on the islands, undisturbed forests harbour a higher number of unique species than disturbed forests. Finally, this study suggests that the diversity of herbivorous beetles on islands is strongly affected by the different levels of forest cover encountered.

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Abbreviations

CBD	Convention on Biological Diversity
CCA	canonical correspondence analysis
CNESS	chord-normalized expected species shared
DCA	detrended correspondence analysis
ETIB	Equilibrium Theory of Island Biogeography
FF	undisturbed forest
FIT	flight interception trap
FSF	disturbed forest habitat
IPC	island principal component
IUCN	International Union for Conservation of Nature
MLR	multiple linear regression
NMDS	non-metric multidimensional scaling
PC	Principal Component
PCA	Principal Components Analysis
PT	pitfall trap
RDA	Redundancy analysis
SD	Standard deviation
SS	settlement
SSF	settlement on mixed habitat island
SSR	species sampling relationship
SAR	species area relationship
UNEP	United Nations Environmental Programme

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Chapter 1. Introduction

1.1. <u>Insect Diversity</u>

1.1.1. The importance of insects

Insects are important because of their diversity, ecological role, and influence on agriculture, human health, and natural resources. They have been used in landmark studies in biomechanics, climate change, developmental biology, ecology, evolution, genetics, paleolimnology, and physiology. Because of their many roles, they are familiar to the general public.

Insects create the biological foundation for all terrestrial ecosystems. They cycle nutrients, pollinate plants, disperse seeds, maintain soil structure and fertility, control populations of other organisms, and provide a major food source for other taxa (Majer, 1987). Virtually, any depiction of a food web in a terrestrial or freshwater ecosystem will show insects as a key component although food web architectures of these two ecosystems are quite different (Shurin et al., 2005).

Insects are of great importance as a source of food for several predators. Aquatic insect larvae serve as food for fishes, and many stream fish appear to be limited by the availability or abundance of such prey, at least on a seasonal basis (Richardson, 1993). Insects provide the major food supply of many lizards. Many amphibia are carnivorous, especially after they reach maturity, and insects form the bulk of their animal food (Brues, 1946). Birds of many families take insects as their staple food, at least during part of the year (Carpenter, 1928; Orians, 1966). Mammals, such as the American anteater, sloth bear, and the African and Oriental pangolins are especially tied to ants and termite colonies, and some mammalian predators use insects as food (Scudder, 1976).

Insects are important supplementary human food source of calories and protein in many regions in the world (Bodenheimer, 1951; DeFoliart, 1989, 1992, 1999), with some 500 species in more than 260 genera, and 70 families of insects known to be consumed (DeFoliart, 1989; Groombridge, 1992). Insects of most major orders are eaten, but the most widely used species are those, such as termites, that habitually occur in large numbers in one place, or that periodically swarm,

such as locusts, or large species such as saturniid moth larvae (Scudder, 1976). The seasonal abundance at certain times of the year makes them especially important when other food resources may be lacking (Groombridge, 1992).

As many, or perhaps more, entomophagous insects exist as do prey or hosts (DeBach, 1974). The habit of feeding upon other insects is found in all major insect orders (Clausen, 1940). Included here are predators and parasitoids, both of which are involved in the natural and effective control of insects (Koul and Dhaliwal, 2003). The control of the cottony-cushion scale *Icerya purchasi* Maskell in California by the predatory vedalia beetle *Rodolia cardinalis* (Mulsant) imported from Australia established the biological control method in 1888-1889 (DeBach, 1974, Caltagirone, 1981; Caltagirone and Doutt, 1989).

Conservatively, some 400,000 species of known insects are plant feeders (New, 1988). Thus, phytophagous insects make up approximately 25% of all living species on earth (Strong et al., 1984). The members of many orders of insects are almost entirely phytophagous (Brues, 1946), conspicuous orders being the Hemiptera, Lepidoptera, and Orthoptera. The influence of insects, as plant-feeding organisms, exceeds that of all other animals (Grimaldi and Engel, 2005).

Under natural conditions, insects are a prime factor in regulating the abundance of all plants, particularly the flowering plants, as the latter are especially prone to insect attack (Brues, 1946). More thoroughly than any other animals, insects have exploited their food supply and profited thereby (Scudder, 2009).

Miller (1993) have categorised how insects interact with other organisms as providers, eliminators, and facilitators. Insects serve as food or as hosts for carnivorous plants, parasites, and predatory animals. They also produce byproducts, such as honeydew, frass, and cadavers that sustain other species (Scudder, 2009). As eliminators, insects remove waste products and dead organisms (decomposers and detritivores), consume and recycle live plant materials (herbivores), and eat other animals (carnivores).

Many insect taxa are coprophagous and well-known dung-feeders (Hanski and Cambefort, 1991). African dung beetle species have been introduced into North America to improve the yield of pasture land through effective removal of dung and to limit the proliferation of flies and nematodes that inhabit the dung (Fincher,

1986). Dung beetles in the tropical forests also play an important role in secondary seed dispersal because they bury seeds in dung, protecting them from rodent predators (Shepherd and Chapman, 1998).

The process of insect pollination is believed to be the basis for the evolutionary history of flowering plants, spanning at least 135 million years (Crepet, 1979, 1983), although the origin of insect pollination, which is an integrating factor of biocenosis (Vogel and Westerkamp, 1991), is still being debated (Kato and Inoue, 1994). Approximately 85% of angiosperms are pollinated by insects (Grimaldi and Engel, 2005). Yucca moths (*Tegeticula* spp.) exhibit an extraordinarily adaptation for flower visitation, and the yuccas depend on these insects for pollination (Addicott et al., 1990; Powell, 1992). Similarly, figs and chalcid wasps have a significant association (Janzen, 1979; Wiebes, 1979). Orchid species have developed floral colour, form, and fragrance that allow these flowers to interject themselves into the life cycle of their pollinators to accomplish their fertilisation (Dodson, 1975).

1.1.2. Global insect diversity and distribution

Considerable debate continues over how many species of insects are in the world. Estimates range from 2 to 50 million (Stork, 1993). The lower figure is from Hodkinson and Carson (1991). The higher figure is up to 50 million is from Erwin (1988; 1993), and as an earlier estimate of 30 million (Erwin, 1982; 1983), is based on number obtained from canopy fogging in the tropical forest of the Americas. These high estimates have been questioned, however, because of the assumption made and the lack of real evidence for a vast number of undescribed species (Stork, 1993). Other methods of estimation have been used by May (1990), and from these other data, Stork (1993) concluded that a global total of 5-15 million is more reasonable than the previous estimation. Gaston (1991) gave a figure of about 5 million, and this estimate was accepted by Grimaldi and Engel (2005), although Hammond (1992) gave an estimate of 12.5 million species.

The number of insects described at present is estimated to be 925,000 (Grimaldi and Engel, 2005), in a total biota described to date of 1.4 to 1.8 million (Stork, 1988; 1993; May, 1990; Hammond, 1992). Using the 925,000 species described,

versus the estimate of 5 million total, Grimaldi and Engel (2005) suggested that only 20% of the insects are named.

A majority of the species on earth are insects. Hammond (1992) calculated that arthropods constitute 65% of the total known biodiversity, and Grimaldi and Engel (2005) put the figure at about 58% while Samways (1993) noted that they constitute 81.3% of described animal species, including the Protozoa. Thus, from a modest beginning some 400 mya, insects have become the dominant component of the known diversity on earth, with 100 million species having ever lived (Grimaldi and Engel (2005).

Wheeler (1990) in his 'species scape' pictorially illustrated the current dominance of insects, and Samways (1993) noted that if all insect species in the world were described, the beetle representing the proportion of insect species in the world might have to be drawn up to 10 times larger. Wheeler (1990) used a beetle to depict the arthropods in his species scape because the Coleoptera are the dominant insect group, constituting 40% of the estimated total number of insects (Nielsen and Mound, 2000). The dominance of the Coleoptera was said to have led J. B. S. Haldane when asked what he could infer from the work of the Creator, to respond that the Creator must have had 'an inordinate fondness for beetles', although there is some doubt about the provenance of this phrase (Fisher, 1988). The success of the order Coleoptera is claimed to have been enabled by the rise of flowering plants (Farrell, 1998).

So systematists continue to debate the issue without any hope of consensus. Even the number of insects already described, a number that would seem to be robust and beyond dispute, is contentious. On one hand, there are problems with synonymies. Alroy (2002) has estimated that '24-31% of currently accepted names eventually will prove invalid' due to synonymies or *nomina dubla* (that is, 30% of named species are illusions created by unsettled taxonomy). On the other hand, new molecular results of tropical parasitoid flies in the family Tachinidae found that the 16 generalist species apparently represent nine generalist species and 73 specialist lineages. Given that parasitoids are thought to represent 20% of all insect species, gross underestimates of parasitoid species diversity may mean that global species richness of insects also may be grossly underestimated.

While there may not be a consensus on how many insect species remain to be described, an examination of known numbers is an argument for stepping up the inventory effort. According to the Red List (http;//www.redlist.org/), 9932 species of birds have been described, of which 1005 have been evaluated as to their ability to survive; of the 4842 species of mammals that have been described, 4782, almost 97%, have been evaluated. By contrast, of the 1,004,898 or so species of insects that have been described, only 768 – about 0.08% - have been evaluated. Of the mammal species that have been evaluated, 1130 of 4782, or 23.6%, are threatened; of the 9932 bird species, 1194, or 12%, are threatened. By contrast, of the 768 insect species that have been evaluated, 563, or 73%, are threatened (Figure 1)

(a)

(b)
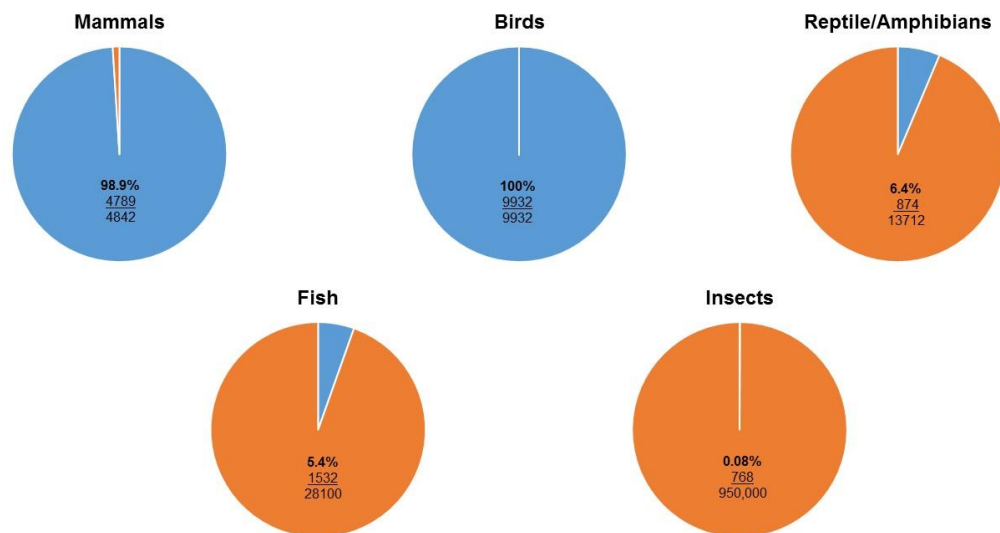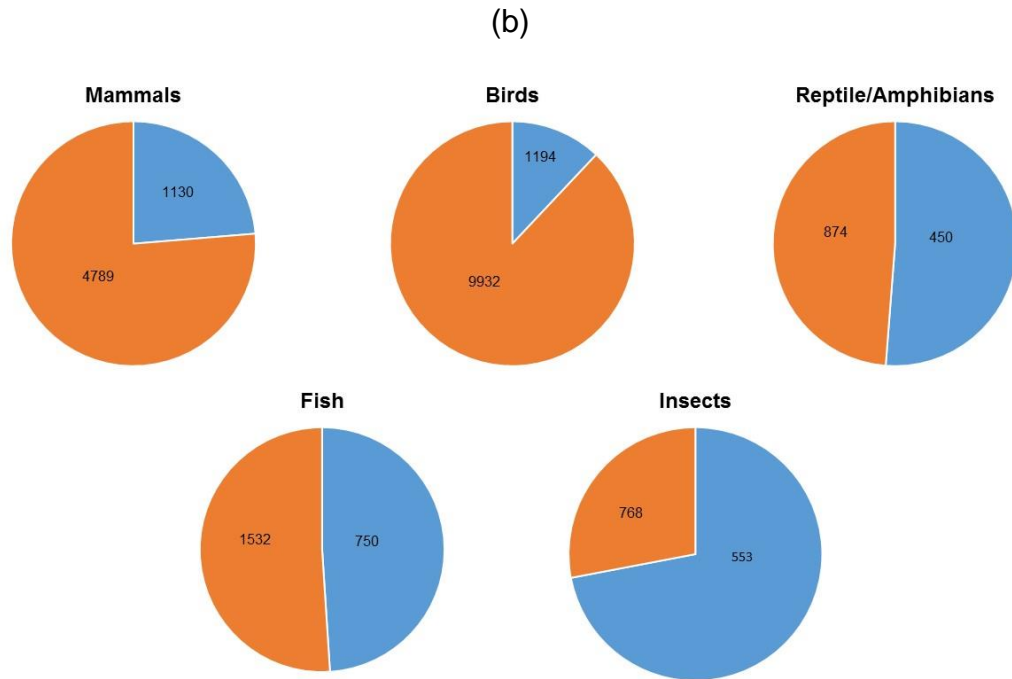
Figure 1 Taxa redlisted (in blue) with extinction worldwide, (a) number
evaluated as percentage of the species described, (b) number redlisted as a
percentage of those species evaluated (data from www.redlist.org.2004).

Insects, then, despite their almost ungraspably large numbers, are at
disproportionate risk of extinction. How disproportionate is an open question in
that, of all the major animal taxa on the planet, they are the least well-
characterised group. To characterise even the majority of insect species would
be a massive undertaking, but the fact that the rate at which species are being
described has steadily increased since Linnaeus's day suggests that it is not an
impossible one. If there is a general consensus that conserving biodiversity is a
good thing, then a necessary first step is to inventory that which is to be
conserved. It would be unfortunate that one of the most durable and time-tested
biological observations – that there are a lot of insects – may cease to be true in
the foreseeable future.

1.1.3. The relationship of insect to human

In attempting to characterise public attitudes toward invertebrates, Kellert (1993)
administered a questionnaire to determine the 'level of knowledge' of

invertebrates in general. Individuals surveyed included randomly selected residents of the New Haven, Connecticut, area, along with subsamples of farmers, conservation organisation members, and scientists. Of the various categories of knowledge investigated, the general public revealed the least knowledge of taxonomic differences among invertebrates. Taxonomic confusion extended beyond the phylum Arthropoda.

While biologists passionately debate the number of species awaiting discovery, the general public appears blissfully unaware of and indifferent to this discussion. In fact, the business of differentiating among insect species has been long regarded as the pursuit of trivial value. Insect species as numerous and as seemingly similar as they may appear, are not ecologically interchangeable, and failing to recognise that fact has had tremendous economic and public health consequences over the centuries (Barenhaum, 2009).

Examples of the importance of differentiating among arthropod species are legion. In agriculture, identifying pest species correctly is often key to understanding their life histories and developing approaches to managing them. The varroa mite, for example, is a devastating parasite of European honeybee *Apis mellifera*. When mites first appeared attacking honeybee in North America in the 1980s, they were assumed to be *Varroa jacobsoni,* a species native to Indonesia and Malaysia that had hitherto been thought to attack only *Apis cerana*, the Eastern honeybee. However, Anderson and Trueman (2000) conducted morphological and molecular studies and determined that the mite attacking bees in North America is a distinct species, which they name *Varroa destructor*. Unlike *V. jacobsoni*, *V. destructor* infests *A. cerana* throughout much of Asia and is also capable of parasitizing *A. mellifera* throughout the world to devastating effect.

No less important than identifying pest species to control them is identifying and appreciating the diversity of potential biological control agents that can be used in pest-management programs. Many programs have failed or experienced decades-long delays simply because the diversity of potential control agents was not fully recognised (Caltagirone, 1981). California red scale *Aonidiella aurantii*, for example, is an important pest of citrus that was accidentally introduced into California in the nineteenth century, most likely from Southeast Asia. For close to 60 years, biocontrol efforts ignored ectoparasitoid wasps in the genus *Aphytis* as

potential control agents because *Aphytis chrysomphali* was already present in the state, having been accidentally introduced at the turn of the twentieth century, and apparently had little impact on the pest. Thus, dismissing ectoparasitoids as ineffective, entomologists concentrated on potential predators and endoparasitoids, without much success. Eventually, the taxonomic study of the genus revealed a complex of species, including two, *A. lingnanensis* and *A. melirus*, which, once introduced, proved to be significantly superior biocontrol agents for the scale (Price, 1984).

Just as biocontrol agents are not interchangeable, neither are insect-pollinating agents. Establishing a fig industry in California, today second only to Turkey in the production of figs worldwide, was stymied for a decade in the late nineteenth century until entomologists recognised that one particular agaonid fig wasp species, one of the hundres in the genus, had to be imported to pollinate the trees. Similarly, cacao cultivation in Africa, outside its area of indigeneity in Mexico, was not profitable until the specific pollinators – midges in the genus *Forcipomyia* – were imported (Young, 1981).

There have been significant public consequences of the failure to recognise and differentiate among insect species. *Anopheles gambiae*, for example, was long regarded as the most important vector of malaria in Africa south of the Sahara. The species, however, turned out to be in reality a complex of seven essentially morphologically identical species, some of which are efficient vectors and other are not vectors (White, 1973; Hunt et al., 1998). These species also differ in the degree to which they are resistant to insecticides, which has major implications for control efforts (Davidson, 1974). Effective management of vectors of malaria, a disease that kills 2 to 3 million people worldwide annually, requires precise identification of species (Oringanje et al., 2011).

Even such unglamorous ecosystem services as waste disposal depend on a diversity of non-interchangeable arthropods. The introduction of placental mammals such as cattle and sheep into Australia led to significant problems with dung accumulation; Australian dung beetles, adapted to using dung of marsupial mammals, could not process the dung of introduced placental livestock species. The accumulated dung threatened the livestock industry by taking a substantial amount of pastureland out of commission but also led to a population explosion

of *Musca vetustissima*, the bush fly, whose larval stage thrived in the dung of the introduced species. Ultimately, over 50 species of dung beetles, with different habitat requirements, food preferences, and phenologies, were imported to manage the dung problem (Doube, 1990).

Insects, as the most diverse group of animal with which we share our world, add substantial variety and diversity to the extraordinarily rare veneer of life on Earth. Yet, this insect diversity, the manifestation of millions of years of evolution, is under threat of attrition, as populations are lost, genetic diversity reduced, species go extinct, and the biomes and resources on which they depend succumb on human cupidity. It has been estimated that perhaps a quarter of all insect species are heading for extinction over the next few decades. In a mere blink of a geological eyelid, the ecological impact of humans is causing the demise of a vast amount of Earth's biodiversity. This variety not only has intrinsic value but also may have much practical, utilitarian value that is only starting to be explored.

1.2. <u>Insect taxa selected in this study</u>

In this study, the beetle fauna (Coleoptera) has been selected for two reasons. Firstly, beetles represent the greatest proportion of described insects, which would be helpful for the identification of specimens. Secondly, the beetle fauna is not known equally well in all parts of the world. Studies of beetles in restricted area such as islands can provide important data on biodiversity at a finer scale. Species lists from distinct areas or habitat types are useful not only because they give a snapshot of current ecosystem health and function, but also because they can be compared to lists generated at different periods to monitor changes over time (Howden and Howden, 2001).

1.2.1 *Beetle diversity, habitat, and life cycle*

The estimated number of described species of beetles is between 300,000 and 450,000 (Nielsen and Mound, 1999). Although Arnett and Thomas (2001) and Arnett et al. (2002) showed in *American Beetles* that the figure is more than 375,000 species. Of the described species, many are known only from a single

locality or even from a single specimen (Stork, 1999; Grove and Stork, 2000). Beetles are so diverse, and most species are poorly known, that an estimate of how many species exist remain difficult.

Erwin (1982) first proposed an estimate of the total number of beetle species on the planet, based on field data rather than on catalogue numbers. The technique used for his original estimate, possibly as many as 12,000,000 species, was criticised, and revised estimates of 850,000 – 4,000,000 species were proposed (Hammond, 1995; Stork, 1999; Nielsen and Mound, 1999). Some 70-95% of all beetle species, depending on the estimate, remain undescribed (Grove and Stork, 2000).

Yeates et al. (2003) estimated that the known beetle diversity of Australia includes 23,000 species in 3265 genera and 121 families. This estimate of species is slightly lower that that reported for North America, a land mass of similar size: 25,160 species in 3526 genera and 129 families (Marske and Ivie, 2003). While Marske and Ivie (2003) predicted that there could be as many as 28,000 species in North America, including currently undescribed species, a realistic estimation of the true diversity of the little-studied Australian beetle fauna could be 80,000 – 100,000 (Yeates et al., 2003).

Patterns of beetle diversity can illustrate factors that have led to the success of the group as a whole. Based on estimates for all 165 families, more than 358,000 species of beetles haven been described and considered valid. Most species (62%) are in six megadiverse families, each with at least 20,000 described species: Curculionidae, Staphylinidae, Chrysomelidae, Carabidae, Scarabaeidae, and Cerambycidae. The smaller families of Coleoptera account for 22% of the total species in the group and include 127 families with 1-999 described species and 29 families with 1000-6000 described species (Bouchard et al., 2009) (Figure 2)
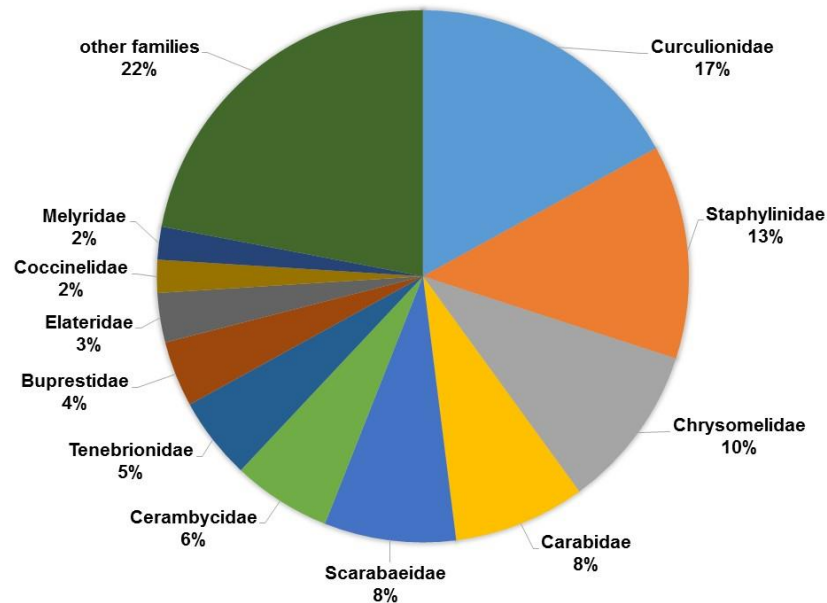
Figure 2 Coleoptera biodiversity using the estimated number of described species. The 11 largest beetle families (each with 6000+ described species) are shown. The remaining 154 families (each with fewer than 6000 described species) are combined into 'other families.' but together represent a significant proportion of beetle diversity (Bouchard et al., 2009).

Body length of beetles ranges from 0.4mm (Sorensson, 1997) to more than 17cm. Larvae of some of the larger beetles can weight more 140 g and are the heaviest insects known (Acorn, 2006). The most common life cycle type in beetles is holometaboly, where individuals emerge from eggs as larvae, develop through several instars, pupae, and eventually emerge as adults (Bouchard et al., 2009). Sexual reproduction is predominant, although partigenesis (i.e., production of viable, unfertilised eggs) also occurs. More specialised or unusual life cycles, which include the occurrence of active and inactive larval instars in parasitoid species, are also known in Coleoptera (Lawrence and Britton, 1994).

Beetles occur in most terrestrial and freshwater habitats (Lawrence and Britton, 1994), and a few occupy marine environments (Doyen, 1976; More and Legner, 1976). They are an important part of these habitats, have important effects on agriculture and forestry, and are useful model organisms for many types of science. A better understanding of beetle diversity will enhance our knowledge and provide many practical applications.

1.2.2. Overview of beetle taxa

The order Coleoptera is divided into three suborders: suborder Archostemata and Myxophaga, suborder Adephaga, and suborder Polyphaga. Suborders Archostemata includes about 40 species of small to medium-sized beetles in five families of Ommatidae, Crowsoniellidae, Micromathildae, Cupedidae, and Jurodidae (Hornschemeyer, 2005). Myxophagan are small beetles (usually shorter than 2.5 mm) that feed on algae or blue-green algae in freshwater and riparian habitats (Beutel, 2005). The four myxophagan families include approximately 100 species worldwide.

The suborder Adephaga includes three terrestrial families (Carabidae, Rhysodidae, and Trachypachidae), eight freshwater families (Gyrinidae, Haliplidae, Noteridae, Amphizoidae, Hygrobiidae, Dytiscidae, Aspidytidae, and Meruidae), and more than 40,000 species worldwide (Ball and Bousquet, 2001; Beutel and Ribera, 2005). Most species are predators in both the larval and adult stages, although several species of Carabidae are parasitoids (Ball and Bousquet, 2001). The most diverse family of adephagan beetles associated with freshwater habitat is the Dytiscidae, with approximately 4000 species worldwide. Because of their predatory habits, dytiscids are thought to play an important role in the control of larval mosquitoes that, as adults, often are infected with a variety of disease agents transmittable to humans (Lopez et al., 1997; Bellini et al., 2000; Lundkvist et al., 2003).

The Carabidae, commonly referred to as 'ground beetles', represent the most diverse family in this suborder, with an estimated 40,000 known species (Erwin, 1991). Ground beetles are by far the most important adephagans regarding anthropogenic interactions. Studies of ground beetles have enhanced our understanding of the ecological effects of agricultural practices (Freuler et al., 2001; Duan et al., 2006), forestry practices (Niemela et al., 1993; Magura et al., 2003), habitat fragmentation (Magagula, 2003), pollution of natural ecosystem (Freitag, 1979), and many more human activities. Ground beetles are also important for research on habitat conservation (Bouchard et al., 2006) and biogeography (Marshall and Liebherr, 2000).

Suborder Polyphaga includes several series: Staphyliniformia, Scarabaeiformia, Elateriformia, Bostrichiformia, and Cucujiformia.

Series Staphyliniformia includes the superfamilies Hydrophiloidea, and Staphylinoidea. The phylogenetic evidence is mounting that the superfamily Scarabaeoidea also should be included in this series (Hansen, 1997; Beutel and Komarek, 2004; Korte et al., 2004; Beutel and Leschen, 2005; Caterino et al., 2005, Hughes et al., 2006). However, the exact relationship of the Scarabaeoidea to the Staphyliniformia and the monopholy of the series Staphyliniformia, as presently defined, have yet to be determined. Bouchard et al., (2006) decided to treat the Scarabaeoidea as a separate series to follow current classification schemes. The total number of described species of Staphyliniformia is about 90,000, or roughly a quarter of all beetles and considerably more than all Vertebrata combined.

The superfamily Hydrophiloidea unites four families: Hydrophilidae, Histeridae, Sphaeritidae, and Syntellidae (Archangelsky et al., 2005). The Sphaeritidae and Syntellidae include fewer than 20 species each. These families are associated with decaying organic matter, and each includes a single genus distributed in both North America and Eurasia. The Histeridae (330 genera and 4000 species) and Hydrophilidae (170 genera and 2800 species) are two large, cosmopolitan families that are most diverse in the tropics (Beutel and Leschen, 2005). Hydrophiloid beetles are primarily aquatic, although the Sphaeridiinae are secondarily terrestrial and found in dung and leaf litter. Larvae of the Hydrophilidae are normally aquatic, go through three instars, and are predators. Pupation, however, takes place in the soil (Hansen, 1991). Unlike the Hydrophilidae, the Histeridae are strictly terrestrial predator in the adult stage, and their larvae have only two instars.

The superfamily Staphylinoidea includes seven families. Beutel and Leschen (2005) hypothesised that the Hydraenidae and Ptiliidae for a sister group of the Agyrtidae plus Leiodidae while these four families are together a sister group of the Staphylinidae and Silphidae plus Scydmaenidae. Six of these families are worldwide in distribution while the Agyrtidae are known only from northern temperate areas, with one genus in New Zealand (Newton, 1997). The family Hydraenidae comprises some 1300 described detritus-feeding species in 40

genera. However, the true species richness is probably higher (Jach et al., 2005). Most hydraenid species occur in freshwater habitat, some are terrestrial and either riparian or associated with wet forest leaf litter. The Ptiliidae (feathering beetles) are strictly terrestrial and mycophagous and include more than 550 described species in about 70 genera (Hall, 2005). .

The Silphidae, also known as the large carrion beetles, include fewer than 200 species in 15 genera (Sikes, 2005) and are efficient carrion decomposers. The Scydmaenidae mainly prey on mites and have about 82 genera with more than 4600 species, more than half of which belong to the genus *Euconnus* (O'Keefe, 2005). The family Staphylinidae includes 47,744 described species. The Staphylinidae are predominantly mycophagous, saprophagous, and predaceous, although some species are phytophagous. The Staphylinidae are organic components of healthy ecosystems, both natural and modified by humans (Bouchard et al., 2009).

The series Scarabaeiformia, as currently classified, consists of 12 families (Pleocomidae, Geitrupidae, Belohinidae, Passalidae, Trogidae, Glaresidae, Diphyllostomatidae, Lucanidae, Ochodaeidae, Hyborosidae, Glaphyridae, and Scarabaeidae), 43 subfamilies, and 118 tribes (Smith, 2006). Recent estimates of the number of described species in this group range from 31,000 to 35,000 (Jameson and Ratcliffe, 2002; Scholtz and Grebennikov, 2005). Scarab beetles are terrestrial with their larvae inhabiting soil, detritus, or decaying wood. Scarab species can be found in most terrestrial habitats worldwide and are most diverse in tropical forests. Hundreds of species of scarab beetles are nectar feeders and pollinators of a diverse assemblage of plant species. The benefits of dung removal and burial by dung beetles worldwide are well documented from the perspective of pastureland productivity, nutrient recycling, and health (Mittal, 1993; Tyndall-Biscoe, 1994).

The series Elateriformia contains five superfamilies: Scirtoidea, Dascilloidea, Buprestoidea, Byrrhoidea, and Elateroidea (Lawrence et al., 1995), and at least 40,000 sepcies. Of these, about 30,000 species belong to the three largest families, the Buprestidae, Elateridae, and Cantharidae. Elateriform beetles are found throughout the world and most diverse in tropical regions (Bouchard et al., 2009). Elateriform beetles have a wider diversity of larval feeding habits than for

any other series, which include feeding on deadwood (e.g. Buprestidae), herbivory (e.g. Buprestidae), fungivory (e.g. Elateridae), carnivory (e.g. Elateridae), and ectoparasitism (e.g. Rhipiceridae).

Although the major known economic effects of elateriform beetles are negative (e.g. Buprestidae as forest pest and Elateridae as an agricultural pest), many are likely beneficial but unknown. Among the beneficial species, only a few elaterids have been introduced for biological control (Clausen, 1978). Similarly, the role of elateroids and buprestoids as pollinators is probably also undervalued (Bouchard et al., 2009).

The series Bostrichiformia are composed of seven families, each contains relatively few species. The Jacobsoniidae, Derondotidae, Nosodendridae, and Endecatomidae, each contains fewer than 100 species worldwide, whereas Bostrichidae, Dermestidae, and Anobiidae contain between 500 and 2500 species each. Some of the species of less diverse families are very small, their biology is essentially unknown, and they are collected only by using specialised tools such as the Berlese funnel. Overall, the species-poor families Jacobsoniidae, Derodontidae, Nosodendridae, and Endecatomidae have diverse feeding habits and habitat preferences. They occur in fungi, rotten wood, under bark, in leaf litter, and in bat guano (Lawrence and Hlavac, 1979; Leschen, 2002; Ivie, 2002).

The larvae of most Bostrichidae are wood borers, and several are major pests. The grain borers (*Prosthephanus* and *Rhyzopertha*), powder post beetles (*Lyctus* and *Trgocylon*), and bamboo powder-post beetles (*Dinoderus*) are especially important economically (Ivie, 2002b). The Dermestidae include primarily scavengers of dried animals and plant material. This family includes some of the most important pests of stored products and museum specimens. In addition, some dermestids are used in forensic entomology.

The family Anobiidae, which the most diverse in tropical and subtropical habitats, includes more than 2000 species worldwide (Bouchard et al., 2009). The larvae of Anobiidae can be separated into two groups. The first group of species bore into plant materials such as bark, seed, dry wood, and galls, while the other group feed on dry animals and plant detritus (Philips, 2002).

The series Cucujiformia includes six superfamilies: Cleroidea, Lymexyloidea, Cucujoidea, Tenebrionoidea, Chrysomeloidea, and Curculionoidea (Lawrence and Newton, 1995). The superfamily Lymexyloidea is the smallest, containing the single family Lemexylidae with more than 50 predominantly tropical species are organised into seven genera (Wheeler, 1986). Larvae of at least some Lymexylidae burrow into wood and cultivate ambrosia fungi believed to be their only larval food source. This larval lifestyle causes some damage to forestry in temperate areas, whereas, in the tropics, *Promelittomma insulare* is a pest of coconut palms (Brown, 1954).

The superfamily Cleroidea is a group of ten families and about 10,000 species. Adults and larvae of most species are predators. The larvae of some species pursue and attack wood-boring insects inside the tunnels, benefiting the forestry industry. The Acanthocnemidae have a single extant species, *Acanthocnemus nigricans* native to Australia (Lawrence et al., 1999). The Chaetosomatidae include four genera in New Zealand and Madagascar (Lawrence et al., 1999). Cleridae is the second largest family in this superfamily, with about 3500 species worldwide (Kolibac, 2004). The Melyridae have about 5000 species worldwide (Kolibac, 2004).

The superfamily Cucujoidea includes about 20,000 species in about 1500 genera (Pakaluk et al., 1994), which are classified in the following 35 families (Leschen et al., 2005): Agaphytidae, Alexiidae, Biphyllidae, Boganiidae, Bothrideridae, Byturidae, Cavognathidae, Cerylonidae, Coccinellidae, Corylophidae, Cryptophagidae, Cucujidae, Cyclaxyridae, Discolomatidae, Endomychidae, Erotylidae, Helotidae, Hobartiidae, Keteretidae, Laemophloidae, Latridiidae, Lamingtoniidae, Monotomidae, Myrabolidae, Nitidulidae, Passandridae, Phalacridae, Phoeostichidae, Priasilphidae, Propalticidae, Protocucujidae, Sivanidae, Smicripidae, Sphindidae, and Tasmosalpingidae. Some species prey on phytophagous arthropods, benefiting human by protecting beneficial plants. Other species are invasive or otherwise detrimental (Bouchard et al., 2006)

The superfamily Tenebrionoidea is composed of 27 families. The families Aderidae, Anthicidae, Ciidae, Meloidae, Mordellidae, Oedemeridae, and Zopheridae are moderately diverse within the Tenebrionoidea, each containing 550-3000 described species. The adults are some important pollinators of wild

and cultivated plants (Bouchard et al., 2009). A large proportion of these beetles develop in dead wood, fungi, and leaf litter and are uncommonly encountered by people. A few species in the family Anthicidae prey on the eggs and small larvae of pest species and can be useful as biological control agents (McCutcheon, 2002).

The most diversity of tenebrionoid family is Tenebrionidae, with nearly 20,000 described species worldwide.Tenebrionids play a significant role in food webs (Crawford et al., 1993). Several tenebrionid species have been transported across the world by humans because of their association with stored products (Chaddick and Leek, 1972). Some Tenebrionidae, especially those who have lost their ability to fly, are recognised as endangered and in need of habitat conservation to avoid extinction (Bouchard et al., 2009).

The superfamily Chrysomeloidea is a group of seven beetle families (Beutel and Leschen, 2005) with more than 50,000 species arranged in the cerambyciform (Cerambycidae, Vesteridae, Oxypeltidae, Disteniidae) and chrysomeliform (Megalopodidae, Orsodacnidae, Chrysomelidae) lineages. Because they are almost exclusively phytophagous, many of these beetles are important to humans, mainly as plant pests or biological agents against unwanted plants (Bouchard et al., 2009). Although the majority of species in the Cerambycidae are winged and have arboreal habits, specialised adaptations to ground-dwelling habits are known in the flightless genus *Dorcadion* and related genera (Plavilstshikov, 1958).

The herbivorous superfamily Curculionoidea contains seven smaller families with fewer than 4500 described species each (Nemonychidae, Anthribidae, Belidae, Caridae, Brentidae, and Ithyceridae), as well as the most diverse family of beetles, the Curculionidae. Most species in this superfamily have a distinctive cylindrical extension of the head that leads to the buccal cavity. This adaptation, the rostrum, is used to prepare cavities in plant tissues for the deposition of eggs. The evolution of the rostrum is thought to be one of the reasons for the success of this group because it allows species of the Curculionoidea to exploit plant tissues that other groups cannot access (Anderson, 1995).

The family Curculionidae is one of the most diverse groups of organisms, with more than 60,000species described and thousands more to be described. Their close association with flowering plants is one of the main factors explaining their great diversity. Curculionids feed on plants of any terrestrial or freshwater habitat and any plant tissue, from roots to seeds (Anderson, 2002). Because of these characteristics, curculionids are important economically as serious pests of agricultural and forestry plants.

1.2.3. Beetle of economic importance

In agriculture, hundreds of species beetles, including many from family Curculionidae, Chrysomelidae, Elateridae, and Scarabaeidae, feed on crops and ornamental plants in their larval or adult stages or both (Campbell et al., 1989). One of the best-studied pest is boll weevil (*Anthonomus grandis grandis*), which reduces cotton production. This species is native to tropical and subtropical America but has been established in the USA since the late 1800s (Burke et al., 1986). In the last 100 years, yield losses and control costs against this species have been estimated at more than $22 billion (Kaplan, 2003).

Blister beetles that contaminate animal feed also affect agriculture. These meloid beetles are sometimes abundant in hay fields and possess cantharidin compounds that they use for defense against predators. Farm animals (cows, emus, goats, horses, and sheep) have become ill or died after consuming alfalfa contaminated by dead blister beetles (Capinera et al., 1985).

Beetle are important vectors of pathogens to crops and livestock (Harris, 1981). The striped cucumber beetle, *Acalymma vittatum*, is a specialist herbivore that feeds on plants of the cucumber family Cucurbitaceae. The association of these beetles with the wilt-inducing plant bacterium *Erwinia tracheiphila* has led to major losses in the past (Garcia-Salazar et al., 2000).

Hinton (1945) stated that the Coleoptera was the most important order of insects attacking stored products. More than 600 species of beetles are associated with stored products all around the world. Although many of these species eat the stored products, others feed on the fungi or other animals that inhabit warehouse

(Bousquet, 1990). Some of the most problematic groups of beetles in stored products are the Laemophloeidae, Dermestidae, and Tenebrionidae.

Beetles from family Dermestidae are also one of the greatest threats to the world's museum collection. Species of *Anthrenus* and *Dermestes* commonly attack and destroy preserved animals such as pinned insects and preserved pelts and skins, as well as cultural artefacts that incorporate hair, wool, fur, leather, feathers, and other animal derivatives (Campbell et al., 1989).

Many species of Coleoptera are also forest pests. Up to 45% of the annual wood volume grown in Sweden was estimated to be lost to only two bark beetles, *Tomicus piniperda* and *Ips typographus* (Eidmann, 1992). Weevils of the subfamilies Scolytinae and Platypodinae, with 5812 and 1463 species, respectively (Wood and Bright, 1992), are the most infamous forest pests. Many bark beetles use chemical signals (pheromones) to schedule a synergic attack by many individuals on a single tree, thus overcoming its resistance and killing it, making it suitable for beetle reproduction (Paine et al., 1997).

On the other hand, many important ecological services are provided by beetles. Confining large mammals in small areas creates challenging waste-management problems. Cattle production in the United States provides a particularly pertinent example, because nearly 100 million head of cattle is in production (NASS, 2004), and each animal can produce over 9000 kilograms (kg) (Fincher, 1981), or about 21 cubic meters (BCMAF, 1990), of solid waste per year. Fortunately, beetles in the family Scarabaeidae (Ratcliffe 1970) are very efficient at decomposing this waste. In doing so, they enhance forage palatability, recycle nitrogen, and reduce pest habitat (Fincher 1981), resulting in significant economic value for the cattle industry (Losey and Vaughan, 2006). The importance of this service is illustrated by the success of dung beetles introduced into Australia to deal with the dung of non-native cattle brought to that continent in 1788 (Australian Bureau of Statistics 2005).Before the introduction of dung beetle species that were adapted to feed on cattle dung, Australia had no insect fauna to process cattle faeces. Consequently, rangeland across the country was fouled by slowly decomposing dung (Bornemissza, 1976). In addition, this dung provided fodder for pest species. Recent research in Western Australia has revealed that populations of

the pestiferous bush fly (*Musca vetustissima*) have been reduced by 80% following dung beetle introductions (Dadour and Allen, 2001).

Another important service provided by dung beetles is promoting decomposition of dung into labile forms of nitrogen that can be assimilated by plants and thus function as fertilizer when the dung is buried. In the absence of dung beetles, cattle feces that remain on the pasture surface until they are dry lose a large proportion of their inorganic nitrogen to the atmosphere (Gillard, 1967). Experiments in South Africa and the United States have shown that approximately 2% of cattle dung is composed of nitrogen and that 80% of this nitrogen is lost if the dung dries in the sun before it is buried (Petersen et al.,1956; Gillard, 1967).

Many cattle parasites and pest flies require a moist environment such as dung to complete their development. Burying dung and removing this habitat can reduce the density of these pests (Fincher, 1981). From field observations that reflected current levels of removal, Fincher (1981) estimated the annual losses due to mortality, morbidity, and medication of beef cattle, dairy cattle, and other livestock with internal parasites is about $428 million annually because of parasites and pests.

Plant-feeding beetles, primarily of the families Curculionidae and Chrysomelidae, have been used successfully to control the spread of invasive alien plant species throughout the world. Weeds have been transported accidentally throughout the world for centuries, and the trend is increasing with the global trade (Mason et al., 2003). Careful studies of the biodiversity and biology of beetles in the weed's country of origin are necessary for safe and efficient control (Lindgren et al., 2002).

Beetles, along with other insects groups, are critically important in the pollination of cultivated and wild plants. Pollination by beetles is often referred to as cantharophily. The Coleoptera are considered as the most primitive pollinators (Kevan and Baker, 1983). Thirty-four families of flowering plants contain at least one species that is pollinated primarily by beetles (Bernhardt, 2000). In some ecosystem, such as cloud forests, more than 45% of palms and herbs rely on beetles for pollination (Serez and Ramirez, 1995).

1.2.4. Threatened beetles

Many beetles are especially vulnerable to local and global extinction. These beetles often have low powers of dispersal (flightless), only occur in extreme or specific microhabitats, or occur over small geographical areas. Beetles on islands, isolated dunes, caves, mountains, and other ecological islands fit into this category. In addition to beetles considered threatened locally or globally, 69 globally threatened species appear on the International Union for Conservation of Nature and Natural Resources' Red List of Threatened Species either as vulnerable (27), endangered (16), critically endangered (10), or extinct (16). These species belong to 13 families and occur in 60 countries. Human activities, such as habitat destruction and the introduction of invasive alien species, continue to threaten many of the world's natural ecosystems and the myriad of beetle species in them (Spence and Spence, 1988; Martikainen and Kouki, 2003; Munks et al., 2004; Davis and Philis, 2005; Bouchard et al., 2006). The number of species currently listed as vulnerable, threatened, or extinct represents a gross underestimation of the number that should be targeted for conservation. Thus, studies on beetle diversity and the conservation of their habitats are necessary to ensure the sustainability of natural ecosystems and critical human activities.

1.3.   The biogeography of island life

1.3.1. Island environments and the significant of island biodiversity

Island topography is primarily determined by the geophysical origins of the island. Marine islands may be subdivided into two geophysically distinct categories: continental shelf islands (land-bridge islands) and oceanic islands. Continental shelf islands are likely to be physically connected to the mainland during low sea level periods. Due to their connection, these islands have similar geological structures to the nearby mainland (Williamson 1981). This similar topography, coupled with the island's proximity to the continent, results in the proliferation of similar flora and fauna (biota) (Yu and Lei, 2001).

Continental islands have often been compared with habitat fragments. A study by Walter (2004) showed that they resemble the latter in some respects: their

limited size and disconnection from the mainland will result in similar biodiversity losses and downsizing over time as can be experienced in continental remnant habitats. However, the different nature of the surrounding matrix – the seawater barrier – keeps many continental mortality factors affecting mainland fragments off the island, potentially lowering the extinction rate compared with what might occur at the place–taxon interface of a mainland remnant isolate. In addition, there is no terrestrial edge effect. Often, there are no endemics on such islands, but some island populations may have become independent from their mainland conspecifics thereby achieving full functional insularity (Walter, 2004). In other cases, continental islands may harbour relict taxa already extinct on the mainland or taxa that only exist on islands regardless of their connection to a mainland (white-crowned pigeon *Columba leucocephala* in the Gulf of Mexico). Thus, continental or near-shore island biotic space must be considered separate from that of oceanic islands as well as from any mainland isolate patch (Walter, 2004).

Oceanic islands are typically more isolated, and may have never been physically connected to a continental landmass. Williamson (1981) divided three main types of oceanic islands: oceanic ridge islands, hot-spot islands, and the individual islands of island arcs. Oceanic ridge islands and hot-spot islands are volcanic islands because they are formed from ocean floor volcanoes. Islands that are part of island arcs also have a volcanic origin, involving the collision of continental and oceanic plates, resulting in islands that consist of both basalt and granite rock (Williamson 1981).

Rosenzweig (1995) came up with the definition 'an island is a self-contained region whose species originate entirely by immigration from outside the region'. The first part of this definition is acceptable because it underlines the uniqueness and isolation of many island ecosystems. The second part is only valid where there has been no in situ evolution of taxa which is true for almost all recently formed land bridge islands (British Isles, Elba, Dalmatian islands) but not for thousands of oceanic islands. In fact, for Rosenzweig, all regions 'whose species originate entirely by speciation within the region' are considered mainlands. He insists that Hawaii is a mainland; logically then, so should most other islands with endemic taxa. It would be more useful to term such islands as novel centres of diversity. From the perspective of functional aerography, Rosenzweig's approach

fails to acknowledge the all-important biotic community and physical geocoenosis context in which species evolve and persist on islands (see below). Alfred Russel Wallace (1869, 1881) remains, of course, the patron of island biodiversity studies. The current renaissance of Wallace's works (Berry, 2002) and a new biography (Raby, 2001) will surely lead to greater appreciation of insular biotas and of the diversity of physical, climatic, and cultural island environments. Brown & Lomolino (1998) and Whittaker (1998) review island geography and distinguish several types of oceanic and continental islands. Mayr (1941) had noted that there has been some confusion over the term oceanic island. There is a geologic definition (an island not situated on a continental shelf), and there is a zoogeographical definition: 'an island that has received its fauna across the sea and not by way of land bridges' (Mayr, 1976).

All of the geological processes occurring volcanic islands can produce islands with high elevations, with peaks of at least 2,000 m (Williamson 1981). Volcanic islands are typically steeper and become increasingly separated with age. This phenomenon has important implications for island biota because a wide range of elevational gradients and associated ecological attributes allows for the persistence of diverse habitats. The elevation of islands also has important influences on the climatic regime.

Island climate is determined by both external influences, such as ocean circulation and atmospheric circulation, and internal influences, such as island size, shape, and topography. Ocean circulation and atmospheric circulation consist of water currents and air currents, respectively, that have similar movements of upwelling and sinking. If an island is in the path of a moving current or is located where two currents intersect, this can alter the climate significantly. In addition to circulation influences, the proximity of an island to a continental landmass also affects the island's climate. Islands located close to a mainland, such as land-bridge islands, are likely to be influenced by the continental climate. Remote oceanic islands, on the contrary, are influenced by the maritime climate (Yu and Lei, 2001).

Internal influences, such as island size and elevation, can have a substantial impact on the precipitation regime on the island. Whittaker (1998) states that low islands typically have relatively dry climates, and high islands are wetter through

orographic rainfall, resulting in the creation of extensive arid regions due to the rain shadow effect. These higher islands often contain diverse habitats within a relatively small area. Due to the impact of elevation on island climate, research studies have indicated that elevation is a critical variable in analyzing species diversity on islands. Telescoping, a compression of elevational zones, is fairly common on small tropical islands. Leuschner (1996) proposes that forest lines on islands are generally 1,000 to 2,000 m lower than forest lines on continents. Hence, telescoping creates smaller patches from a variety of habitats favourable to many species, and permits high- and low-elevation inhabiting species to coexist in a relatively small area (Whittaker 1998).

1.3.2. Anthropogenic losses and threats

Islands have also been an issue in conservation biology, mainly due to detrimental human impacts in island environments. There are numerous heated debates as to what type of impact the earliest human colonizers had on island ecosystems. Some ecologists and biogeographers argue that most of the earliest island colonizers were respectful of the island ecosystem and that negative impacts occurred only after secondary arrivals of colonizers conflicted with the interests of the initial inhabitants. Others argue that earliest inhabitants of some islands devastated the environment because of their ignorance and negligence concerning island ecosystems. One rather undisputed fact is that as human communities on islands reached the carrying capacity, humans often modified island landscapes to support the rapidly growing population. A classic example is the terracing of steep terrain on islands to maximize agricultural productivity (Nunn 1994). Through history and into the modern age, negative anthropogenic impacts have continued and increased. Humans can easily damage pristine island environments in five ways: overexploitation and predation, habitat loss, fragmentation, degradation, and the introduction of exotic species and diseases (biological invasions).

Olson (1990) reviewed the prehistoric impact of humans on island birds and concluded that 'analysis of the fossil record has repeatedly shown that prehistoric man has had an extremely adverse effect on insular ecosystems on a global

scale. He documented that on many Pacific islands (from New Zealand, New Caledonia, Oahu, Maui, Managaia, to Huahine in the Society Islands) some 40–80% of the native land bird species had gone extinct in prehistoric and historical times (Steadman, 1997). Olson showed that current distribution patterns have been unnaturally modified by man-caused extinctions 'and have thus led to many fallacious systematic and biogeographic conclusions'. He argued that 'at this point, the only safe generalization in island biogeography is that it is not safe to make generalizations' (Olson, 1990). Similar effects of prehistoric and historic human agency have been discovered in the West Indies (Woods & Sergile, 2001). The severe species and habitat loss experienced by many island ecosystems have been accompanied (and possibly accelerated) by intentional and accidental invasions of exotic biota. Sax et al. (2002) have shown that the species richness of vascular plants has approximately doubled on oceanic islands as a result of the recent human impact.

For centuries, island ecosystems have been the target for habitat loss, fragmentation, and degradation primarily for agricultural reasons (Heywood 1979). Such habitat destruction not only directly damages the island flora but also reduces the faunal biodiversity. As forested areas are diminished, suitable habitats and food resources for fauna also diminish. As habitat fragmentation (deforestation) continues at an alarming rate, it creates major ecological dilemmas on islands such as Madagascar. Another mechanism of habitat degradation or simplification is human-induced fires. Fires are often utilized for hunting purposes or to clear a plot for agricultural purposes. Frequent fires in areas with a low natural fire frequency can be tremendously destructive. Such prescribed burning can clearly destroy the present island ecosystem and permanently transform the island landscape.

As humans travel the globe, different species have been intentionally and inadvertently introduced into new ecosystems. Many island species, also known as the native biota, are particularly vulnerable to biological invasions due to their isolation through evolutionary time. The absence of herbivory, for instance, has resulted in the persistence of many island flora with no defensive mechanisms against grazing pressures. Isolation, in a sense, has protected such plant species that, otherwise, would have become extinct on the mainland (Melville 1979).

Nevertheless, the presence of abundant herbivores, such as cattle, sheep, goats, and pigs, has led to extreme habitat degradation. Historically, humans intentionally introduced these grazing animals to ensure abundant food supply, without even considering the negative ecological consequences. However, many of these animals have become feral and extremely detrimental to the island landscape. Overgrazing has caused massive erosion on the hillsides, leading to large-scale landslides. Similarly, heavy grazing has encouraged the proliferation of exotic species. The introduction of exotic species into an island ecosystem is typically irreversible. Some exotic species, in fact, are more successful in these foreign environments than in their native landscape. Once those exotic species have established, their populations rapidly proliferate, making it nearly impossible to completely extirpate them from the island.

1.3.3. Insect and island ecosystem

Insect diversity on islands is often skewed. Some taxa and endemic insect diversity on islands had rarely been explored (Sugiura et al., 2009). On newly created islands, this is partly the result of the sweepstake effect, where only certain taxa successfully land and colonise an island. Especially on larger isolated islands or archipelagos, many species that naturally invaded new islands or were marooned on islands that became separated from the mainland develop into island endemics. This can be related to the island being separated from neighbouring suitable habitat by a hostile environment, the sea. Besides adaptive radiation, where species have evolved to occupy distinctly different niches and subsequently acquired evolutionary stability, there is also fugitive radiation. This, according to Adsersen (1995), is the appearance of 'weak species', which are very local and have to evolve further to avoid extinction when faced with competition from mainland relatives. Many insects appear to fall into this latter category, maintaining remarkably small populations (Samways, 2003), which presumably are highly susceptible to adverse changes. This emphasizes the risks of synergistic effects of global warming and invasive aliens on island insect assemblages, which are both severely impacting some island faunas (Samways, 2005).

On the other hand, insects are ideal objects for studies of ecological biogeography because of their highly diversified ecology, also in habitats like islands, where some taxa, such as tenebrionidae beetles, are speciose while other animal groups have low diversity (Fattorini, 2002). Because insects also differ in dispersal ability (there are winged, wingless, and wing-dimorphic species, den Boer et al., 1980), they are a popular model in island ecology (Lovei and Sunderland, 1996; Hatteland et al., 2008; Kotze, 2008).

Beetles have been used extensively to study island ecosystems in the past. Ground-beetle species (Coleoptera: Carabidae) have been employed as bioindicators for conservation planning over a wide range of altitudes in the Canary Islands (Gomez, 2010). Dung beetle (Coleoptera: Scarabaeidae) have been studied to look at the small island effects on their richness and communities in north-eastern Peninsular Malaysia (Qie et al., 2011). The study showed that common species and those able to forage on the forest edge have a higher chance of survival on small islands. Qie et al. (2011) also found that species richness and community composition on islands below 35.8 ha in an area clearly exhibited increased variability. A study from Emerson and Oromi (2005) looked at diversification of the flightless beetle genus *Tarphius* (Coleoptera: Colydiidae) and its evolutionary origins of island endemicity in the Canary Islands. The result suggested that the Canary Island species assemblage is of some antiquity, however, much of this species diversity is relatively recent in origin. It also indicated that colonization events between islands have probably been a significant factor in the evolutionary history of the Canary Island species assemblage (Emerson & Oromi, 2005). Study on *Bothrometopus huntleyi,* a flightless weevil endemic to the volcanically-formed sub-Antarctic Prince Edward Islands, showed that the genetically discrete *B. huntleyi* complexes on each of the islands of the Prince Edward Islands archipelago together with the low levels of inter-island gene flow reaffirm the need to control alien invasive mice, which are restricted to Marion Island, and which prey on this weevil species.

1.4. The development of The Equilibrium Theory of Island Biogeography (ETIB)

1.4.1. Historical perspective of Island Biogeography Theory

Research on islands has long played a fundamental part in developing our basic understanding of ecology and evolution. Both Darwin's and Wallace's insight into evolution and speciation were shaped by studies on islands (Darwin, 1859; Wallace, 1881). The reasons why islands are useful in ecological studies are manifold. Island populations, communities and ecosystems are self-maintaining entities with well-defined geographical limits that contain the fundamental processes, properties, and interactions of ecological systems - but they often do so in simpler ways, without the complexity of most continental systems. Moreover, the influence of particular factors that control ecological phenomena can be studied against a relatively simple environmental setting in island ecosystems (Eliasson, 1995; Kaneshiro, 1995). More practically, islands provide clear records of anthropogenic interactions with biological diversity in contained areas, and of the consequences of those interactions (MacDonald and Cooper, 1995).

The field of Island Biogeography was particularly stimulated by the equilibrium theory of extinction and immigration of species on islands formulated by MacArthur and Wilson (1967). They stated that, while immigration rates should be mainly influenced by island isolation from a source landmass, extinction rates should mainly depend on island size. As a result, species richness on islands should be negatively affected by increasing island isolation as well as decreasing island size. An equilibrium state will eventually be reached when extinction and immigration rates level and lead to a constant species richness.

MacArthur and Wilson's equilibrium theory revolutionised the field of island biogeography and, to a large degree, ecology as well. Although their classic foundation for the Equilibrium Theory of Island Biogeography (ETIB) has been largely superseded by new field data and more realistic concepts, there are still key aspects of the ETIB paradigm that continue to influence basic biogeographical thinking and its application in conservation science today (Walter, 2004).

Brown & Lomolino (2000) argued that MacArthur and Wilson's equilibrium theory has not kept pace with relevant theory and our growing appreciation for the complexity of nature, especially with empirical findings that species diversity on many islands. Their study found that species diversity on islands is not in equilibrium, influenced by differences in speciation, colonization, and extinction among taxa, and influenced by differences among islands in characteristics other than area and isolation. They also recognised that the discipline of biogeography itself is in a state of disequilibrium. Wherever this shift may take us, the next generation of biogeographers will still look to islands for insights into the forces that shape biological diversity.

A large body of work (Brown & Lomolino, 1998; Lomolino, 1984, 1986, 1993, 2000; Fox & Fox, 2000) shows clearly that the differences among both species and islands (in characteristics other than area and isolation) matter. Species differ in their ecological interactions with other organisms and their abiotic environment. These differences affect the assembly of insular biotas by influencing the capacity to disperse across different kinds of barriers, and to establish and persist on islands with different abiotic conditions and species composition. In addition to area and isolation, characteristics of islands that affect species diversity and composition include the influence of currents, ice formation, human transport, and other factors which affect the permeability of barriers, and habitat heterogeneity, disturbance regimes and the presence of humans and other interacting organisms, which affect both the establishment of colonists and the persistence of natives. The rescue effect, a major influence on island biogeography and underlying metapopulation dynamics (e.g. Brown & Kodric-Brown, 1977; Lomolino, 1986; Gilpin & Hanski, 1991) shows that immigration and extinction cannot be regarded as independent processes.

A new theoretical framework to develop such an alternative: a species-based theory of island biogeography (Lomolino, 1986; 2000b) is required. This formulation focuses on the importance of differences among species (and also, implicitly, on differences among islands) in determining the assembly of insular biotas, and the resulting patterns of species richness and composition. This model is much less revolutionary than MacArthur and Wilson's original theory. Yet, it seeks to preserve some of their most valuable insights, especially the

observation that insular biotas reflect the interplay between recurrent immigration and extinction events, but not necessarily an equilibrium between these processes. By aiming to be more realistic and more general than MacArthur and Wilson's theory, such efforts might aspire to be stepping stones towards a better understanding of island biotas and towards new paradigms.

1.4.2. Island species-area relationship

The species–area relationship is one of the most studied patterns in ecology, often being referred to as one of ecology's few laws (Schoener, 1976; Rosenzweig, 1995, 2003; Lawton, 1996, 1999). According to this 'rule', the number of species increases with area, and the rate of increase of species richness usually declines as area increases. There are a number of classifications for the different types of species–area relationships, depending on the scale at which they are analysed or whether they are measured from nested areas or not (Rosenzweig, 1995; Scheiner, 2003; Gray et al., 2004; Whittaker & Fernández-Palacios, 2007; Dengler, 2009).

The species richness of small islands may be relatively independent of area and isolation (Lomolino & Weiser, 2001). On larger islands, one of the most atypical datasets concerns the avifauna of the Canary Islands (Lack, 1976). An arid climate and volcanic soil and surface have a drastically depressed bird and plant richness of Lanzarote and Fuerteventura compared with the other islands. Among land snails (see above, Solem, 1982, 1990) SAR was inverted on some oceanic islands. Differences in species–area relationships may provide important clues about the composition, history, and function of biotic communities on continents. An example is Keeley's (2003) comparison of Australian and Californian shrub communities

In addition, Minelli (1990) found that area was often less important for the observed species diversity than habitat diversity, elevation, climatic diversity, floristic diversity, and habitat disturbance regimes. Species diversity is positively increased by speciation given suitable conditions of size, time, and isolation. The classical ETIB model operates in ecological time omitting speciation processes. Minelli then scrutinized the sampling procedures used to assess equilibrium and

turnover states (see also Gilbert, 1980; Brown & Lomolino, 1998; Whittaker, 1998). He questioned the census accuracy and species selection of published case studies (what is a proper census interval, what is the exact source pool of species, do we count only within or between habitats, taxon levels, guilds, native and introduced species?). The conclusion reached was that the available evidence is riddled with uncertainty because of inappropriate or non-comparable sampling procedures and taxon selections.

Regional factors acting on the whole of an archipelago (such as archipelago isolation, age, origin of the islands) are thought to have a consistent effect on the local patterns of diversity at the island level. Therefore, archipelagos are usually considered to be homogeneous entities, and it is thus not surprising that many authors have used complete archipelagos as single data points in their analyses (e.g. Adler et al., 2005; Biber, 2002; Hamilton et al., 2009). In his discussion, Rosenzweig (1995) argued that 'the diversity and the area of whole archipelagos fall in the same species–area curve as the separate islands that constitute them', although stating that this hypothesis deserves further examination.

Where an archipelago is composed of different groups of islands with differing characteristics, the processes building up island biotas might vary amongst the constituent islands. This can be hypothesised to happen in archipelagos in cases where the proximity to the source(s) of colonizers allows inter-island variation in colonization rates and/or the arrival probability of particular species or lineages (thus, different sets of widespread species will be found in different clusters of islands), one or some of the islands show higher speciation rates (Losos & Schluter, 2000), some islands suffer anomalous pulses of extinction (Whittaker & Fernández-Palacios, 2007) and islands vary strongly in relation to anthropogenic influences, for example with humans acting as deliberate or accidental vectors of organisms. All these cases will produce anomalous patterns of species accumulation with area, and the departure of the overall richness of the archipelago from the island species-area relationship of its constituent islands.

1.4.3. The distance effect

Isolation is a critical component when examining evolutionary processes since it allows for allopatric speciation to occur. Islands offer prime examples of isolation effects on biota (Cox and Moore 1993). Specific adaptations, such as seed parachutes, are necessary for plants to disperse across large bodies of water. Such dispersal invokes survival of a sweepstakes route, an extensive barrier permitting only a stochastic set of immigrants to successfully colonize the island (Brown and Lomolino 1998). The more remote the island is from a continental landmass, the more severe the sweepstakes route and the smaller the number of species that would successfully colonize and become established on the island. This is known as the species-isolation relationship on islands. The number of species would decrease exponentially as a function of isolation because the species isolation correlation should account for a pool of species (Brown and Lomolino, 2000).

Conceptual models in island biogeography commonly consider isolation as the 'distance to', or more generally as 'isolation from' an unspecified source pool. However, correlative studies require a precise metric quantifying isolation. Many different metrics have been tested. The vast majority of studies have used the distance between a target island and the nearest mainland coast (Case, 1975, Abbott, 1978, Chown et al., 1998) since continental landmasses harbour large species pools for potential island colonization. The validity of this approach is supported by phylogenetic studies indicating long-distance dispersal events from continents to even remote islands (Alsos et al., 2007, Harbaugh and Baldwin, 2007). However, islands may also serve as sources for immigration to other islands and to the mainland (Bellemain and Ricklefs, 2008, Keppel et al., 2009). The distance to the nearest island (Johnson and Simberloff, 1974), the nearest large or larger island (McMaster, 2005), the nearest older island (Cardoso et al., 2010), or the mean distance to other islands (Borges and Hortal, 2009) have therefore been used in correlative studies. The UNEP isolation index (Dahl, 2004), another frequently used metric (Boyer and Jetz 2010, Kisel and Barraclough 2010), incorporates the distances to the nearest mainland, nearest island group and nearest equally sized or larger island. However, nearest landmasses are not necessarily suitable source areas because colonization also

depends on the favourability of island environmental conditions, especially on climate (Steinbauer et al., 2012). Price (2004) therefore used the distance to the nearest island with analogous habitats as isolation metric. Moreover, long-distance dispersal depends on dispersal vectors and is influenced by wind and ocean currents (Muñoz et al., 2004). Similarly, Abbott (1974) found the distance to the nearest landmass in a westerly direction to be a strong predictor of plant species richness for a set of islands within the west wind zone of the southern hemisphere.

Weigelt and Kreft (2012) concluded in their study that isolation is comprised of multiple components that cannot be captured in a single metric. In fact, a range of different immigration mechanisms influence island biogeographic patterns. The ordinary distance to the nearest mainland is an adequate and simple-to-calculate measure. However, accounting for stepping stones, climatic similarity and the area of surrounding landmasses increases the explanatory power of isolation for species richness. At a global scale, the proportional landmass within certain buffer distances around an island is the best metric. The effect of isolation depends on the degree of isolation of the considered system and the dispersal mode of the studied taxa (Lomolino 1982) as well as on abiotic factors. Weigelt and Kreft (2012), therefore, suggested choosing metrics for a study system on an empirical basis. They argued that multiple isolation metrics may be useful not only in analyses of species richness but also of other biogeographic patterns such as gene flow and genetic diversity (Slatkin 1993), speciation (Kisel and Barraclough 2010), endemism (Bunnefeld and Phillimore 2012), phylogeography (Cook and Crisp 2005), species composition and turnover (Hausdorf and Hennig 2005), community structure (Santos et al. 2011) or species traits (Meiri, 2005).

1.5. Indonesian archipelago

1.5.1. Geography and geology

In 1996, the Republic of Indonesia officially defined itself as an archipelagic nation. The approximately 17,000 islands and the seas between the islands shape the country.The country is the largest archipelagic state of the world with an area of about 5,219,000 km^2 including East Timor. About 17,500 islands, 6000

of which are inhabited by humans, form the landmass of about 1.919,000 km^2 (land: 1,826,000 km^2, inland water: 93,000 km^2), encircled by about 3.3 Mio km^2 of territorial seas (Rigg, 1996). After Greenland, the biggest islands of the globe belong partly to Indonesia, like the Western part of New Guinea (West Papua) and the Southern part of Borneo (Kalimantan) (Figure 3).

Figure 3 Indonesian archipelago (Nations Online Project, 2012). Indonesia is highlighted in white colour.

1.5.2. Biogeographic importance

Indonesia covers only 1.3% of the Earth's surface. Yet, it harbours 10% of all flowering plant species, 12% of the world's mammal species including four threatened endemic mammal species and subspecies, the Sumatran tiger, orang-utan, rhinoceros and Sumatran elephant, 17% of all bird species and more than 25% of known marine and freshwater fish species, in addition to 16% of the world's reptile and amphibian species (Stone, 1994). Particularly in relation to amphibians, Indonesia is a global hotspot, harbouring 392 of the world's amphibian species in its vast area. Indonesia also has the second highest

number of endemic species in Asia, with 175 amphibian species endemic to its rainforest habitats (IUCN, 2009).

The flora and fauna of most of the islands of this archipelago are proof of ancient affiliations. The animals of the Great Sunda Islands of Java, Sumatra and Borneo are characteristically Asian origin comprising tigers, elephants, tapirs, deer, monkeys and squirrels. In contrast, the island of New Guinea has no indigenous placental mammals other than bats, rats, and the sea-living dugong, but harbours tree kangaroos (Stabach et al., 2009). Fossil evidence shows that lowering and raising of the sea level happened several times, resulting in connections between mainland Asia and the islands of the Sunda Shelf, and between Australia and the islands of the Sahul Shelf, which were subsequently broken again. During periods of connectivity, many of the respective continental species spread and filled vacant niches on the respective shelve areas (MacKinnon, 1992).

The important feature of colonisation and specialisation of plants and animals in Indonesia was systematically documented for the first time by the Victorian naturalist and voyager Alfred Russel Wallace. In Indonesia, Wallace noticed that Lombok and islands in the east were inhabited by cockatoos, parrots and marsupials. In contrast, monkeys, tigers, elephants and rhinoceros were found in Bali and on islands further west. He recorded these findings in his book "The Malay Archipelago" (Wallace, 1869).

This important faunal boundary, separating Bali from Lombok and extending northwards through the Makassar Strait, here separating Borneo from Sulawesi, is dubbed the "Wallace Line" (Figure 4). Not only the Indonesian fauna and flora is remarkable, but Central Java is also the place where the oldest remains of mankind in Asia, *Meganthropus* sp. and *Homo erectus*, have been excavated. Another significant finding was from excavations at Liang Bua, on the Indonesian island of Flores, that yielded a stratified sequence of stone artifacts and faunal remains spanning the last 95 k.yr., which includes the skeletal remains of two human species, *Homo sapiens* in the Holocene and *Homo floresiensis* in the Pleistocene (Morwood & Jungers, 2009).
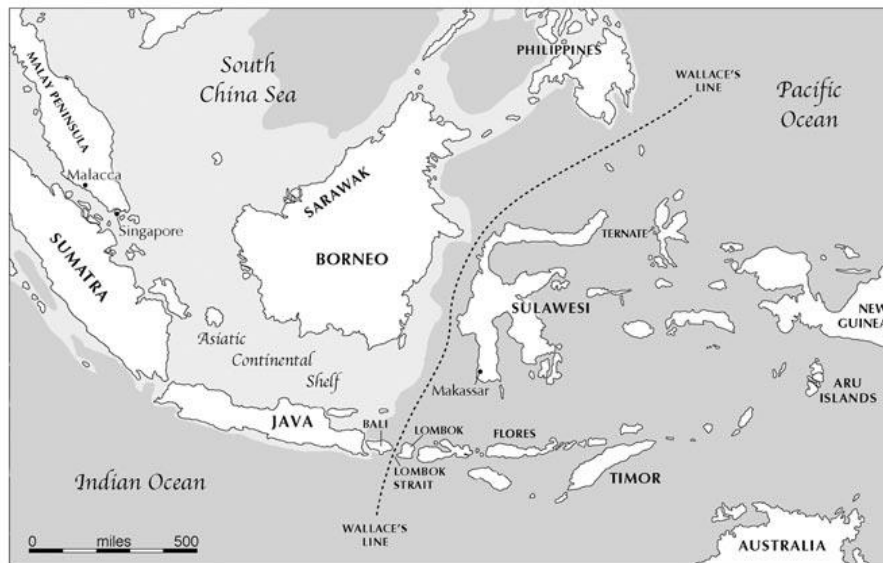
Figure 4 Wallace Line on Indonesian archipelago (Encyclopaedia Britannica, Inc., 1997)

1.5.3. Small islands region in Indonesia

Indonesia as an archipelagic country with many small island regions has attempted to adopt the sustainable development framework though Integrated Coastal Zone Management (ICZM), which has been activated under the Indonesian Cooperation Law, Act No. 27 in 2007. At present, the quantification of sustainable development for the coastal and island management is a critical problem.

Farhan & Lim (2011) found that several main issues of ICZM in Indonesia are socio-economic issues - where the emphasis is put on new infrastructure development regardless of the consequences to the environment, rather than optimizing the existing infrastructure. Poverty is widespread, as lack of knowledge and use chiefly of traditional and destructive fishing methods. These authors also mention that there are observation, monitoring and evaluation issues, where there are only a few ocean and coastal observation equipment (such as oceanographic buoys and tidal gauges). Moreover, problems facing the coastal and island ecosystems in Indonesia have been worsened by the lack of policy and financial support, continuous overfishing and overexploitation of

natural resources, erosion, abrasion, pollution, losing and declining biodiversity and mismanagement (Sukardjo, 2002).

Figure 5 Small island regions in Indonesia (Farhan & Lim, 2012)

Small island regions in Indonesia (Figure 5) are the regions particularly threatened by the direct or indirect results of the negligence of the government and the coastal society. The rapid development in the five major islands has made the small island regions overlooked and underdeveloped. Poor accessibility and poor infrastructures such as lack of electricity, housing, waste areas and ports underline the disadvantageous situation in the small island regions (Farhan and Lim, 2012).

1.6. Kepulauan Seribu Marine National Park

The Kepulauan Seribu Marine National Park is used as research location because it represents tropical islands with varying land use patterns, sizes and

distance to Java as the main source area for potential colonizing species. The National Park is located in the northern sea of Jakarta Bay and consists of 105 islands, each being smaller than 1 km^2 and with a maximum elevation of less than 3m (Yates, 1994; Nur et al., 2001; Alamsyah 2003). The total number does not include islands that already became submerged in recent years, with their disappearance being linked to climate change and anthropogenic effects (Farhan & Lim, 2012). Many of the remaining small islands are still unexplored and may serve as a home for endangered and endemic species.

The islands of Kepulauan Seribu are all coral cays with reefs that reach a maximum depth of between 15 and 20 m (Yates, 1994). Until the early 1970s, they supported a diverse ecological community, yielding an abundance of environmental resources for the local population. They featured more than 130 species of coral, which provided a habitat for a variety of reef-associated fish, including groupers and snappers, hawksbill turtles, and green turtles. In May 1981, for example, 95 turtle nests were counted on seven small islands, with 51 encountered on Gosong Rengat Island alone (Salm et al., 1982).

This archipelago can be considered as an inner island region that is located 30 km away from the north of Jakarta and supports a population of about 22,700 people (The Centre of Indonesia Statistic, 2009). Administratively of Kepulauan Seribu Marine National Park region is divided into two districts and six villages. Most of the people live only on the main 11 islands, and one of the main islands is Pramuka Island as the center of the local government of the islands region.

According to the Centre of Indonesia Statistic (2009), the islands have an average slope of 15% with a height of less than 2 m above the sea surface. They are influenced by both the East Monsoon between December and March and the West Monsoon between June and September. Wet seasons usually occur from November to April, with the annual rainfall amounting to approximately 1700 mm, and the number of raining days ranges between 10 and 20 days/month. Air temperature in these islands is ranging between 26.5 and 28.5 C and the humidity from 75 to 99%.The land use in these islands can be classified into several categories including settlement areas (housing, industry, government and private office), farmland and forest plantations (Rizali et al., 2010; Farhan & Lim, 2011).

Although the region is very close to the Indonesia's capital city, Kepulauan Seribu Marine National Park is a typical example of a protected area lacking a general concept, design, central planning and development plans. It has turned out to be overburdened by the increased population (Verstappen, 1988), pollution (oil spill in Pabelokan Island by a multinational oil company), illegal unregulated and unreported fishing (IUUF) and marine debris originating from seven major rivers in Jakarta Bay (Bird and Ongkosongo, 1980).

Due to its proximity to the capital Jakarta which is a metropolitan city of about 12 million inhabitants, the sanctuary serves as an important holiday destination for people in Jakarta and vicinity. The area offers a relatively noise- and air-pollution free environment, something not commonly found in the areas surrounding the crowded capital city. In addition to their use for water sports and recreation, the islands are utilized for educational and military training purposes. They are therefore overall subjected to considerable pressure from human use (Fauzi & Buchary, 2002).

1.6.1. The environmental degradation in the Jakarta Bay and Kepulauan Seribu

Jakarta's Office of Urban Environmental Study reported in 1997 that marine pollution and beach litter are the main chemical pollutions in the Jakarta Bay. The 'inland' area, inhabited by 20 million people, is considered the primary source of Jakarta Bay's degradation. The heavy metal content in its water especially of copper (Cu), lead (Pb) and mercury (Hg) has been increasing since 1983. Razak (1994) also reported that in relation to organic pollutants, the total polychlorobiphenyls (PCBs) content in the water of the Muara Sunter area of Jakarta Bay is higher than the recognized water quality standard, with a tendency to further increases.
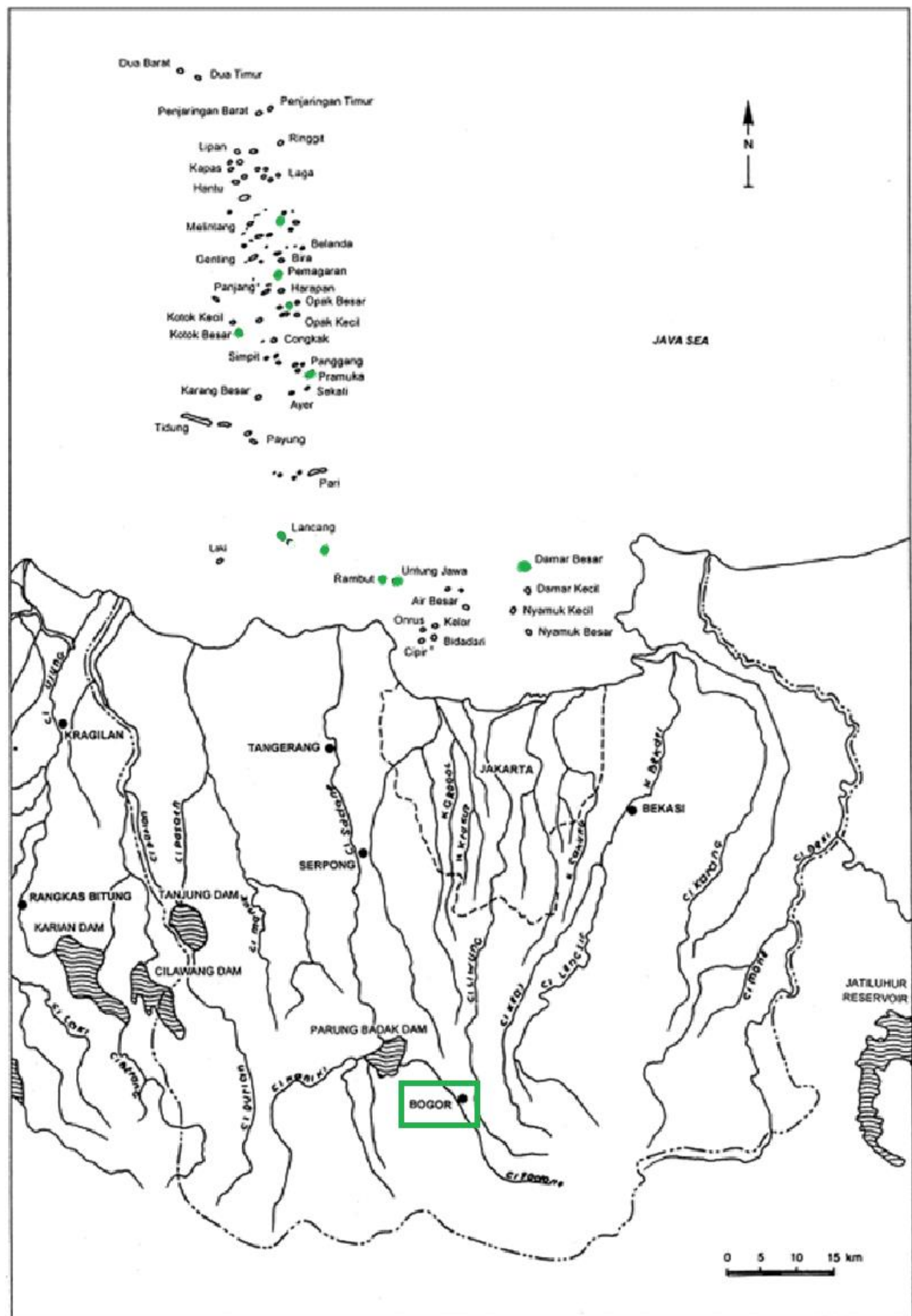
Figure 6 Jakarta Bay and Kepulauan Seribu archipelago (Nur et al., 2001), with the studied area highlighted in green.

The transformation of natural ecosystems has taken its toll in Jakarta Bay and Kepulauan Seribu National Park (Figure 6). During the last decades, a rapid increase in urbanization along Jakarta Bay has taken place. An enormous reclamation project is envisaged along the Jakarta Bay coastline, both for housing as well as for business projects (Nur et al., 2001).

The growing population in Jakarta Bay has also effected mangrove ecosystems in Jakarta. This region harbours the only mangrove conservation program in Jakarta. In 1960, the conservation area of mangroves was 1335 ha, but the remaining current mangrove protection area comprises only 173 ha. Residential and fishpond developments have had the greatest impact on mangrove areas (Nur et al., 2001).

Another unsustainable coastal resource exploitation is blast fishing. This technique of using explosives to stun or kill fish is an extremely damaging practice. In addition to indiscriminately killing target and non-target fish and invertebrates of all but the largest size classes, blasts commonly damage or outright destroy the reef framework itself. Cyanide fishing practice using sodium cyanide solution to stun fish for live collection is another widespread destructive fishing practice in Kepulauan Seribu National Park. Before 1990, the main targets of cyanide fishing were ornamental fish and invertebrates for the aquarium trade. In the years following 1990, cyanide fishing was also used to catch live fish food. Unfortunately, cyanide fishing may be the most destructive practice observed in Kepulauan Seribu National Park (Nur, et al., 2001).

Large-scale sand mining has taken place during the construction of the harbours in the Jakarta Bay area. In the 1970s, sand extraction for building activities occurred on a small scale and was carried out manually. From the 1980s onwards, extraction became more and more intensive (Nur et al., 2001). It is becoming an activity of great importance for the economies of various small communities along the coastline. Extensive dredging activities have been allowed to proceed, despite regulations banning the exploitation of sand, gravel and boulders by the local government, to provide construction material for the new international airport at Cengkareng (Nur et al., 2001).

Nur et al. (2001) also found that the exploitation of coral from the reefs started from the early part of the century. In the 1990s, 12,000–25,000 m^3 of coral reef were exploited annually. In the 1930s, the annual removal of coral reef was 8500–20,000 m^3 in Kepulauan Seribu National Park. With time, it has been estimated that the scale of exploitation has escalated with values in 1982 double those recorded in 1979. The most significant removal of coral reef in the Jakarta Bay has been around the island of Air Kecil and Ubi Kecil. As a result of subsequent erosion, both islands have now disappeared. The island Ubi Besar is currently rapidly being eroded as the reef is dredged around it.

1.6.2. Sustainable Development and Biodiversity Status in Kepulauan Seribu Marine National Park

Several studies on sustainable development have been conducted in the Kepulauan Seribu Marine National Park (Nur et al., 2001; Farhan & Lim, 2011). Farhan and Lim (2011) conducted a vulnerability assessment to measure the ocean and coastal sustainability to have a better evaluation and redesign of the land development as well as policy making. The results of their study were measured only on the urban islands. It proved that the constructions and robust developments in the islands reduced the weathering process.

Biodiversity studies conducted in the national park to date have either mostly focussed on the marine area, did not compare different terrestrial habitats on the islands in detail, nor have they looked at habitat complexity and changes caused by anthropogenic activities. General studies of terrestrial habitat using insects as indicators have been conducted by Rizali et al. (2010) and Spengler et al. (2011), looking at the effects island size and isolation and 'tramp' ant species have on the overall ant communities and the effects of island size and isolation on bee and wasp ensembles, respectively.

1.7.   The beetle research gap on small islands in Indonesia

Indonesia is known as one of the mega-diverse countries in the world, and the study of insect diversity in Indonesia has great value. Some estimated insect diversity in Indonesia of about 250,000 species account for 15% of the total

species number in Indonesia (National Development Agency, 1993). Beetles accounted for more than 40% of the total insect species described in Indonesia, and 10% of the total global species number (Noerdjito, 2003), indicating an even bigger contribution. However, very limited attention has been given to the country's beetle communities, their conservation status, and the likely influence of habitat fragmentation and anthropogenic activities on these communities.

As the largest island country in the world, surprisingly, there has been very limited research on island ecosystem. Land use intensity, habitat changes, and anthropogenic activities on the tropical islands also has strong effects on the diversity and abundance of functionally important beetles such as ground beetle (Rainio and Niemela, 2003; Kotze, 2008), bark and ambrosia beetle (Jordal et al., 2002; Kirkendall and Jordal, 2006), and dung beetle (Qie et al., 2011; Silva and Hernandez, 2014). Research on beetles in Indonesia has been dominated by several groups, including dung beetle and ground beetle, but mostly in forest, agroforest, and agriculture habitats (Shahabuddin et al., 2005; Shahabuddin et al., 2010).

Understanding the island ecology with human-dominated landscapes provides critical insights into functional diversity in the tropical islands because most species experience their surroundings at spatial scales beyond the plot level. Given this importance for island ecology and conservation, this study provides a comparison overview of important considerations shaping beetle functional groups with and without human settlement.

The main research area of this study is located in Kepulauan Seribu Marine National Park. Insects from order Hymenoptera, ants and wasps, have been studied in some of the islands in the national park (Spengler et al., 2011; Rizali et al., 2010). These studies, however mainly focused on the effects of island isolation and area on the insect assemblages on the islands. None of these investigations compared different taxa compositions in Java and islands, and no comparison on different beetle feeding guilds and habitat specialisation were investigated. In addition, analyses on how the diversity of the taxa linked to anthropogenic factors, such as human population were not discussed. The authors also encouraged more works to highlight the destructive role of human disturbance on the islands (Rizali et al., 2010).

1.8.   <u>Research aim and objectives</u>

In this thesis, I aim to establish the diversity patterns of beetle assemblages in ten islands in Kepulauan Seribu Marine National Park in relation to island area and island isolation from Java, and how human settlement affects the distribution patterns of beetle with different feeding guilds and habitat requirements. The resulting patterns furthermore form the basis for assessment of the effects of different land use and habitat change scenarios on biodiversity patterns, as well as providing a baseline for biodiversity studies in the tropical islands of Indonesia. The following research questions hence will be addressed:

1) How is the diversity of beetles on islands affected by island size and isolation?

2) How is the alpha diversity and composition of beetle communities affected by the presence of human settlements on small islands?

3) Do alpha- and beta-diversity patterns of different beetle families differ according to their trophic level and habitat requirements?

In particular, the main hypotheses will be tested in the following chapters:

Hypothesis 1.1: Beetle assemblages on islands in Kepulauan Seribu Marine National Park effectively form impoverished subsets of the communities encountered on Java but retain unique island beetle species.

Hypothesis 2.1: Beetle diversity on the studied islands decline with a decrease in island size, with a log-log relationship describing this relationship.

Hypothesis 2.2: Inter-island faunal exchanges linked to the distance to the nearest small island are more important for faunal turnover in the island setting than the distance to Java.

Hypothesis 3.1: Islands with settlements are expected to have higher beetle species richness.

Hypothesis 3.2: Forest habitats on undisturbed forested islands will harbour more unique and distinct beetle faunas, containing species that only occur in a particular island setting.

Hypothesis 3.3: When comparing disturbed forest habitats in mixed forest and settlement habitat islands with undisturbed forest habitats, the former will contain a larger proportion of beetle generalists.

Chapter 2. Methodology

2.1. <u>Study area</u>

The main study area is located on ten islands in The Kepulauan Seribu Marine National Park (the Thousand Islands Archipelago; 106º20' - 106º50' E and 5º20' - 6º00' S). This island group consists of several hundred small islands near Java; each with an area of < 1km^2 (Alamsyah, 2003). The islands have different characteristics of island size, island isolation from 'mainland', i.e. the much larger island of Java, and of dominant land cover types (forest, settlement, or a combination of both), (Rizali, 2010; Spengler, 2011).

Table 1 Surveyed Islands in Kepulauan Seribu Marine National Park

| No | Island | Coordinates | | Type of Land-use | | |
				Forest	Human Settlement	Tourism
1	Rambut	05°58.68 S	106°41.57' E	+	-	-
2	Untung Jawa	05°58.61' S	106°42.18' E	-	+	+
3	Damar Besar	05°57.45' S	106°50.58' E	+	-	-
4	Bokor	05°56.74' S	106°37.92' E	+	-	-
5	Lancang Besar	05°55.87' S	106°35.23' E	+	+	+
6	Pramuka	05°44.72' S	106°36.90' E	-	+	+
7	Kotok Besar	05°41.98' S	106°32.25' E	+	+	+
8	Opak Besar	05°40.23' S	106°34.92' E	+	-	-
9	Pamagaran	05°38.09' S	106°34.74' E	+	-	-
10	Putri Barat	05°35.55' S	106°33.40' E	+	-	-

Beetles were surveyed on all 10 islands, as well as at Java, using a combination of pitfall traps and flight interception traps as outlined below. Geographic coordinates provided for all islands were measured with a GPS at the center of

each surveyed island (Table 1). Distances between islands were generated from topographical maps. Island isolation measurements were defined in three categories, the distance between the respective island and the nearest coastline of Java, the distance to the nearest island, and mean distance to islands within the radius of 5km (Table 2). Data on island size, human population and land-use changes were provided by the authorities of Kepulauan Seribu Marine National Park.
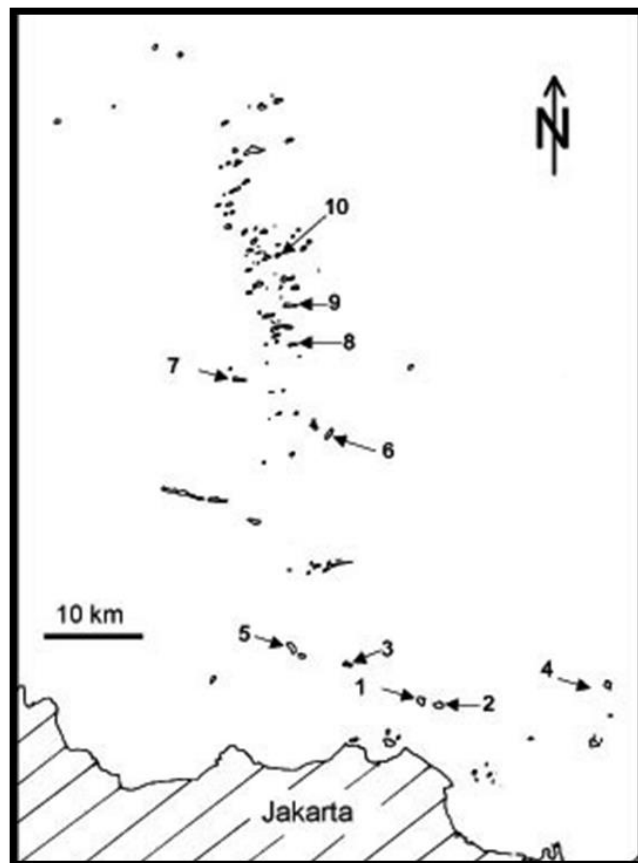
Figure 7 Surveyed islands in Kepulauan Seribu Marine National Park: (1) Untung Jawa, (2) Rambut, (3) Bokor, (4) Damar Besar, (5) Lancang Besar, (6) Pramuka, (7) Kotok Besar, (8) Opak Besar, (9) Pemagaran, (10) Putri Barat.

Islands were categorized by looking at three main aspects: isolation, island size, and level of human activities. Although I expect that the intensity of human activities would generally decrease with distance from Java as well as with

decreasing island size, islands were selected with view of minimizing the respective correlations (see also Table 2).

Untung Jawa Island, Lancang Besar Island, and Pramuka Island represent islands with high human population and activities. Data from Pemerintah Kecamatan Kepulauan Seribu (report of the government activities of Kecamatan Kepulauan Seribu in 2010) reported on the demography of Untung Jawa Island (Figure 8) with a total population of 1698 and density of 50 people/ha. Lancang Besar Island (Figure 9) was reported to harbor a total population of 1554 and a density of 116 persons/ha.
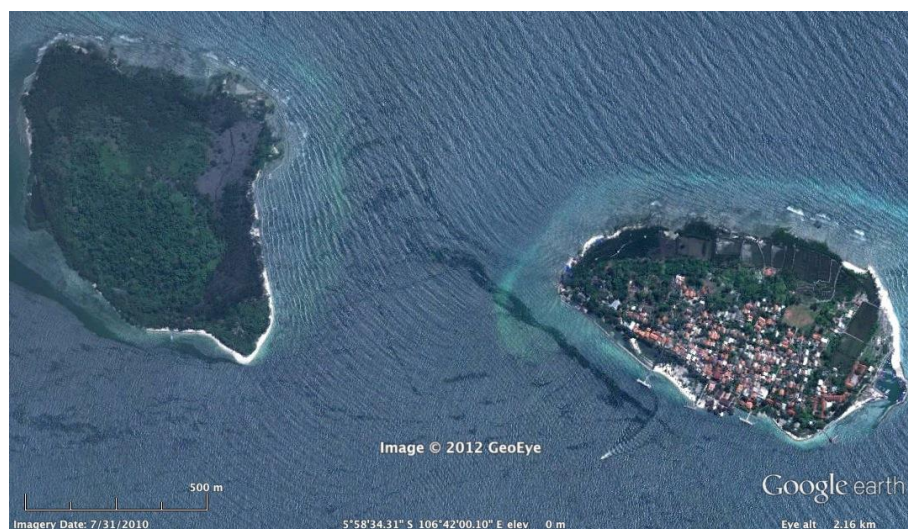
Figure 8 Rambut Island (left) and Untung Jawa Island (right)

Figure 9 Lancang Besar Island

Meanwhile, Pramuka Island (Figure 10), harboured a total population of 1004, including the national park's 41 staff, with 25 in the field and 16 in administrative positions. Pramuka Island not only hosts the Kepulauan Seribu Marine National Park headquarter, it also serves as information and visitor centre for the national park (Yates, 1994).

Figure 10 Pramuka Island

Rambut Island (Figure 8) and Bokor Island (Figure 11) are important nature reserves. There are three types of the forest ecosystem in Rambut Island; coastal forest, mixed secondary forest and mangrove forest. The island is set as protected area because thousands of local birds permanently breed on the island, while some stop over during their migration journeys. Around 24,000 birds of 54 species can be encountered there during the breeding season, particularly water bird species, and is one of the important breeding location for Milky Stork (*Mycterea cinerea*), which is a critically endangered species (www.redlist.org.2011). From only 6,000 individuals of this bird left on the planet, 42 nests have been recorded on the island (Birdlife International, 2012). Other species commonly found in Pulau Rambut are the Grey Heron (*Ardea cinerea*), Oriental Darter (*Anhinga melanogaster*), Black-crowned night heron (*Nycticorax nycticorax*), Purple Heron (*Ardea purpurea*), Great Egret (*Casmerodius albus*), Little Egret (*Egretta garzetta*), Intermediate Egret (*Mesophoyx intermedia*),

Pacific Reef-egret (*Egretta sacra*), Cattle Egret (*Bubulcus ibis*), Glossy Ibis (*Plegadis falcinellus*), and Black-headed Ibis (*Threskiornis melanocephalus*). The island is famously called the "Island of Birds' Paradise" and the need for intervention to protect the area has made the government change the status in 1999 from a nature reserve to Wildlife Reserve and to be included in the Essential Ecosystem Management by Presidential Instruction Number 3/2010 on Sustainable Development (Birdlife, 2012).

Pulau Bokor was established as a nature reserve by the Dutch Government in 1931 because of its flora diversity and mature lowland forest. This establishment was later adopted by the Indonesian Government after Indonesia's declaration of independence in 1945. Some of the dominating plants on this island include *Terminalia copelandii, Casuarina equisetifolia, Guettarda speciose*, and *Triphasis trifolia*, which is native to South-East Asia, Malaysia, and Christmas Islands.
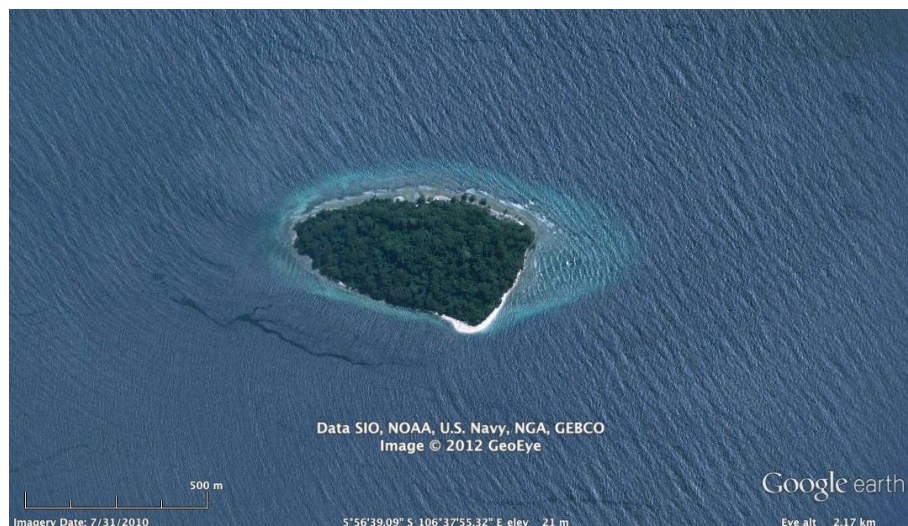
Figure 11 Bokor Island

Opak Besar Island (Figure 12) is an uninhabited island. The island also has no docks. Hence, it is very difficult for boats to reach the island. Opak Besar is dominated by mangrove and coastal plants including palm and coconut trees.
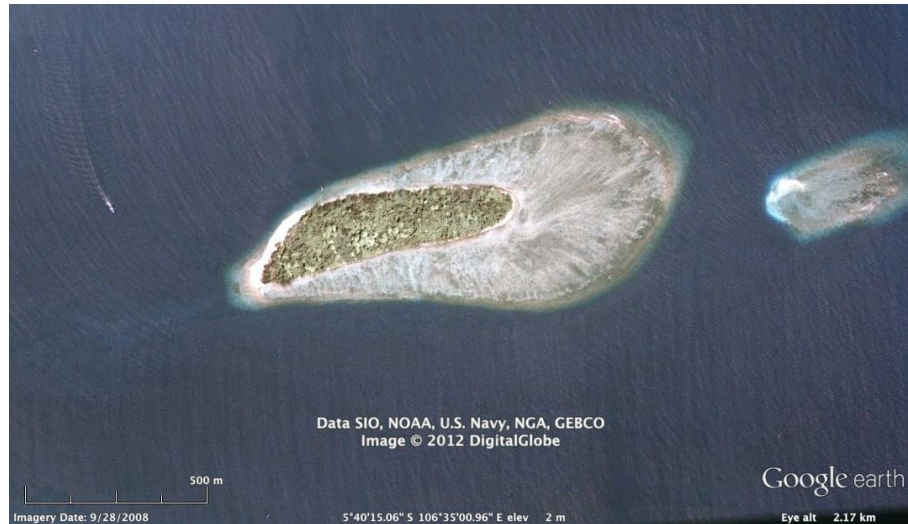
Figure 12 Opak Besar Island

The name 'Damar Besar' has been given to this island by local fishermen because the island was originally dominated by Dammar trees from the Dipterocarpaceae family. Although the island has no permanent settlement, the Indonesian National Navy has an office on this island for its perimeter checking point. The island (Figure 13), used to be called Edam Island, has been used for different purposes for the last 130 years. In 1879, the Dutch built a 60m lighthouse in Damar Besar Island to help ships navigate when entering Tanjung Priok, Jakarta's biggest port. During the Second World War, the Japanese built a fortress on the island as frontline defense. At present, the island's lighthouse is still functioning well, and the ruins of the Japanese fortress can be found across the island, that is otherwise covered in forest.
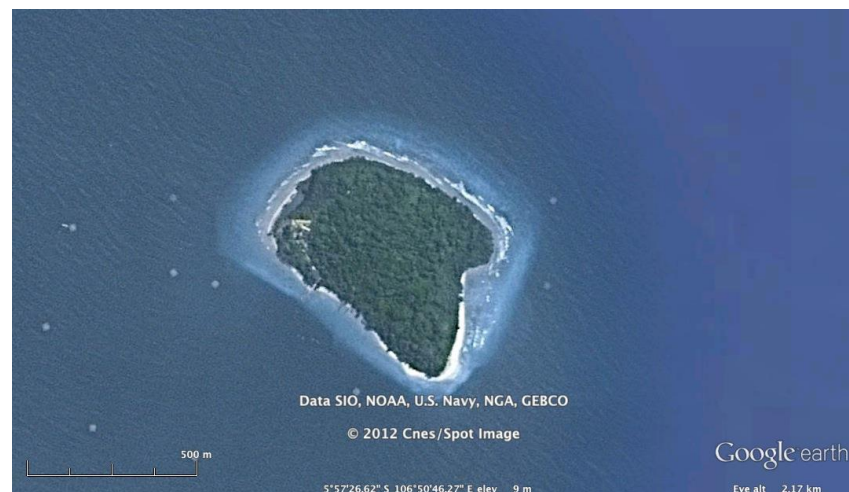
Figure 13 Damar Besar Island

Kotok Besar Island (Figure 14) has been developed mostly for tourism. However, Kotok Besar Island still keeps some of its forests to serve as Raptor Rehabilitation Centre, supported by Jakarta Animal Aid Network (JAAN) (JAAN, 2012). Meanwhile, Putri Barat Island, up until my last sampling, was a forested island. Recently, however, the island is being developed to attract tourists from Jakarta.
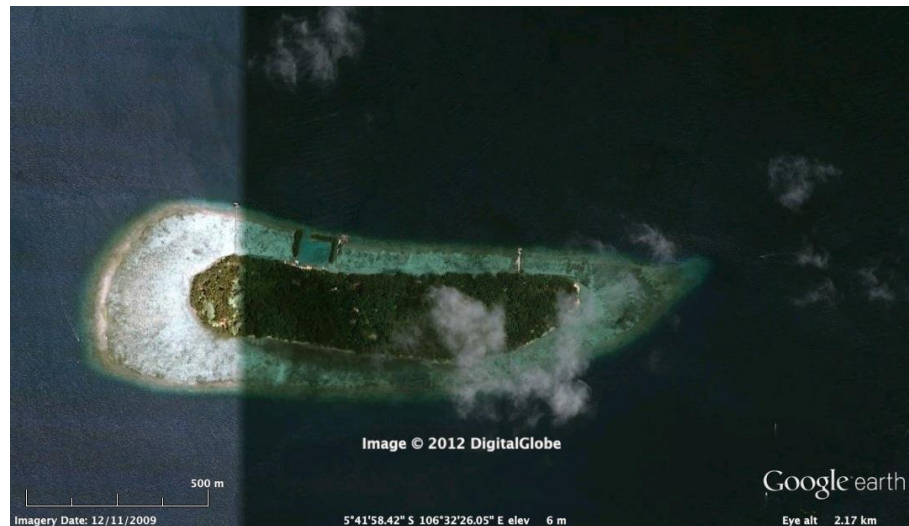
Figure 14 Kotok Besar Island

In Java, Dramaga Research Forest (DRF) (Figure 15) was used as sampling location to represent a large-island forest habitat and potential source area for the colonization of forests on the smaller islands. Dramaga Research Forest measures for 60 ha and was established in 1956 by the Forestry Investigation Bureau (Badan Penyelidikan Kehutanan). It is located in Bogor, West Java, about 70km from the Jakarta Bay. This secondary forest was initially developed as an introduction site for new tree species from all around Indonesia and outside Indonesia. At present, the forest is home to 128 tree species, one bamboo species, and one rattan species (BPPK, 2010). The forest is also home to CIFOR (Centre for International Forest Research), which was based in Dramaga Research Forest in 1993. Collaboration between DRF, CIFOR and a local University, Bogor Agricultural University (IPB), has successfully promoted the area as a research forest (BPPK, 2010). Sampling was conducted inside the forest and in the surrounding area that includes agricultural land and settlement areas.
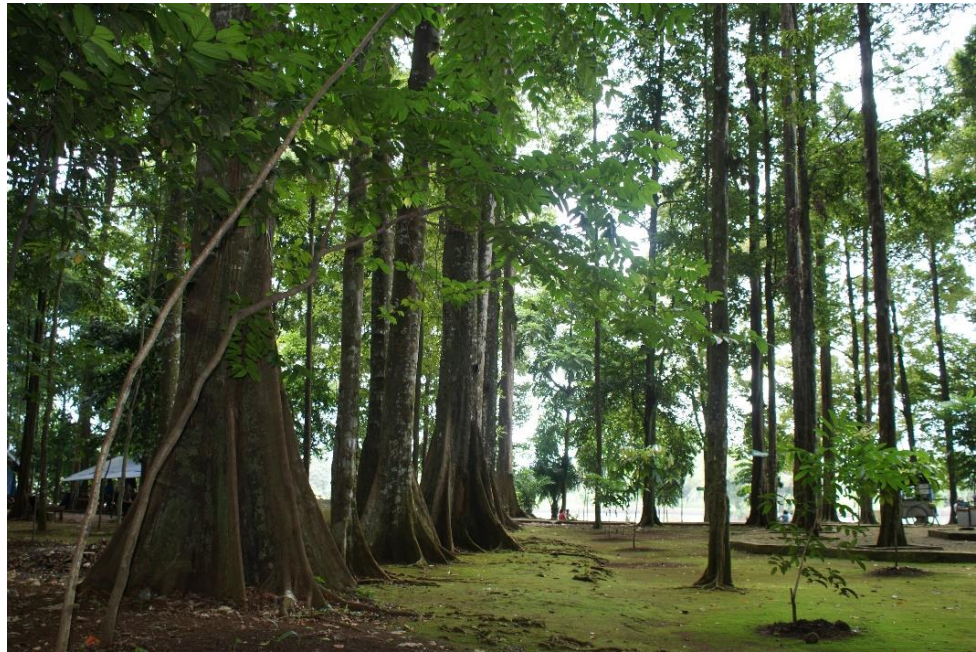
Figure 15 Darmaga Research Forest, Bogor, West Java, Indonesia (Puskonser, 2012)

2.2 Sampling plot design

Fieldwork was conducted in 2010 and 2011, between April and June. Beetle sampling was stratified by dominant habitat types on each island and on the sites at Java, differentiating forest and settlement areas. The forest habitat was classified as disturbed or undisturbed forest. Meanwhile, settlement habitat included both settlements by local fishermen and tourism infrastructure.

Entomological sampling methods can be characterized by some criteria that enable the method or methods to be chosen in accordance with assigned objectives. One of the main differentiations in insect sampling methods is into passive and active sampling (Brustel, 2004). Active exploration of specimens found in collected litter or sediment, sweep netting   and a manual search of micro-habitats and sight identification are examples of active sampling. Species are determined either from a distance such as in typical butterfly transects, or following capture directly in the field or in the laboratory. Typical target groups of active sampling include diurnal Lepidoptera, Hymenoptera, Odonata, floricolous Coleoptera, Orthoptera, Hemiptera and Neuroptera. Functional groups typically

sampled actively include diurnal pollinators, phytophagous and many floricolous, saproxylic and terricolous insects (Bonneil et al., 2009).

Table 2 Surveyed islands in Kepulauan Seribu Marine National Park in 2010 and 2011

Island	Distance to Java (km)	Area (km²)	Number PF plots§		Number FIT plots		Dates of sampling
			Forest	Settlement	Forest	Settlement	
Java Forest	0	n/a	5	0	2	0	21-24.IV.2011
Java Settlement	0	n/a	0	5	0	2	3-6.VI.2011
Rambut	5	0.4580	5	0	2	0	11-14.IV.2010 27-30.IV.2011
Untung Jawa	6	0.3912	0	10	0	2	8-11.IV.2010 26-29.IV.2011
Bokor	7	0.1634	5	0	0	0	9-12.IV.2010 28.IV-1.V.2011
Lancang Besar	10	0.2643	5	5	0	0	9-12.IV.2010 28.IV-1.V.2011
Damar Besar	18	0.2951	5	0	2	0	10-13.IV.2010 27-30.IV.2011
Pramuka	27	0.1992	0	10	0	2	22-25.IV.2010 6-9.V.2011
Kotok Besar	32	0.2265	5	5	0	0	24-27.IV.2010 8-11.V.2011
Opak Besar	37	0.0974	5	0	2	0	24-27.IV.2010 8-11.V.2011
Pamagaran	40	0.1556	5	0	2	0	23-26.IV.2010 7-10.V.2011
Putri Barat	45	0.0963	5	0	2	0	23-26.IV.2010 7-10.V.2011

§: each plot contained two baited and three non-baited pitfall traps

This study, however, was conducted primarily using passive sampling, which is based on the movement of the focal taxa towards a trapping device, with the surveyor remaining passive. Passive traps allow relatively unbiased estimates of species activity densities in insect populations when insects are neither attracted nor repelled by the traps. Sampling is commonly entrusted to standalone traps left in the field for varying periods between installation and collection. It includes all kinds of continuous traps such as pitfall traps, flight interception traps, malaise traps, pan traps, fixed suction traps, sticky traps, light traps and emergence traps (Grootaert et al., 2010).

In this study, the sampling was conducted using pitfall traps to collect ground-dwelling beetles in the terrestrial environments in Java and on all ten islands. In

addition, flight interception traps (FITs) were used to capture dispersive beetles in Java and on seven of the islands (Table 2).

On each island, pitfall traps were set in 5m x 5m plots, with three non-baited pitfall traps and two fish-baited pitfall traps on each plot (Figure 16). Mature forest and settlements were sampled depending on their presence on each island, and plots were randomly selected within habitat types. The number of plots per island ranged from 5 to 10, depending on island size and habitat types occurring on each island. Beetle sampling on each plot lasted for three days, as it was logistically very difficult to allow for a longer sampling period particularly at the very remote sites. The samples therefore represent rather a snap-shot than a complete sample of the beetle fauna on each island. Nonetheless, the number of specimens collected indicate that the sampling approach overall was extremely successful, and allowed for meaningful analysis of the resulting data.
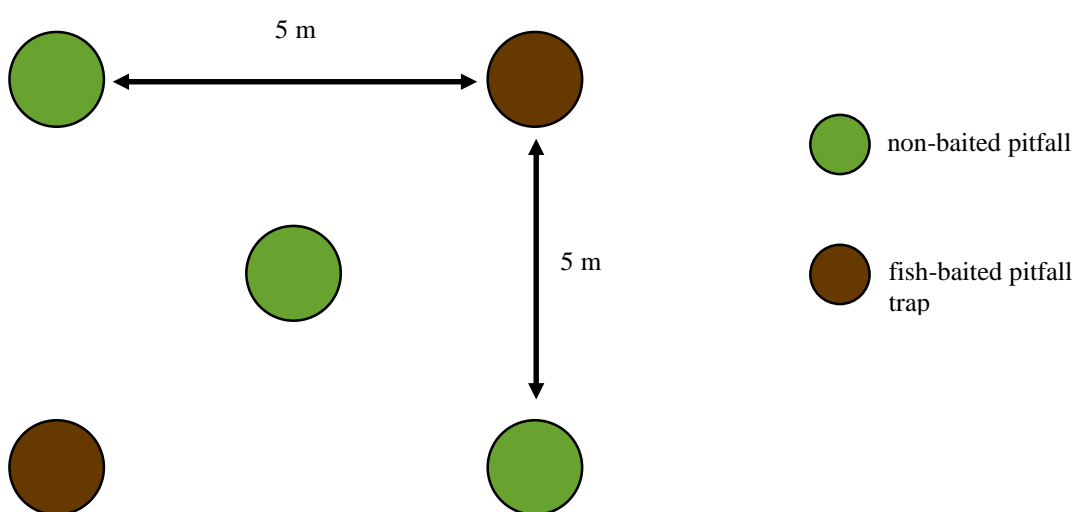
Figure 16 Pitfall trap setting

The FITs were set on seven islands, with two replicate nets placed in each habitat type. The islands selected for FIT sampling were Untung Jawa, Rambut, Damar Besar, Pramuka, Opak Besar, Pemagaran, and Putri Barat. The FITs were set on 3 pairs of islands, with 2 replicate nets placed in each habitat type. Islands that are paired for FITs are within the same distance range from Java, similar in size, but comprise of different habitat. The pairing islands were Untung Jawa

Island and Rambut Island, Damar Besar Island and Pramuka Island. The last group of islands comprised of Opak Besar, Pemagaran, and Putri Barat Island, which were in the same distance range from Java.

2.3 Sampling methods for beetles

2.3.1 Pitfall Traps

Pitfall traps have been used to obtain information on the structure of invertebrate communities (Hammond 1990), habitat associations (Hanski & Niemela, 1990), relative abundance and distribution ranges (Giblin-Davis et al., 1994). Pitfall traps are the most frequently used technique to collect epigeal invertebrates (Woodcock, 2005). Ground beetles (Coleoptera: Carabidae), rove beetles (Coleoptera: Staphylinidae), and ants (Hymenoptera: Formicidae) are the most commonly sampled epigeal invertebrates using this trap type (Woodcock, 2005). One of the greatest advantages of pitfall traps is that they sample continuously, requiring only periodic emptying, which can remove biases associated with other techniques that sample only at specific points in time (Topping & Sunderland, 1992). This makes the technique particularly useful for sampling invertebrate occurring at low density (Melbourne 1999). The low levels of disturbance, both physically and aesthetically, which pitfall trap installation and collection causes, has made then useful for sampling environmentally sensitive area (Melbourne, 1999). Moreover, this type of sampling is low price, simple to use and easy to set up. It has a high efficiency regarding the ratio between the number of individuals and species captured and the time required. It is also in very widespread use; hence results are easily comparable (Woodstock, 2005).

However, as the rate of capture of most invertebrate is proportional to their activity (Curtis, 1980), the number of each species caught in pitfall traps will not reflect their true abundance (Woodcock, 2005). Instead, their rate of capture will be proportional to the interaction between their abundance and activity; expressed by the concept of activity abundance (Thiele, 1977). Species that are largely sessile, but occur at high abundance, may be under-represented in pitfall traps compared to less abundant, but more active species. Furthermore, these traps chiefly catch ground-dwelling arthropods, and while most species of Carabidae are ground surface-active species and hence easily accessible with pitfall

trapping, members of the genus *Dromius* are arboreal, and such species are going to be largely absent from pitfall catches (Terell-Nield, 1990). Overall, without specific information on the activity of each species, it is almost impossible to relate pitfall catches to the true relative abundances of different species (Woodcock, 2005).

Although glass cups can potentially catch more specimens (Luff, 1975), plastic cups (250ml) were selected because they are cost-effective, light and robust and hence easy to carry and extremely solid when buried in soil in forests for several months (Figure 17). Transparent plastic roofs were used to cover the mouth of traps. As the study area experiences high levels of precipitation during the sampling period, the roof was seen as essential to protect the killing solution from dilution by rain and litter contamination. The roofs were supported by wooden sticks so that they rested 3-4cm above the soil surface to allow free access to the traps. Although roofs cause bias in the catches of pitfall traps, the use of transparent materials for roof coverings minimizes the influence of roofs on the catches of invertebrate (Baars, 1979).

Techniques for preserving and maintenance of insect specimens have been developed for well over a century and are described for example by Smithers (1982), Uys and Urban (2006) and Cooter and Barclay (2006). Preservatives also stop predation from predatory species and reduce levels of escape (Lemieux & Lindgren, 1999). At present, one of the most commonly used preservatives in ecological research is ethylene glycol (antifreeze).

Ethylene glycol is not ideal for use in the Kepulauan Seribu Marine National Park, because it is sweet-tasting but toxic to both birds and mammals, which actively consume it (Hall, 1991), and can hence be a serious hazard for the animals inhabiting the area. This is especially important for sampling on Rambut Island, which serves as habitat for many bird species including the endangered milky stork. Another reason for not using this preservative is due to the distance from the mainland, which makes transporting a large quantity of liquid preservative in small boats problematic.

Water and salt were used as a preservative in the pitfall traps and proved to be suitable as pitfall trap preservatives in taxonomic studies (Sasakawa, 2007). Based on 1 week of pitfall trapping using water and salt by Schmidt et al. (2006) demonstrated low evaporation rates (>75% of sample volume was retrieved) and

strong preservative effects (>85% of samples were preserved without appendage damage). Water and salt was also cost-effective and minimized attractant bias (Kotze et al., 2011). A small quantity of unscented detergent was added to the solution to reduce surface tension. This increases the efficiency of traps, as insects drown more easily and quickly (Clarke & Bloom, 1992).

Alcohol with 70% solution was used in this study to store all beetle specimens in small tubes - 70% alcohol is a cheaply available, good preservative, and safe to be used within the national park. Every tube was given a label in the field before specimens were sorted and identified in the laboratory.

Carrion bait, from fish, was used in this study (Figure 17). Human dung was strictly prohibited to be used on the islands for ethical reasons. Approximately 20g of fish was suspended in the middle of the roof, immediately above the trap (Woodcock, 2005). To avoid ants eating the baits, Vaseline was applied on the roof stands.

Figure 17 Fish-baited pitfall trap

2.3.2 Flight Interception Trap (FIT)

This trap type uses a collection receptacle placed under an interception surface comprising a single vane (bidirectional interception), or two crossed vanes (multidirectional interception) oriented vertically. The trap will intercept mobile, flying insects whose flight is heavy and which allow themselves to fall on collision with an obstacle. This trap is often used in studies aiming to catch saproxylic insects, with taxa like Coleoptera, Hymenoptera, Diptera, Homoptera, and Heteroptera commonly caught (Bonneil et al., 2009).

The advantages of this sampling method include capturing a representative selection of active insects including rare and cryptic species. It has low survey costs and is easy to construct. This trap can also be combined with other methods. However, some drawbacks can be created when plant debris, such as leaves and twigs, obstructs the collection pan or funnel, allowing insects to escape. This trap is also highly visible and may be vulnerable to vandalism.

Many flying insects fall to the ground when they collide with a vertical surface. Flight interception traps utilize this behaviour to trap them. A vertical screen is stretched between two stakes and drop trays containing preservative fluid are arranged below its bottom edge. Ideally, the traps should be positioned so that they are either blocking a corridor or be placed perpendicular to a flight barrier (Peck & Davis, 1980). Flight interception traps are particularly useful for collecting beetles, which typically close their wings on encountering the barrier and, therefore, fall into the drop tray (Masner & Goulet, 1981). The traps are also very effective at trapping slow-flying insects such as cockroaches and crickets (McGavin, 1997).

The flight interception traps used in this study acted by literally intercepting insects' flight. The traps I used consisted of very thin black net measuring 1.5 x 4 m, which was placed above six plastic containers filled with water and salt as preservatives, with detergent added to reduce the surface tension (Figure 18).

Figure 18 Flight Interception Trap

2.4. Insect Specimen Sorting and Identification

I looked at two taxonomic levels in our samples; family and species level. An identification at morpho-species level was conducted for all specimens, but subsequently more detailed family-level analysis focused chiefly on three families, Scarabaeidae, Carabidae, and Scolytidae. These families were chosen based on their important roles in the ecosystem, number of specimen's collected, available data and references, and access to specialists aiding in the species identification.

Specimens from this study were all sorted and labelled, with information such as habitat and method of collection also recorded on the label. A second label was used to note the taxon name given to the respective insect species.

Figure 19 Beetle specimens were stored in tubes with 70% alcohol, dried, pinned and labeled

Collections were protected from light, heat, humidity and attack from other insects, with naphthalene added to the storage containers. All specimens collected in this study were sorted and identified to species or morpho-species level at the Hope Entomological Laboratory, Museum of Natural History, in Oxford (Figure 19).

2.5. <u>Data analysis</u>

The analysis of the data was conducted according to the specific research questions and hypotheses addressed in each chapter. These are therefore explained individually in the respective sections in the three data chapters.

Chapter 3. Beetle family diversity and assemblage structure at small islands of the Kepulauan Seribu Marine National Park and nearby Java

3.1. <u>Introduction</u>

Since the formulation of the equilibrium theory of island biogeography by MacArthur & Wilson (1963, 1967) the comparisons of the composition of island and mainland biotas have been, and remain, a stimulus for ecologists, conservation biologists and biogeographers (Williamson, 1981; Foufopoulos and Ives, 1999; Knapp et al., 2003; Siliceo & Diaz, 2010; Stuart et al., 2012). These comparisons are often done by a direct comparison of species lists, but two major methodological problems make this approach unjustified. First, island and mainland habitats often differ from each other (Williamson, 1981; Jarvinen and Haila, 1984) and, consequently, all species included in the mainland pool are not potential colonists of the islands: some of them may be excluded by the lack of suitable habitats. Second, the colonizing propensity of a species is probably influenced by its abundance in the source area. A study on the breeding land birds of the island Ulverso showed that there are importance of various factors leading to faunal impoverishment, including the effect of rarity that accounted for 75% of the absences on the island (Jarvinen and Haila, 1984). Unfortunately, population sizes have mostly been neglected in insular studies (Jarvinen and Haila, 1984; Williamson, 1981; Simberloff & Abele, 1982).

In this study, I compare beetle communities in similar habitat patches on nearby Java and islands in the Kepulauan Seribu Marine National Park on the basis of quantitative data. I limited the study to two definable, habitat types (forest and settlement patches) to make it possible to get a realistic estimate of the pool of 'actual colonists' by using samples from equivalent habitats on the nearby Java. Many island-mainland comparisons have been inherently unrealistic because of difficulties in defining the pool of colonists adequately (Williamson, 1981; Jarvinen and Haila, 1984).

Beetles have been used extensively to study island ecosystem in the past (Fattorini, 2002; Gomez, 2010; Chatzimanolis et al., 2010; Grobler et al., 2011). They represent the most diverse insect order, and different families have been used as bioindicators in biodiversity, environmental, and ecological studies (Werner and Raffa, 2000). Comparative studies of beetle communities between "mainland" and island biotas can form an important basis for recommendations for conservation measures (Neimela et al., 1985; Palmer, 2002; Lazaro et al., 2005; Ikeda et al., 2008; Da Silva & Hernandez, 2014).

The islands in the Kepulauan Seribu Marine National Park have a long history of use by communities from mainland Java that have affected their biotas (see Chapter 2 on Study Area). Several of the islands have been strongly altered over time by settlements, tourism, military forts and the construction of other institutional buildings, and by a wide range of further activities relating to fishing, but also tourism. The resulting degradation of the islands' ecosystems, including the disappearance of fish species, giant clam, and hawksbill turtles, was caused by increasing population on the islands that put unsustainable pressure on the fishery. More than 250 small and 80 medium-sized fishing boats were based in the south of the park in the early 1980s. The use of increasingly destructive fishing techniques (Salm et al., 1982) was damage to the coral reefs that supported the fishery, and thus the cycle of degradation intensified. The area has also been exposed to threats arising from developments in resource extraction not centred on the islands, exemplified by small oil slicks and tar balls from oil drilling rigs in the North Java Sea (Yates, 1994), and to domestic pollution from Java. At present, some of the islands are protected as nature reserves while others are used for permanent settlements, as tourist destinations, or are privately owned and inaccessible (Pemerintah Kecamatan Kepulauan Seribu, 2010).

Island's limited size and its disconnection from the mainland with its diverse assemblages will also likely see high levels of endemism (Whittaker and Palacios, 2007). The different nature of the surrounding matrix, including the seawater barrier, keeps many continental mortality factors affecting mainland fragments off the island (Walter, 2004). Thus, islands may harbour relict taxa already extinct on the mainland, or small island specialist taxa that only occur in

island ecosystems regardless of the availability of mainland habitats in the vicinity (Walter, 2004). The finding of high levels of unique species diversity on islands may also suggest two important, non-exclusive explanations. First, it is quite possible that contemporary mainland populations are in fact more significantly depressed due to anthropogenic impacts (Caterino et al., 2005). Mainland populations, especially in coastal species, have been extirpated in many areas due to a combination of beach, recreational use, and invasive plants (Powell 1992). However, islands are also simultaneously acknowledged for their lower species richness compared to mainland areas (Whittaker and Palacios, 2007). As well as island's resource limitations, partial release from competition and predation, are suggested as major factors affecting population dynamics and morphological adaptations of island biota.

The fragility of island life is well documented in the record of historical extinctions of plants and animals, which is characterised by a highly disproportionate loss of insular vs. mainland forms; most of this resulting from direct human actions and from impacts of introduced species that devastated native insular biota before they were able to adapt (Lomolino, 2010). Even in more recent times, when local extinctions on continents has arguably started to converge with that of islands (Lomolino et al., 2009), extinctions will often again be insular in nature. In this case, because human civilisations, technologies and land-use changes have converted once expansive continental landscapes of natural habitats to archipelagos of remnant habitat isolates within seas of anthropogenic ecosystems (Ellis & Ramankutty, 2008; Lomolino, 2010). Thus, it is hypothesised that beetle assemblages on islands in Kepulauan Seribu Marine National Park effectively form impoverished subsets of the communities encountered on Java but retain unique island beetle species.

A primary purpose and mission of the Kepulauan Seribu Marine National Park is to preserve and protect the island system it contains, along with associated natural, cultural, and historical resources (Pemerintah Kecamatan Kepulauan Seribu, 2010). However, the focus of attention has been chiefly in the marine areas and resources, as is the case with most marine national parks in Indonesia, while relatively little is known about the park's terrestrial natural resources. While surveys of marine diversity are ongoing, the largest component of biological

diversity, the terrestrial invertebrate fauna, has received extremely little attention in past regional research activities. The insect faunas of these islands are very poorly known and have not attracted any significant conservation efforts. Limited research has been conducted on assemblages of hymenopterans (Sprengler, 2011, Rizali, 2010), whereas compositions of other orders have remained virtually unknown. Moreover, these previous srudies did not compare the results with Java assemblages. This chapter gives significant information and comparisons on overall ground-dwelling and dispersive beetle assemblages. Moreover, it identifies endemic and unique beetle species on Java and islands in Kepulauan Seribu Marine National Park.

3.2.   Sampling plots and data analysis

All beetle data from the 70 pitfall trap plots and 11 flight interception traps (FITs) employed on the ten islands in Kepulauan Seribu Marine National Park were included as a basis for the investigations conducted here. Pitfall trap sampling was carried out from April to June 2010, and from April to June 2011; FIT sampling was carried out from April to June 2011. More details of the study area and the sampling design have already been provided in previous chapters.

The abundance of all beetle families from all islands over the entire sampling period was pooled but differentiated based on the type of traps used in sampling. Specimens from baited and non-baited pitfall traps from all islands and both forest and settlement habitats were combined and represented the island's pitfall trap specimens. FIT specimens on all islands and habitats were combined to represent island's FIT's specimens. The same methods were also applied to specimens from Java to generate sufficient sample sizes for robust statistical analyses. All specimens that were identified to species and morphospecies level will be called 'species' throughout this chapter.

I calculated the alpha-diversity of beetle families on each island as the Shannon index (Shannon, 1948) and the Simpson's index (Simpson, 1949). Shannon's index more strongly emphasizes the species richness component of diversity, while Simpson's index puts more emphasis on the evenness component. The exponential form of the Shannon index (Jost, 2006) was used in this study

because it weighs elements by their frequency without disproportionately favouring rare or common elements. Hill numbers were used to measure these diversity indices by simple algebraic transformations (see Appendix 1).

Hill numbers are a mathematically unified family of diversity indices (differing by changing values of the exponent q) (Chao et al., 2014). Hill numbers incorporated relative abundance and species richness and overcome many shortcomings often associated with the use of diversity indices. They were first used in ecology by MacArthur (1965), further developed by Hill (1973), and recently re-emphasized by Jost (2006). Indices linked to the Hill numbers were developed to overcome sampling problems. Observed species richness in mobile organisms is highly sensitive to sample size. When most species in an assemblage are rare, biodiversity samples are usually incomplete and undetected species are a common problem (Chao et al., 2014). As a consequence, the observed number of species in a standardized sample (Gotelli and Chao, 2013; Chao et al., 2014) is known to be a biased underestimate of true species richness. It is also highly sensitive to the area surveyed, the number of individuals counted, and the number of samples scored for species occurrence (Chao et al., 2014). Another problem with observed species richness as a measure of biodiversity is that it does not incorporate any information about the relative abundance of species (Chao et al., 2010). By counting all species equally, species richness weights rare species equal to common ones. Incorporating abundance into a biodiversity index is critical for studies of many aspects of ecosystem function because rare species usually make smaller contributions to ecosystem functioning (Schwartz et al. 2000). On the other hand, rare species sometimes play key roles in ecosystem functioning (Terborgh et al. 2001). These species are generally of greater conservation and management concern than common ones (May, 1988; Holsinger and Gottlieb, 1991; Gaston and Fuller, 2008). Thus, from a statistical perspective, species richness can be very difficult to estimate accurately from a finite sample. Hill numbers can be effectively generalised to incorporate taxonomic, phylogenetic, and functional diversity, and thus provide a unified framework for measuring biodiversity (Chao et al. 2010, Gotelli and Chao, 2013) (see Appendix 1).

Individual-based rarefaction (Gotelli and Colwell, 2001) was furthermore employed to evaluate whether the relationship of beetle species richness was strongly driven by changing abundances. Rarefied species numbers were calculated as a measure suitable to compare species richness for samples of highly variable size (Liu et al., 2007; Axmacher et al., 2004).

Sampling rare and unique species is especially challenging because they may only represent a small part of the total number of specimens caught. With five pitfall traps per plot, this study tried to increase the rare and unique species detection by using a relatively high number of traps per plot (Parmain et al., 2015). However, since beetle inventories of rare and unique species on tropical islands in Indonesia have never been conducted before, and data on beetle taxa from Indonesia is rather limited, the classification of species into these two groups proved challenging. I subsequently defined rare species as those poorly represented in all combined samples, following the approaches taken by Novotny and Basset (2005) and Grove et al. (2000). Species only found on small islands and absent from all Java plots were considered to belong potentially to a unique small island fauna.

To assess the number of unique species on the small islands, specimens from all small islands were pooled, regardless of the type of traps used. The same approach was also used for Java specimens. The significance of the unique species was established by looking at the proportion of the overall species pool they represent and their distribution across the studied islands.

Rarefied species richness was computed using Species Diversity and Richness (Henderson and Seaby, 2002). All other calculations and statistics were carried out in R language version 3.1.2 (R Development Core Team, 2011) with the use of the 'vegan' package (Oksanen, 2015).

3.3. <u>Results</u>

3.3.1. *Beetle family compositions on small islands and Java*

All specimens taken on the islands have no references and are poorly understood. Only a limited number of specimens could be identified to species level. In total, 6370 beetles belonging to 34 families and separated into 236 morphospecies were caught in the studied islands and Java, combined. Among these, 4929 beetles representing 25 families captured in the pitfall traps. The remaining 1441 individuals representing 27 families were caught in the flight interception traps (FITs). Of the 129 species collected in pitfall traps, 17 could be identified to species level and 33 to genus level, while 12 of the 156 species collected by the FITs were identified to species level and 27 to genus level.

In pitfall traps, 292 beetles representing seven families and 32 species were identified in Java, and 4637 individuals representing 24 families and 111 species were captured on the small islands. Rarefaction curves showed that small islands had higher rarefied family richness compared to Java (Figure 20a). Similar patterns were also shown by rarefied species richness, where Java had significantly lower rarefied species richness than small islands (Figure 21a).

(a)

(b)
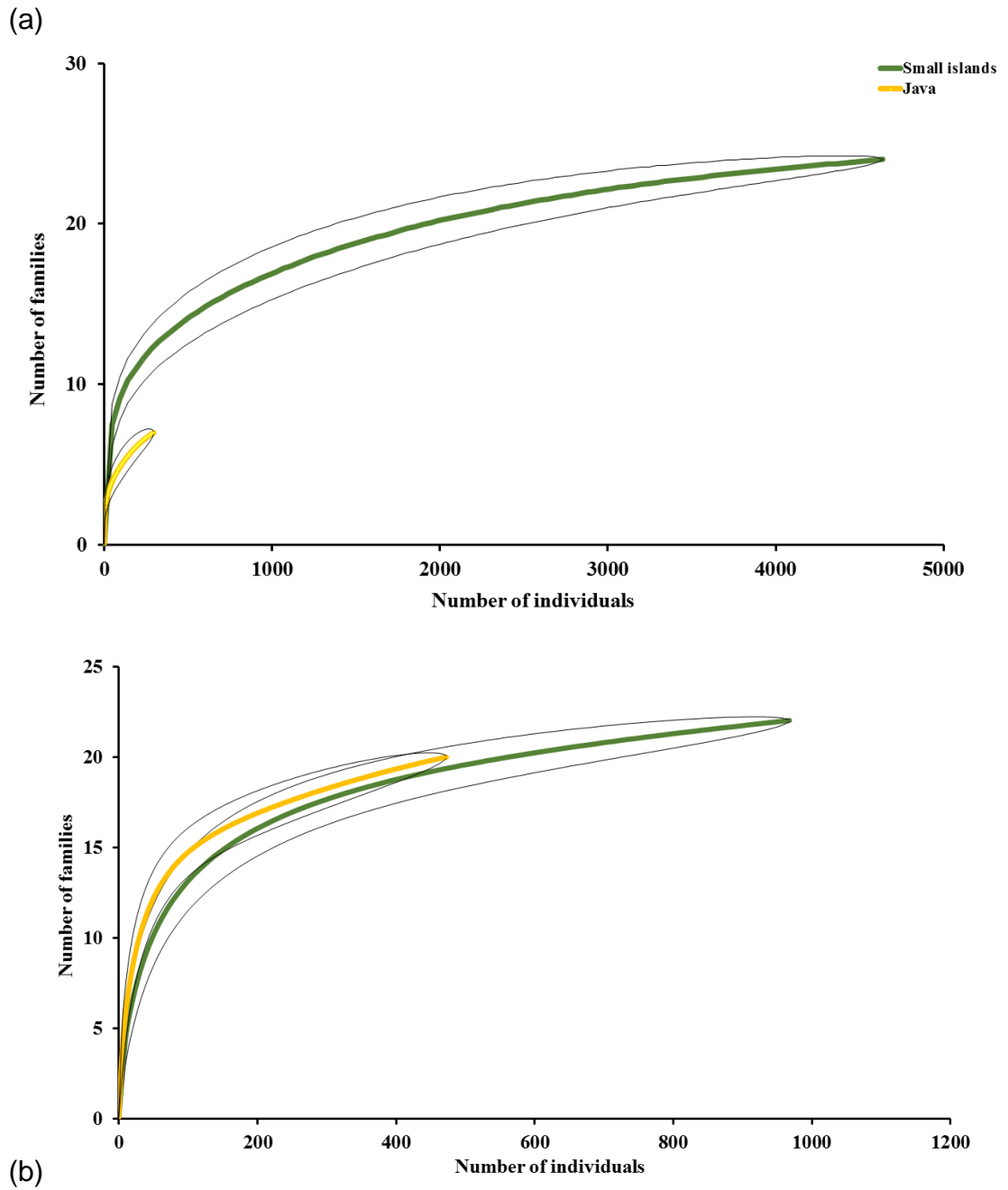
Figure 20 Rarefaction curves of number of families from pitfall traps in Java and small islands from (a) pitfall traps and (b) FITs (black lines represent 95% confidence intervals)

Meanwhile, FITs yielded 473 beetles representing 20 families and 94 species in Java, and 968 beetles representing 22 families and 97 species on the small islands. Rarefaction curves showed similar trends to the observed number of families, where they were closely aligned showing small islands and Java

harbouring a similar number of rarefied family (Figure 20b). Rarefaction curves on species richness showed that, although small islands and Java harbouring a similar number of rarefied species, rarefied species number on small islands appeared to be approaching a plateau, while the number of rarefied species on Java showed a more ascending trends (Figure 21b).

(a)

(b)
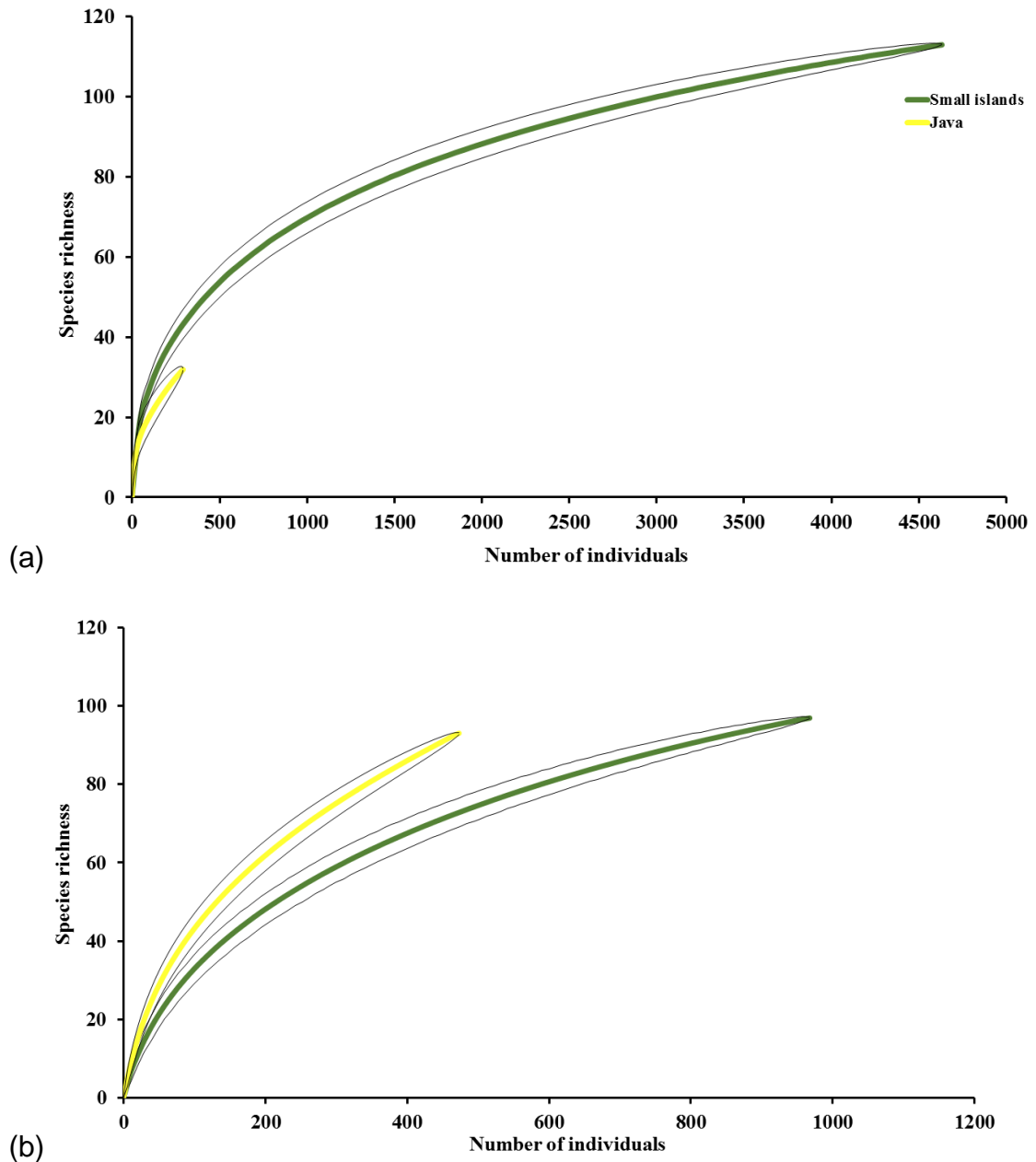
Figure 21 Rarefaction curves of beetle species richness from pitfall traps in Java and small islands from (a) pitfall traps and (b) FITs (black lines represent 95% confidence intervals)

In relation to family abundances, the result from pitfall traps showed that Scarabaeidae (157 individuals) and Scolytidae (113 indiviuals) were the most abundant families captured in Java. In total, Scarabaeidae accounted for 54% and Scolytidae for 39% of all individuals caught in Java pitfall traps. On small islands, Scolytidae (1524 individuals) was the most abundant family, representing 33% of sampled individuals. The next most abundant families were Tenebrionidae (1000 individuals) and again Scarabaeidae (929 individuals), accounting for 22% and 20% of all beetle individuals, respectively (Figure 22a).

The beetle family abundance composition from FITs in Java showed that individuals of Scolytidae (151 individuals) and Scarabaeidae (82 individuals) were again dominating the samples, accounting for 32% and 17% of all individuals, respectively. On small islands, more than half of the total individuals captured were members of the family Scolytidae, with 521 individuals (54%). Scarabaeidae (145 individuals) was the next most abundant families, representing of all individuals (Figure 22b).

In relation to species numbers, 45% of all identified species in Java in the pitfall traps were Scarabaeidae (15 species). Scolytidae (7 species) and Nitidulidae (4 species) were the next most species-rich families, accounting for 21% and 12% of all species, respectively. On small islands, Carabidae (16 species), Anthribidae (15 species), Scarabaeidae (12 species), and Nitidulidae (13 species) yielded almost equal numbers of species, representing 14%, 13%, 11% and 11% of all species, respectively (Figure 23a).

The flight interception traps in Java showed that Scarabaeidae (14 species) and Nitidulidae (14 species) were equally dominant in relation to species richness, representing 15% of all species, each. Scolytidae (10 species) and Hydrophilidae (8 species) were the next most diverse families accounting for 11% and 9%, respectively. On small islands, Anthribidae (18 species) and Nitidulidae (14 species) species represented 19% and 15% of the total species richness, respectively. Scarabaeidae (9 species) on the other hand only accounted for 6% of the total species (Figure 23b).

(a)

■ Java	■ Small islands

(b)
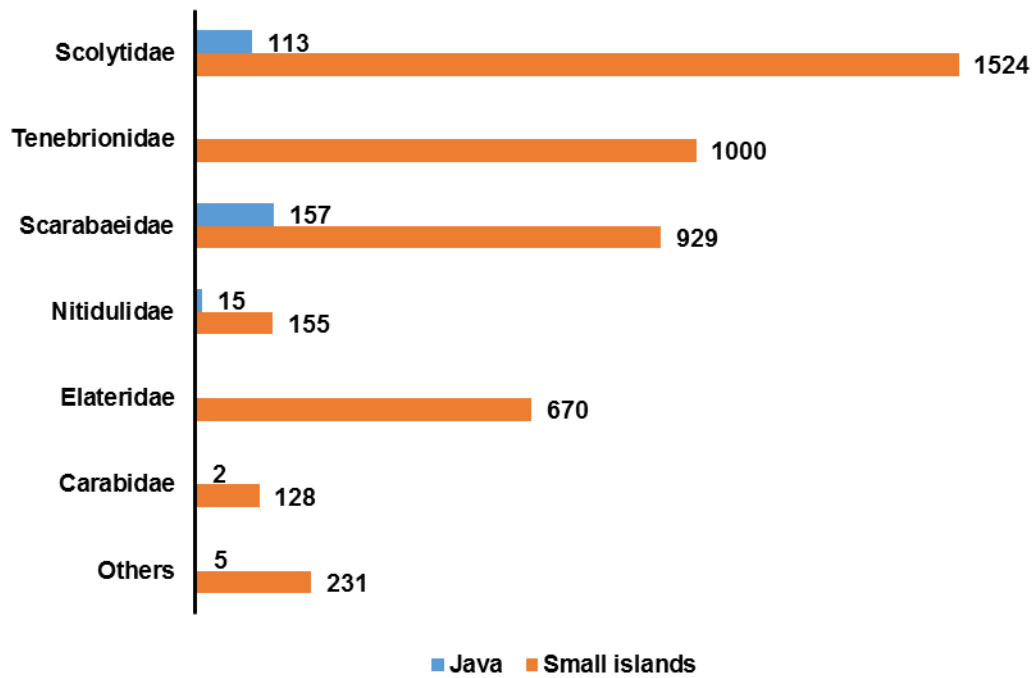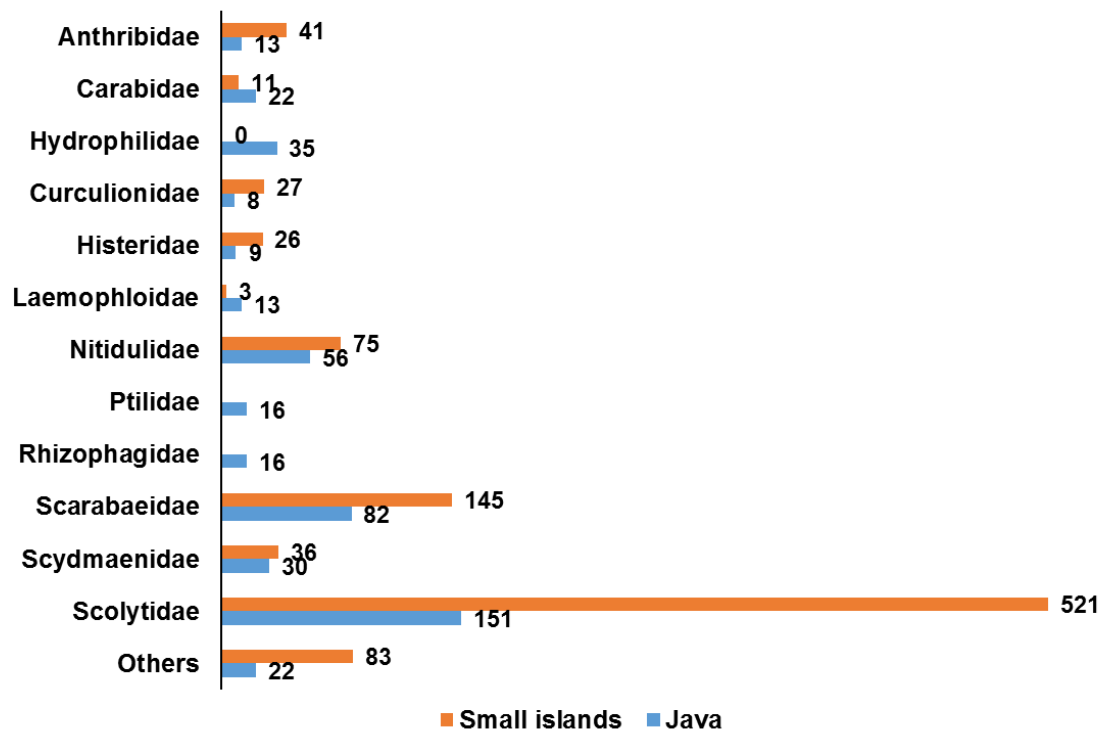
■ Small islands	■ Java

Figure 22 Beetle family composition for number of individuals on small islands and Java from (a) pitfall traps, and (b) FIT

The families Brentidae, Cerylonidae, Ciidae, Coccinellidae, Endomycidae, Laemophloidae, Monotnidae, Ptilidae, and Silvanidae were exclusively sampled from flight interception traps, while members of the families Anthicidae, Cerambycidae, Cucujidae Cryptophagidae, Hyborosidae, Lampyridae, and Trogidae were uniquely encountered in the pitfall traps. The remaining eighteen families were recorded by both methods. All Staphylinidae specimens were excluded in all analysis, because a substantial number of the specimens were lost during a transfer for identification purpose.

(a)
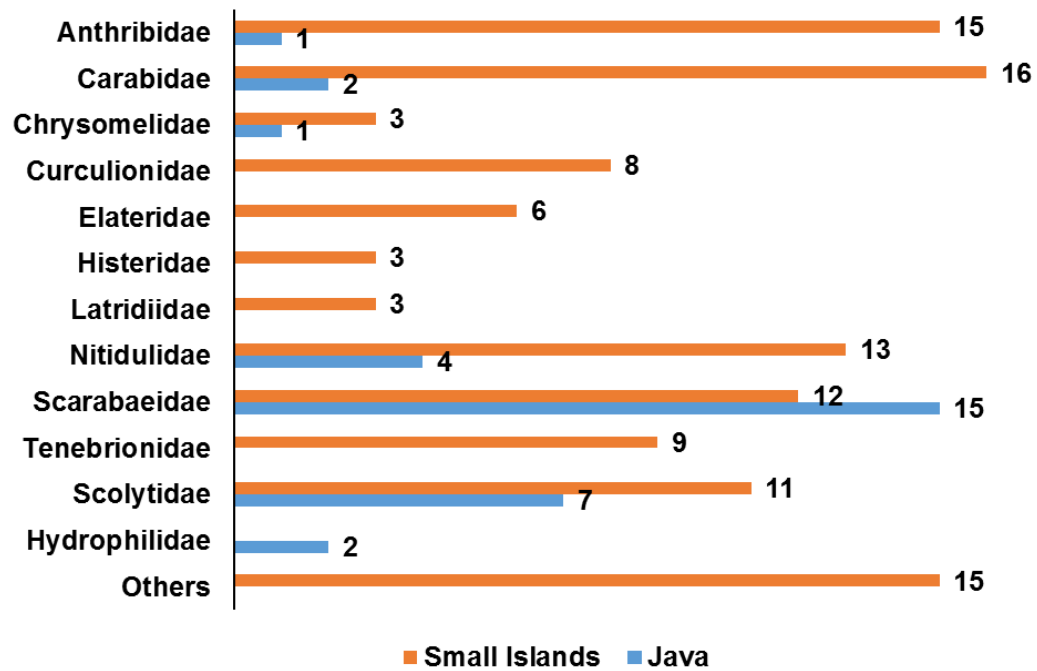
(b)
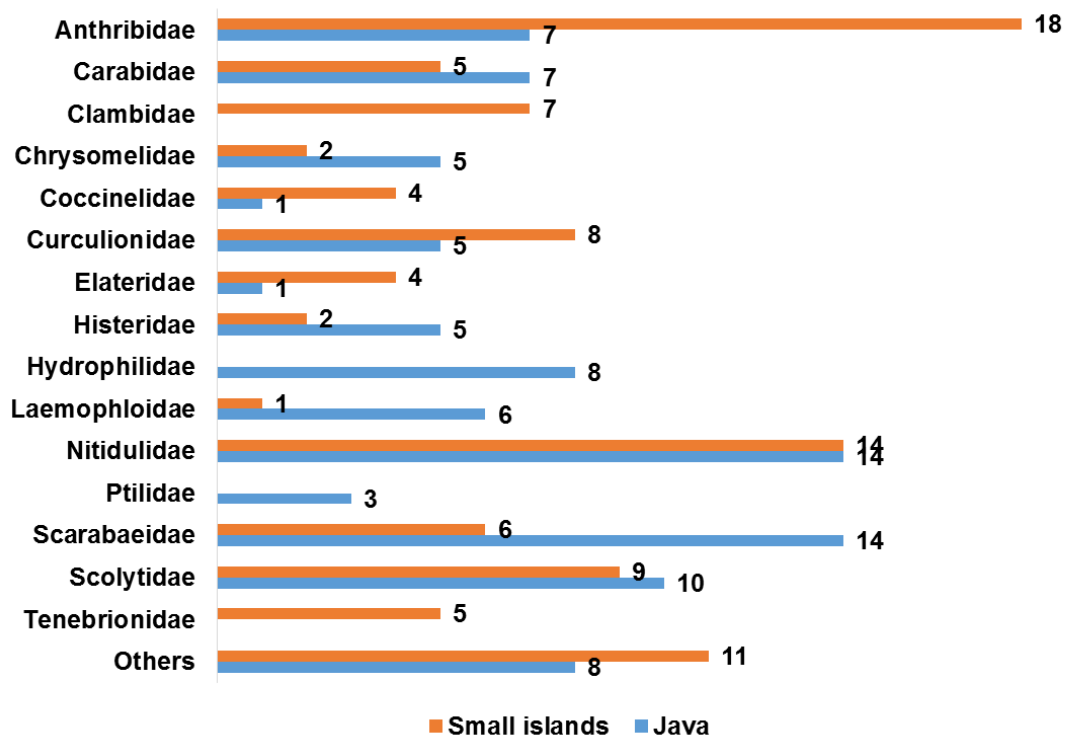
Figure 23 Beetle family composition for number of species on small islands and Java from (a) pitfall traps, and (b) FITs

3.3.2. Comparison of beetle α-diversity between small islands and Java

Beetle diversity from pitfall traps, measured both as Shannon and Simpson's diversity, was higher on small islands. Based on the Shannon index, beetle diversity from pitfall traps on small islands (hexp = 5.83) was higher than in Java (hexp = 2.65). Similarly, the Simpson's index from pitfall traps was also higher for small island assemblages (Ds = 4.60) than for assemblages in Java (Ds = 2.26) (Figure 24a). The results of beetle diversity from FITs showed different patterns. Here, Java is indicated to harbour a higher level of diversity, both for the Shannon diversity (hexp = 9.23) and the Simpson's diversity (Ds = 6.15), compared to small islands (hexp = 5.65 and Ds = 3.09, respectively) (Figure 24b).
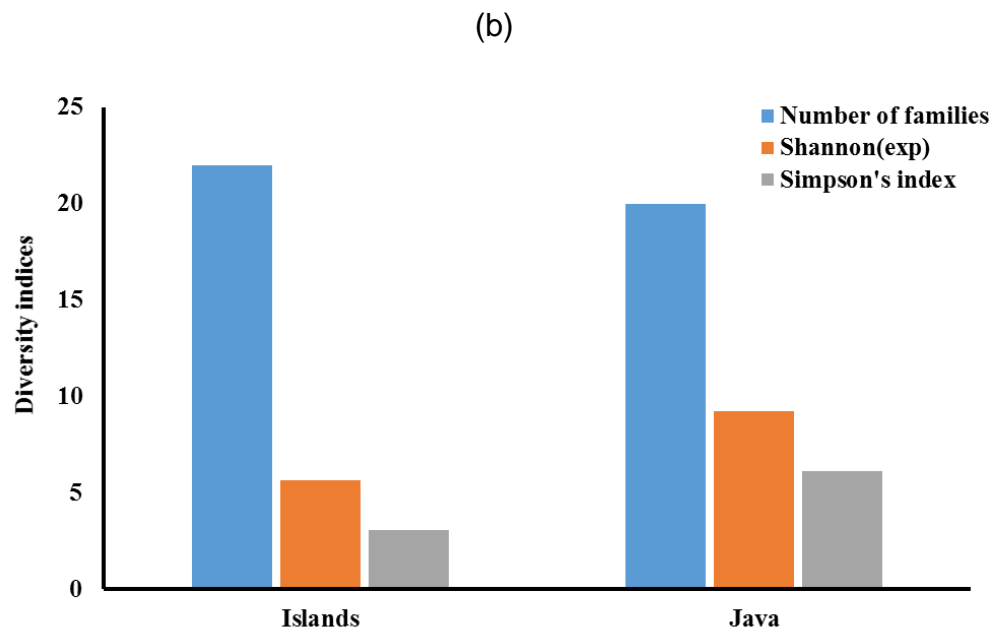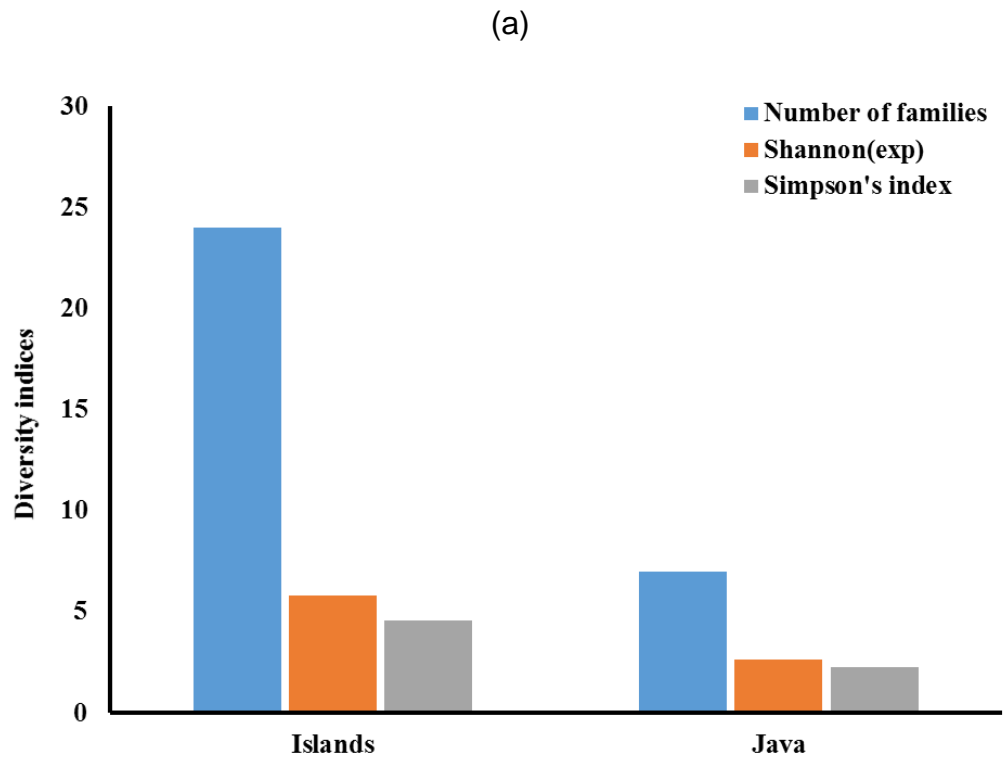
Figure 24 Comparisons of beetle family diversity indices in Java and small islands from (a) pitfall traps and (b) FIT

3.3.3. Small islands family and Java family

When the results from pitfall traps and FITs were combined, 14 beetle families were only recorded on small islands, and five families were only found in Java. All species from family Trogidae, Tenebrionidae, Mordelidae, Monotomidae, Lampyridae, Hyborosidae, Endomycidae, Cryptophagidae, Cucujidae, Clambidae, Ciidae, Cerylonidae, Cerambycidae, and Anthicidae, were only found on small islands. Meanwhile, all species from the families Silvanidae, Ptilidae, Hydrophilidae, Rhizophagidae, and Brentidae were captured exclusively on Java. The rest of the beetle families can be found both on small islands and in Java (Figure 25a).

On the family abundance, although small islands scolytid beetles accounted for more than 30% of the total observed number of Scolytidae species in the study area, they only represented about 2% of the total scolytid individuals captured on both small islands and Java. A similar pattern was also shown by scarabids from small islands. Their abundance was lower (3.5%) in proportion to their overall species richness percentage (23%). On the other hand, carabid beetles from small islands showed the opposite. Their abundance represented about 85% of the total carabid individuals captured in the study area, but the number of carabid beetle species observed on small islands was 65% (Figure 25b).

(a)
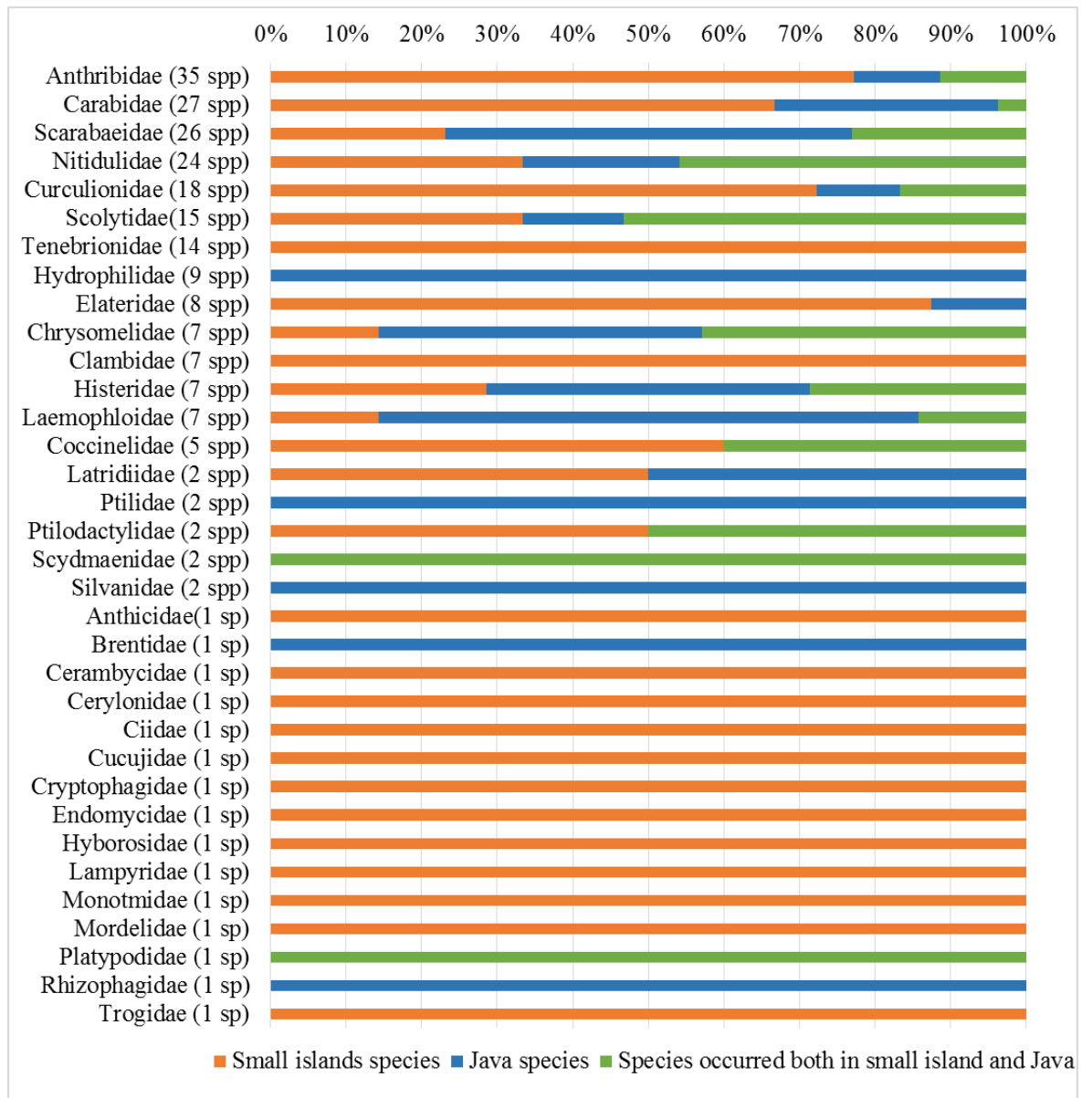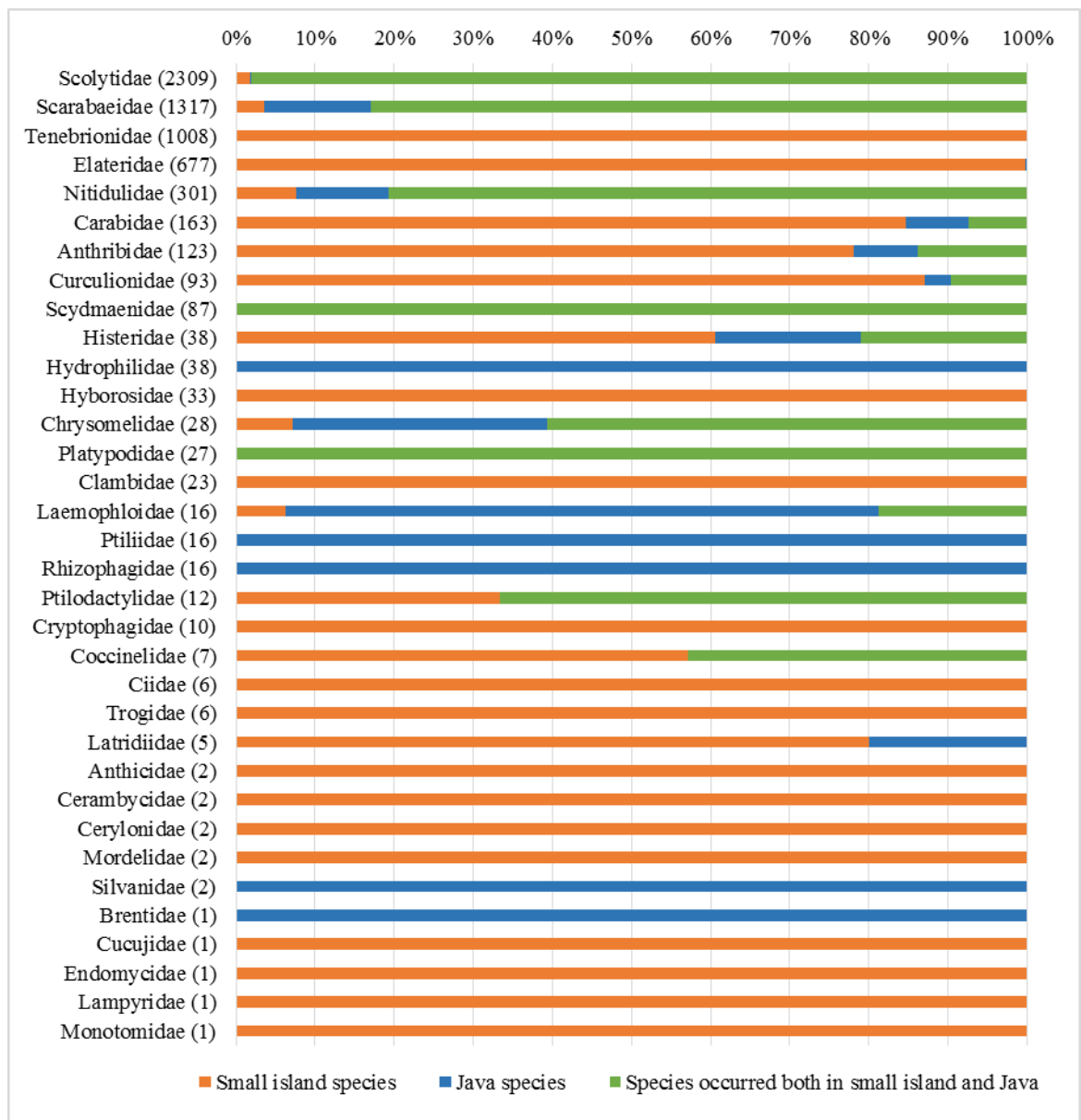
Figure 25 Compositions of small island family, Java family and family occurring in Java and small islands, plotted for (a) the number of species, and (b) the number of individuals.

At the species level, interestingly, the most abundant species both on islands and Java belonged to the family of Scolytidae, *Xyleborus perforans*, with 1023 and 83 individuals collected, respectively. This species has wide distribution throughout tropical parts of the Afrotropical, Australian and Oriental regions (Beaver and Liu, 2010) and is strongly polyphagous (Browne 1961; Schedl 1963; Gray & Wylie

1974; Ohno 1990). Largely due to its abundance, the species can be important timber pest as a result of the 'pinholes' caused by its galleries, and the surrounding black stain caused by the associated ambrosia fungus (Beaver and Liu, 2010).
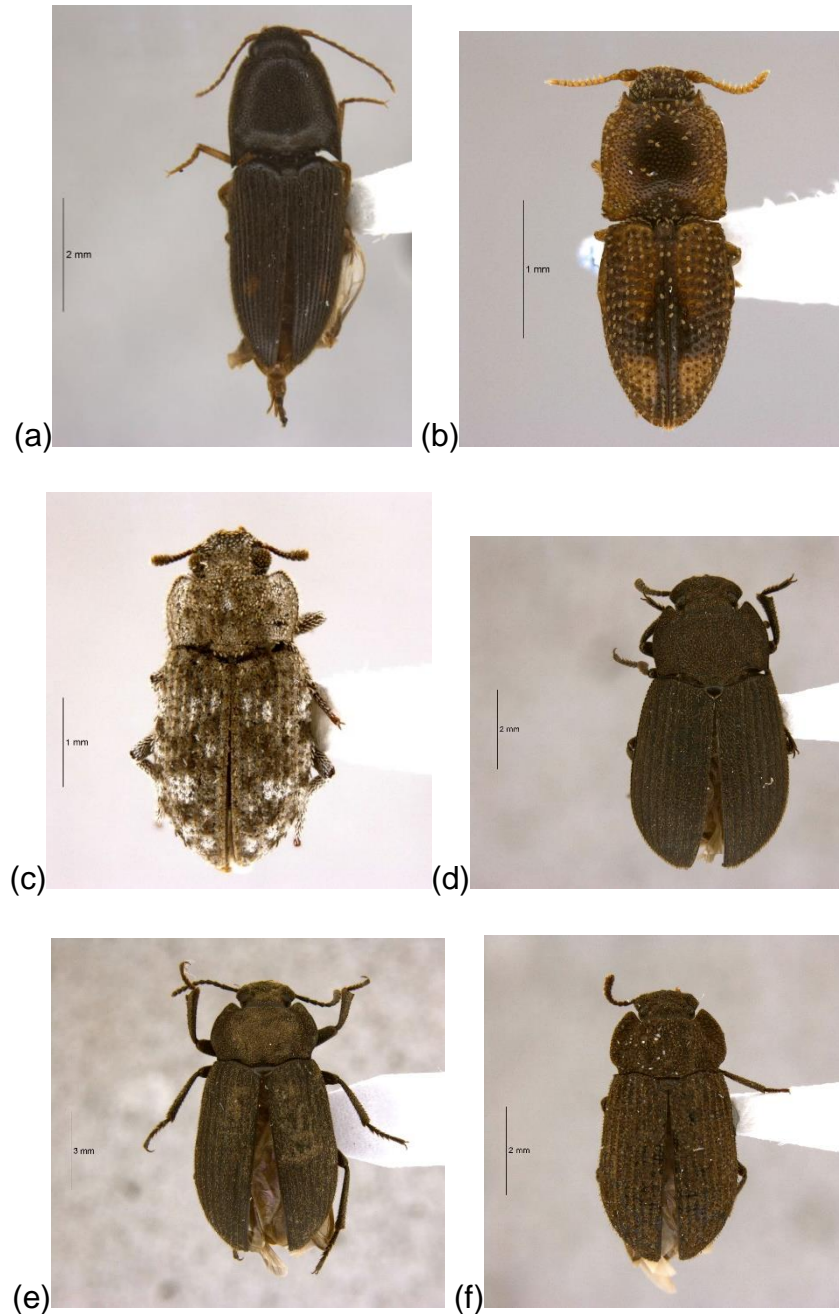
Figure 26 Picture of (a) Elateridae sp. 1, (b) Elateridae sp. 5, (c) *Leichenum* sp. 1, (d) Tenebrionidae sp. 1, (e) Tenebrionidae sp. 2, (f) Tenebrionidae sp. 3

Meanwhile, all species exclusively recorded from the small islands of more than 50 individuals belonged to the family Elateridae and Tenebrionidae. A total of 235 individuals of Elateridae sp. 1 (Figure 26a) and 405 individuals of Elateridae sp. 5 (Figure 26b) were collected on small islands, whereas this species was missing from catches in Java. From the family Tenebrionidae, the species *Leichenum* sp. 1 (Figure 26c), Tenebrionidae sp. 1 (Figure 26d), Tenebrionidae sp. 2 (Figure 26e), and Tenebrionidae sp. 3 (Figure 26f) accounted for 667, 152, 77, 89 individuals, respectively. They were, again, only found on the small islands (Appendix 1).

The most widely distributed small island species belonged to the families Anthribidae and Tenebrionidae, with both Anthribidae sp. 34 and Tenebrionidae sp. 3 recorded on five islands. Three species representing the family Curculionidae; Curculionidae sp. 1, Curculionidae sp. 2 (Figure 27a), Curculionidae sp. 3 (Figure 27b), were found on four islands.

(a)   (b)
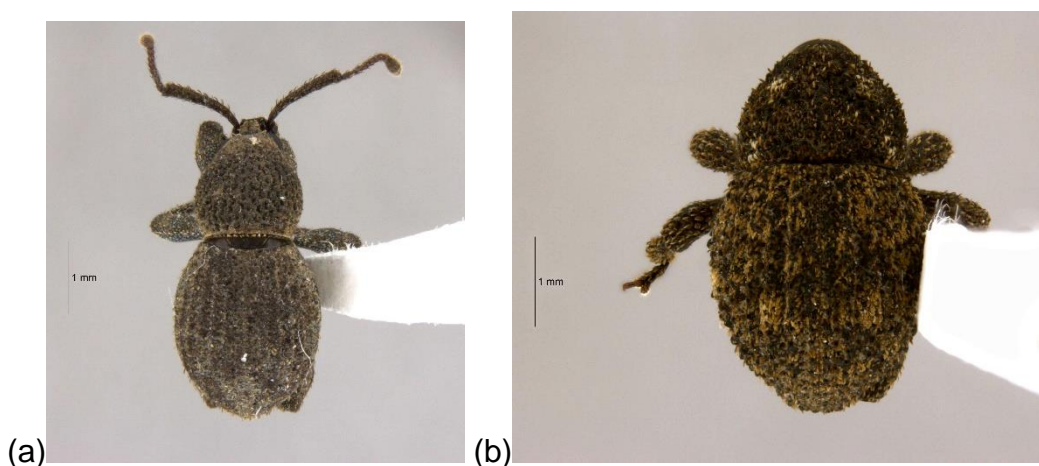
Figure 27 Picture of (a) Curculionidae sp. 2, (b) Curculionidae sp. 3

A more detailed analysis based on members of the three beetle families Carabidae, Scarabaeidae, and Scolytidae showed that eight Carabidae species recorded only in Java compared to 18 species recorded only on small islands. The most abundant small islands carabid species was Carabidae sp.6 with 34 recorded individuals. The only carabid species found both on small islands and in Java was *Perigona* sp.1, with a total recorded individuals of 12. Meanwhile, species from Family Scolytidae were found more and abundantly both on small islands and in Java, with eight species.

Two scolytid species, *Dryocoetiops coffeae* (Eggers, 1923) and *Xyleborinus perminutissimus* (Schedl, 1935), recorded only in Java. Although *Dryocoetiops coffeae* (Eggers, 1923) was only recorded in Java, it is not endemic to Java. Its distribution ranges from India, Indonesia (Java), Japan, Malaysia, New Guinea, Sri Lanka, Taiwan (Beaver and Liu, 2010). It is known as a polyphagous twig borer and has been recorded as a secondary pest of coffee (*Coffea* spp.) (Rubiaceae) by Browne (1961) and Le Pelley (1968). A study by Hulcr and Cognato (2010) only recorded *X. perminutissimus* in Java. However, there were no further information whether this species is endemic to Java or not.

The two most abundant species recorded only from Java belonged to the family Scarabaeidae. Species *Onthophagus* sp. 7 and *Onthophagus javanensis* (Balthasar, 1969) (Figure 28a), which is endemic to Java, accounted for 75 and 33 individuals in the Java samples, respectively (Appendix 1). Another scarabid species endemic to Java, *Onthophagus javacupreus* (Huijbregts & Krikken, 2011) (Figure 28b) was also recorded in the Java samples and accounted for 3 individuals. Both endemic species were only recorded in samples collected in Java.

(a)   (b)
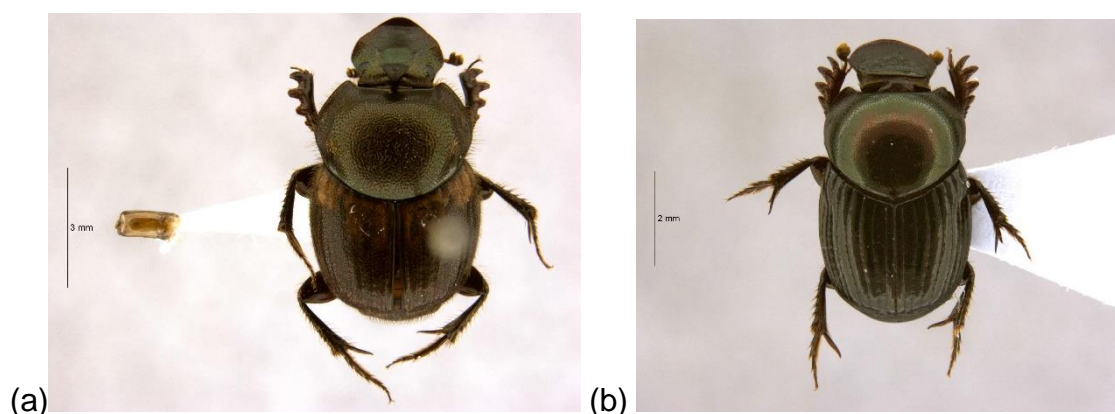
Figure 28 Picture of (a) *Onthophagus javanensis*, (b) *Onthophagus javacupreus*

3.4. <u>Discussion</u>

3.4.1. *Overall beetle compositions on small islands and Java*

To the best of my knowledge, my study represents the first intensive study of beetle communities in Kepulauan Seribu Marine National Park. The recorded 34 families representing 236 species in this study represent a substantial diversity encountered in the relatively small sampling area in Java and the ten islands, selected out of 105 islands in the National Park, and considering the short sampling time (see Chapter 2). Additionally, I combined two different types of traps, pitfall traps and FITs, which are very rarely used jointly in beetle studies and which have never before been used in combination in the study area.

There are three main differences between my Java and small island samples. First, when sampling effort is equal, the number of family and species of ground dwelling beetles were higher on islands than Java. However, Java showed higher family and species diversity of dispersive beetles. Second, the total number of individual beetles caught was significantly larger on small islands than on Java. The third main difference is several species that were very abundant on Java sites were scarce or almost absent from the small islands, and conversely species with high abundance on small islands were missing on Java sites.

The difference in sample size is to a great extent explicable regarding the high number and abundance of unique island species richness on islands, which emphasises their outstanding importance for global conservation of genetic resources. Although some of the studied islands' ecosystem are still susceptible to the anthropogenic activities, such as tourism and settlement, they might have been able to maintain suitable habitat for some beetle species, while Java has not. Geographical barriers, habitat differentiation and ecological speciation have likely played a role in the diversification of island faunas (Ogden and Thorpe, 2002, Thorpe et al., 2005 and Crews et al., 2010). The different colonizing propensity of single species (Niemela et al., 1985), might also explain the high number of beetles captured on islands. A few species are successful in inhabiting the island habitat. It might be that these patterns can be derived from differences in environmental conditions, including habitat composition in the surroundings of the study sites, and in ecological characteristics of the species. This explanation

could indicate that evolutionary assembly of island faunas can reverse the general pattern of reduced species richness on islands relative to Java.

Resource levels between Java and the studied island sites are likely to differ. It could be because the habitats (open sandy area, field, garden and settlement) are relatively high on some islands. It would be tempting to suggest that the observed impoverishment of Java's ground-dwelling beetle communities is at least partly due to food resource scarcity. Unfortunately, no data on resource abundances on Java and island sites are available.

Anthropogenic activities on the studied islands are potentially affecting the number of island's beetle species as well. On the other hand, with almost 58% of total Indonesian's population living in Java, it is continuously experiencing the same problems with habitat alterations and land use changes. When land cover changes driven by either direct human activity (agriculture, deforestation, and urbanization) or climate change predicted for the year 2100 by the Millennium Ecosystem Assessment (2005), an apparent dichotomy surfaced between island and mainland regions. Whereas future habitat loss driven by land-use change is projected to accelerate for island regions, mainland regions are predicted to lose more of their original land cover because of climate change through such as extreme weather.

Further factors potentially leading to an enhanced number of small island specimens relate to the abundance of dominant species. In Java, the three most abundant dispersive beetle species from FITs, Nitidulidae sp.07, *Hypotheneums* spp., and *Xyleborus perforans*, jointly accounted for only 24.7% of the overall individuals. On small islands, however, the most dominant dispersive beetle species *Onthophagus* sp.01, *Onthophagus* sp.03, and *Xyleborus perforans*, represented more than 50% of sampled specimens.

The differences between the most abundance Java species and small island species were most striking for a Tenebrionidae species, *Leichenum* sp.1, and two Elateridae species, Elateridae sp. 1 and Elateridae sp.5, which were profoundly abundant on small islands but were absent completely in Java. It is not easy to explain why these species only occurred on the studied islands with high abundance.

However, the high diversity of tenebrionids on islands had been recorded before on island ecosystem while other animal groups were scarce (Fattorini and Fowles, 2005). As generalist detritivores, they feed primarily on vegetative matter from a variety of plant species (Roberts et al., 2007). Being highly mobile, they wander freely over hundreds of meters (Parmenter et al., 1989; Wiens and Milne, 1989), thereby encountering a variety of habitats at both broad and fine spatial scales. However, there were potentially other factors may seem important or favourable for tenebrionid beetles on the studied islands, such as feeding or oviposition areas, and refugia from predators. Unfortunately, the autecology of the dominance of these species on islands is poorly known. It is possible only to suggest tentatively species-specific mechanisms that might influence their colonizing ability. More data are needed on the exact environmental requirements and over-water dispersal of the species.

The scarcity of most of the Java dominants on the islands might also be caused by lower food resource level and greater isolation of favourable patches from each other. In addition, the habitat in Java and small islands were not structurally simple. Java and most of the sampling plots on islands were located in a mixed habitat of settlement, forest, and vegetated habitat. It is likely that the density of vegetation in some of the sampling areas in Java and islands does not favour the movement of ground-dwelling invertebrates and decreases the sampling efficiency. The vegetation may also increase the number of taxa that avoid pitfall traps by moving through overlying vegetation (Honek et al., 2003).

3.4.2. Distribution of beetle families on islands and Java

This study has showed that some beetle families were only observed in Java, and some were only on islands. In Java, scarabid beetles dominate both the abundance and diversity of the total observed beetles. These results might be suggested by the higher abundance of dung and carrion resources in Java than the islands. Scarcity and limited food sources would suggest that dung and carrion beetles compete intensively as attested by their competitive and combative behaviours (Halffter and Edmonds 1982; Hanski 1991). Although scarabid beetles occasionally use the dung produced by birds and reptiles (Howden and Young, 1981; Young, 1981), which are available on the studied

islands, some other factors might have influenced the overall population of these beetles. Resource partitioning, such as preference for soil and cover (Nealis 1977; Lumaret 1978), diel flight time (diurnality versus nocturnality) and dung size (Peck and Howden 1984), perching heights (Howden and Nealis 1978) and dung removal methods (rollers versus tunnelers; Halffter and Mathews 1966) have been suggested as important factors affecting scarabid beetles population. In general, the high abundance and diversity of dung beetles in Java could suggest an indicator for high biodiversity. By burying the dung and carrion as food for their offspring, dung beetles may increase the rate of soil nutrient cycling (Halffter and Mathews 1966; Bornemissa and Williams 1970; Nealis 1977), they also act as important secondary dispersal agents for the seeds of several tree species in tropical forests, thus participating in the natural process of forest regeneration (Estrada and Coates-Estrada 1991).

The absence of hydrophilid beetles and the low number of scarabid species on the studied islands might be interrelated. The lack of mammal, thus mammal's dung, on the islands (S. Puspitasari, personal observation) potentially explains the low occurrence of scarabid beetles on the islands. Hydrophildae beetles are mostly predatory on dung beetles, which could indirectly affect the absence of these beetles on the studied islands as well. Some hydrophilids are also coprophagous beetles, which are known to have clear habitat associations and preferences to certain type of soils (Davis et al., 2002). Most hydrophilid species enter the soil beneath dung pad to pupate and, perhaps in some cases, to oviposit or escape harsh conditions. Java has fertile soils like Vertisols and Andosols, but also less fertile soils like Ferralsols that are mainly used for paddy rice production. On the other hand, the studied islands were formed by colonies of dead coral. The surface of the islands is dominated by Regosol (coastal sand) (www.fao.org). This is reflected in the domination of coastal plants such as coconut palm (*Cocos nucifera*), *Pandanus* spp., *Casuarina equisetifolia*, *Morinda citrifolia*, *Barringtonia asiatica*, and mangrove forest (Pemerintah Kecamatan Kepulauan Seribu, 2011).

However, dung and carrion beetles from different families, Trogidae and Hyborosidae, were observed only on the studied islands. Their occurrence on the islands might be explained by their succession during decomposition of an ephemeral resource. The dung or carrion decomposition process are

characterised by a particular complex sequence of species arrival and mostly by competition among insects (Weslien et al., 2011). It is perhaps that islands have fewer competitors or predators for this group of insects and that food sources are more available, and these families are hence thriving with high abundances.

The lack of herbivore beetles from family Brentidae and fungivore beetles from family Rhizophagidae on the studied islands might be explained by the different type of vegetation. Although this study did not include vegetation surveys, my general observation showed that most of the studied islands had low vegetation and high exposure to the sun. The lack of tall vegetation on the islands might be attributed to low level of microclimatic variables such as humidity, which is important for the natural habitat of microorganisms such as fungi and bacteria (Howden & Nealis, 1978; Lumaret, 1978; Doube, 1990; Tuomela et al. 2000).

Herbivorous insects depend on plants as a direct food source for their offspring or themselves (Tscharntke and Brandl 2004; Almeida-Neto et al. 2011; Perre et al. 2011). In addition, most herbivorous insects consume only a few phylogenetically related plant species (Ødegaard et al. 2005; Morais et al. 2011). Often, island settlers brought back ornamental plants, fruit plants, and grass from Java. The competition with the introduced plants might have contributed to the loss of host plant for herbivore beetles on islands. Consequently, the availability of host plant and negative impacts of land use intensity on these plants on the studied islands are expected to propagate through higher trophic levels (Fonseca 2009; Pearse and Altermatt 2013), particularly over the herbivore beetle assemblages that are intimately associated with their host plants. However, introduced plants from Java can potentially carry herbivore insects which flourish on the islands. Previous studies have demonstrated that herbivore insects' response to introduced plant species and habitat alteration is often unpredictable due to non-uniform effects on different trophic levels in a community (Kareiva 1987; Kruess and Tscharntke 1994). This suggests that other biotic and possibly abiotic factors, such as immigration/emigration rates, microclimate and predation may also influence their distributions on the studied islands.

On the other hand, other beetle families flourish on the studied islands. The high abundance of scolytids and woodboring beetles from family Tenebrionidae,

Cerambycidae, Endomycidae and Mordellidae can be partly explained by the deadwood accumulation resulting from driftwood washed up from the sea. Such driftwood is one very likely source explaining the mass occurrence of Scolytidae as many species from this family live in dead and dying wood and are known to use rafting on plant material as an effective dispersal method (Kirkendall and Jordal, 2006).

3.4.3. Unique island and Java species

At the species level, two unique island species from family Elateridae, Elateridae sp. 1 and Elateridae sp. 5 were thriving in population, suggesting that suitable vegetation hosts were more abundant on the islands than in Java. However, the number and occurrence of elaterid species do not always differ according to vegetation type. Because the larvae of some elaterid species are generalist predators (Makihara & Ôhira 2005), the difference in vegetation diversity may not affect the number of elaterid species.

More carabid beetle species were found on the islands than in Java. Factors that probably affect the colonization process include environmental differences, especially differences in the composition of habitats in the surroundings of the sampling sites, and autecological characteristics of the species, such as dispersal ability and habitat preferences. Unfortunately, the autecology of the carabid species, especially on the studied islands, is poorly known. It is possible only to suggest tentatively species-specific mechanisms that might influence their colonizing ability. On the other hand, the scarcity of the Javan dominant species on the islands might be caused by lower food resource level and greater isolation of favourable patches from each other. However, more data are needed on the exact environmental requirements and over-water dispersal of the species.

The high abundance of the Genus *Onthophagus* in Java was also found in a study by Kahono and Setiadi (2007). The low degree of food specificity (Shahabudin et al., 2010) potentially makes this genus thriving in population. The occurrence of two endemic species of Java, *Onthophagus javanensis* (Balthasar, 1969) and *Onthophagus javacupreus* (Huijbregts and Krikken, 2011) is expected. The range and ecology of *O. javanensis* and *O. javacupreus* are only on Java and

these species have never been seen from other regions (Huijbregts and Krikken, 2011). They can be found mostly in the forest habitat with an altitude between 700-1700 m, especially *O. javanensis*, which has adaptation to wide range of altitude and different type of dung. Fish carrion traps, which were used in this study, have been known to attract both species (Huijbregts and Krikken, 2011; Kahono and Setiadi, 2007).

Interestingly, Java and the islands share the most abundant species, *Xyleborus perforans*. This species is widely distributed and easily captured in different traps, such as Malaise trap and by hand, yellow pan trap, and FITs. The high abundance of this species both on the islands and Java might be explained by the possible importance of inbreeding (Kirkendall and Jordal, 2006) in this context. Bark beetles are not the only terrestrial arthropods with clades in outbreeding are found – regular close inbreeding occurs in, for example, certain mites, thrips, aphids, solitary bees and wasps, ants and social spiders (Thornhill, 1993; Wrensch & Ebbert, 1993). Although my study did not look specifically at the breeding process of this group, however, they are apparently the only group in which an association between zoogeography and close inbreeding has been documented (Kirkendall, 1993; Jordal et al., 2001). The proportion of the scolytine fauna that inbreeds by repeated sib-mating increases with decreasing latitude, and is highest on tropical islands. In agreement with these patterns, a study by Jordal et al. (2002) showed that three quarters of the known scolytine fauna on Cocos Island were species which regularly inbreed by brother–sister mating.

3.4.4. Synthesis

Several beetle species are more successful and thriving in inhabiting the islands than Java. The explanations for these patterns can be derived from differences in environmental conditions, including habitat composition in the surroundings of the study sites, and in ecological characteristics of the species. My conclusions underline the importance of quantitative data in island-mainland comparisons. At present, I know of no studies on island beetles dealing with quantitative data, but a quantitative approach is necessary to detect important ecological patterns behind the documentation of the apparent differences of insular faunas. Factors

influencing the ability of single species to colonize insular environments deserve attention as well as community-level comparisons.

Chapter 4. Effects of island size and isolation on beetle assemblages: a test of Island Biogeography Theory

4.1. <u>Introduction</u>

According to the equilibrium theory of island biogeography, species richness on islands forms a dynamic equilibrium between the opposing processes of immigration and extinction (MacArthur & Wilson, 1967) (Figure 29). Concurrent with general island biogeography, many studies have confirmed that island isolation and size are both key predictors for the species richness of an island fauna (Gentile & Argano, 2005; Kalmar & Currie, 2006; Ackerman et al., 2007; Fattorini, 2010; Fattorini, 2011). Particularly on large islands, island area was shown to be an important factor in explaining the species richness in a wide range of arthropod taxa like Chilopoda, Orthoptera, and Tenebrionidae (Fattorini, 2011). The number of species unique to islands also increases with island area (Fattorini, 2010). In relation to plants, island area was found to be the strongest contributor towards explaining insular species richness in a large comparative survey of 488 islands and 970 mainland floras (Kreft et al., 2008). Island area is of great importance in determining how many species can be hosted by an island. Large areas also often allow more individuals of a species to exist, hence reducing a species' extinction risk e.g. by catastrophic events killing off the entire island population (Walter, 2004).

However, more recent studies found that island area is not considered to be the main influence of an island's biotic diversity (Rosenzweig 1995, Whittaker and Fernandez-Palacios 2007, Trianties et al., 2005). Instead, larger islands have shown an increasing species richness in response to a wider range and amount of available resources, a wider spectrum of habitats and a higher diversity of microclimates (Walter, 2004). The species richness of an island or any area must, therefore, be seen as the result of many processes acting and interacting across space and time. Moreover, the explanatory power of the factor area for variations in island species numbers is also variable.
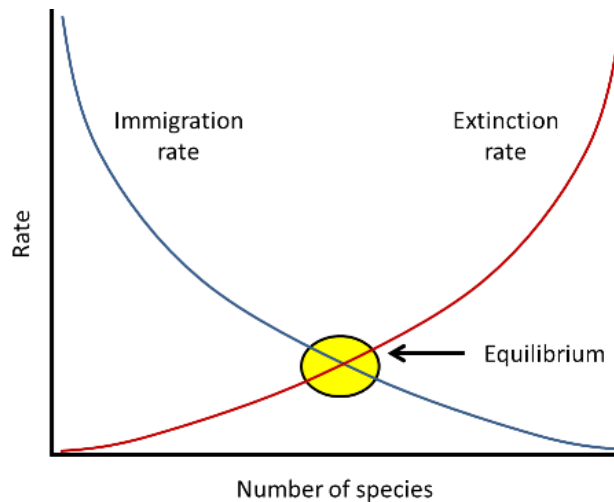
Figure 29 Equilibrium model of the species richness at a single island. The equilibrium species number is reached at the intersection point between the immigration and extinction curves (MacArthur and Wilson, 1967)

Empirical studies demonstrating additional significant and sometimes dominant roles for an array of subsidiary variables, including habitat type, disturbance levels and regimes, elevational heterogeneity and island age, suggested spatiotemporal scale and context-dependency in species-area relationships (Rosenzweig 1995, Whittaker 2000, Whittaker and Fernandez-Palacios 2007, Trianties et al., 2008). Lomolino and Weiser (2001) showed that differences in elevation, the availability of freshwater resources, actual habitat quality and diversity, geological settings and human history are examples of key factors influencing biotic assemblages. With the exception potentially of altitude ranges, these are widely size-independent, hence further complicating the relationship between area and species richness. Overall, habitat diversity is believed to be of particular importance in determining the species richness of island biotas (Hortal et al., 2009). Thus, species-area relationships, as many other highly generalizing patterns describing complex systems, are related to the importance of all the processes above and factors that relate, to highly varying degrees, with this variable. In this chapter, I am looking at the effect of island area without specifically considering the other subsidiary variables. I am effectively testing if the classic area-species richness relationships, inherent to the theory of Island Biogeography, work for insular beetle assemblages on the studied islands. I

hypothesise accordingly that beetle communities on the Kepulauan Seribu Marine National Park will decline with a decrease in island size, with a log-log relationship describing this relationship.

The second key pattern associated with island biogeography relates to the degree of island isolation. MacArthur and Wilson (1967) considered the trend of increasing species richness with decreasing isolation to be the second key trend when predicting island species richness. This prediction was based on the assumption that immigration of sufficient specimens to allow for the successful establishment of a species' viable population occurs more frequently on islands close to the main source area for colonising species. As shown by Kalmar and Currie (2006) for insular bird assemblages, isolation does appear to play a strong role in species richness on islands. A study by Weigelt and Kreft (2012) also found that the isolation metric had the highest predictive power, explaining 86.1% of the variation for vascular plant species.

Most of the conceptual models in island biogeography consider isolation as the 'distance to' or more generally as the 'isolation from' source pools. Many different metrics of isolation have been proposed, including the distance between a target island and the nearest mainland coast (Rizali et al., 2010; Spengler et al., 2011), distance to the nearest neighbouring island (Fattorini, 2010), distance to the nearest island (McMaster, 2005), and the mean distance to a set of other islands (Borges & Hortal, 2009). Another frequently used metric, the UNEP isolation index (Boyer & Jetz, 2010; Kisel & Barraclough, 2010, Weigelt and Kreft, 2012), incorporates the distances to the nearest mainland, nearest island group, and nearest equally sized or larger island.

Previous studies looking into the effect different isolation measures have on different groups of insects showed diverging response patterns to these factors (Fattorini, 2011). Inter-island distances, especially distance to the nearest island, appeared overall to be more important in determining variation in species composition than the distance to the nearest mainland area (Fattorini, 2010; Fattorini, 2011). Therefore, I hypothesise that inter-island faunal exchanges linked to the distance to the nearest small island are more important for faunal turnover in my island setting than the distance to Java.

Taxon-specific dispersal abilities play an important role in island colonisation (Thornton, 1992). Differences in dispersal abilities and population size potentially generate a nested pattern in island biotas. On small and isolated islands where colonization events are rare and frequent extinctions are likely to occur due to small population sizes can hence be expected to harbour subsets of species assemblages of larger islands and islands closer to potential source areas (Wright et al., 1998).

Studies on the effects of island size and isolation have in the past been highly biased towards plant and vertebrate taxa (Weigelt & Kreft, 2012; Kalmar & Curie, 2006; McMaster, 2005; Price, 2004; Kreft et al., 2008). In the following chapter, I will in contrast assess the relative influence of island size and isolation on small, often highly mobile and species-rich tropical beetle assemblages on the small islands in Kepulauan Seribu Marine National Park.

4.2   Methods and data analysis

This chapter was based on all plots located on small islands. As outlined in Chapter 3, a total of 70 sampling plots were equipped with pitfall traps and 11 with flight interception traps (FITs) on the ten small islands within Kepulauan Seribu Marine National Park. Information on island size and distance to Java were gathered from the national park office and had again already been presented in chapter 3. In my analysis, I used three different measurements to assess isolation: the distance to Java as the nearest large source area, the distance to the nearest neighbouring island (Fattorini, 2010), and the mean distance to islands within a 5 km radius (Borges & Hortal, 2009). Measurements for the first two were gathered from the Kepulauan Seribu Marine National Park Office. The two latter distance measurements were made using Google Earth-Pro (Table 3).

Table 3 Isolation and area measurements of the ten islands in Kepulauan Seribu Marine National Park.

No	Island	Area (km²)	Distance 1 (km) *	Distance 2 (km)†	Distance 3 (km)∞	No of Plots	
						PT	FIT
1	Rambut	0.4580	5	0.86	0.86	5	2
2	Untung Jawa	0.3912	6	0.86	0.86	10	2
3	Bokor	0.1634	7	3.44	3.915	5	0
4	Lancang Besar	0.2643	10	0.3	2.345	10	0
5	Damar Besar	0.2951	18	5.25	5.25	5	2
6	Pramuka	0.1992	27	0.69	1.0925	10	2
7	Kotok Besar	0.2265	32	1.02	3.29	10	0
8	Opak Besar	0.0974	37	1.04	2.395	5	2
9	Pemagaran	0.1556	40	0.8	2.965	5	2
10	Putri Barat	0.0963	45	0.57	2.45	5	2

* Distance to Java
† Distance to the nearest island
∞ Mean distance to islands within radius of 5km

The abundances of all beetle species from all islands over the entire sampling period were pooled but differentiated into pitfall trap and FIT samples. Specimens from baited and non-baited pitfall traps on each island were combined and analysed jointly to represent the island's pitfall trap specimens.

The observed number of species depends strongly on sample size and sampling efforts. Consequently, different sets of α-diversity need to be used to assess the sample (Axmacher et al., 2011). The α-diversity of beetle species on each island was calculated using Shannon's diversity (Shannon's H) to emphasise the richness component of diversity and Simpson's diversity (Simpson's D) to emphasise the evenness. As outlined by Jost (2006), Shannon's entropy was converted into diversity measures using an exponential conversion. Simpson's diversity was calculated as the inverse of the Simpson's static, again following the approach outlined in Jost (2006). Hill numbers were again used to measure these diversity indices (Appendix 1).

I computed single-predictor regression models with the rarefied beetle species number per island as the response variable and each environmental parameters in turn as the explanatory variable. Species number per island is adequately accounted for by regression and has been used in many studies (Kohn and Walsh, 1994; Morrison, 2002; Fattorini, 2002; Brose, 2003).

I then used Principal Components Analysis (PCA) to condense data of island size and island distance measurements into principal components (PCs) reflecting the main gradients in the changes of island size and island distance measurements. The resulting sets of principal components and all individual environmental parameters linked with PCs were used consecutively as predictors of beetle species diversity in a series of step-wise multiple linear regression (MLR) models.

Detrended correspondence analysis (DCA) can be used as an indicator whether species responses along the investigated environmental gradient are linear or unimodal (Ter Braak, 1988). In DCA, the axes represent standard deviation (SD) units. If the first axis representation exceeds 2 SD units, then response curves are proposed to follow a unimodal model. On the other hand, if the gradients are less than 2 SD units, then most species responses are assumed to approximate a linear response (Meier, 2007).

For each taxonomic rank and group investigated, a DCA was computed to check for the respective response patterns. The lengths of the major gradient aligned to the first axis were less than 2 SD in some and more than 2 SD in other cases. Thus, redundancy analysis (RDA) and canonical correspondence analysis (CCA) (Leps and Smilauer, 2003) were selected as suitable analytical approaches to measuring the amount of variation (sum of canonical eigenvalues) in the species data that can be explained by the set of environmental variables.

The analysis of changes in the composition of beetle assemblages in relation to island area and distance measurements resulted in similar outcomes for Chord- and Hellinger-distance-transformed geometrid beetle data. Therefore, only results obtained after Chord- transformation will be presented here.

MLR models were calculated using SPSS version 22. DCAs, RDAs, and CCAs were calculated using CANOCO (version 4.5) (Leps & Smilauer, 2003). All other calculations and statistical analysis were carried out in R language version 3.1.2 (R Development Core Team, 2011) with the use of the 'vegan' package (Oksanen, 2015).

4.3. <u>Results</u>

4.3.1 Overall number of beetle species and diversity on small islands

The highest number of recorded ground-dwelling beetle species from pitfall traps was found on some of the larger islands, Untung Jawa, Lancang Besar, and Pramuka, with 51, 38, and 37 recorded species, respectively. Meanwhile, the lowest number of 11 species was recorded at Putri Barat, which is the smallest and the most isolated studied island (Figure 30a). Dispersive beetles from flight interception traps (FITs) recorded the highest number of species on larger islands, Untung Jawa, Pramuka, and Rambut, with 56, 43, and 18 recorded species, respectively. In contrast, only five species were recorded in FIT samples on Opak Besar. Rarefaction curves showed similar patterns of the observed number of species richness (Figure 30b).

(a)

(b)
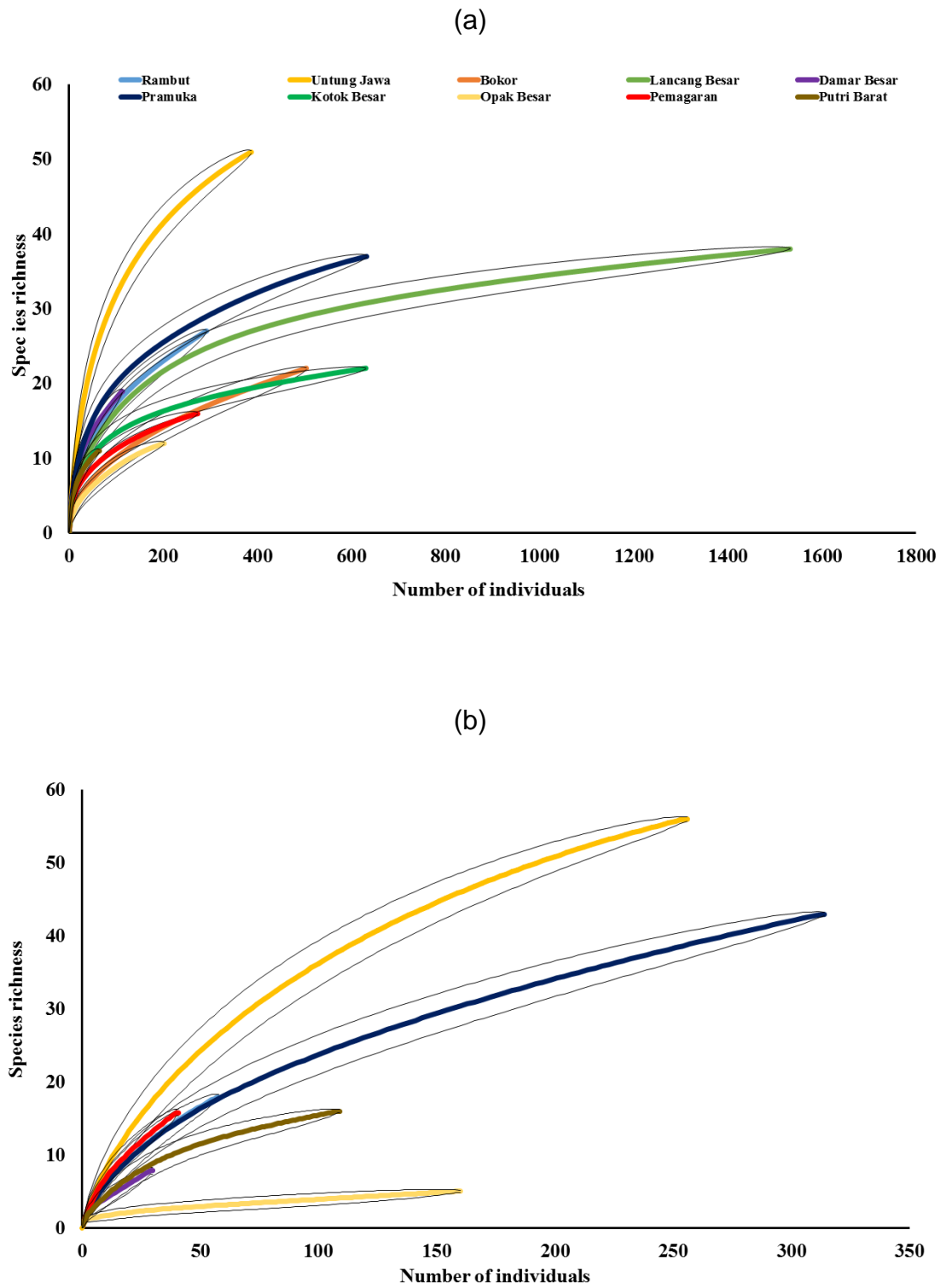
Figure 30 Rarefaction curves of beetle species richness from pitfall traps on studied small islands from (a) pitfall traps and (b) FITs (black lines represent 95% confidence intervals)

Overall, beetle species diversity from pitfall traps, assessed both by the Shannon and Simpson's index, was highest on the larger islands. Untung Jawa Island (h_{exp} = 27.29 and D_S=19.2) recorded the highest beetle diversity, followed by Pramuka Island (h_{exp} = 13.28 and D_S = 8). The lowest beetle diversity was recorded on one of the smallest and more isolated island, Opak Besar (h_{exp} = 2.61 and D_S=1.64) (Figure 31).

FIT samples showed similar patterns to pitfall trap samples, where larger and less isolated islands have higher beetle diversity. Untung Jawa (h_{exp} = 18.48 and D_S=15.89) and Rambut Island (h_{exp} = 9.92 and D_S=5.55) showed the highest diversity both measured using the Shannon and Simpson's index. Meanwhile, Opak Besar island harboured the lowest Shannon (h_{exp} = 1.63) and Simpson's index (D_S = 1.16) (Figure 32).
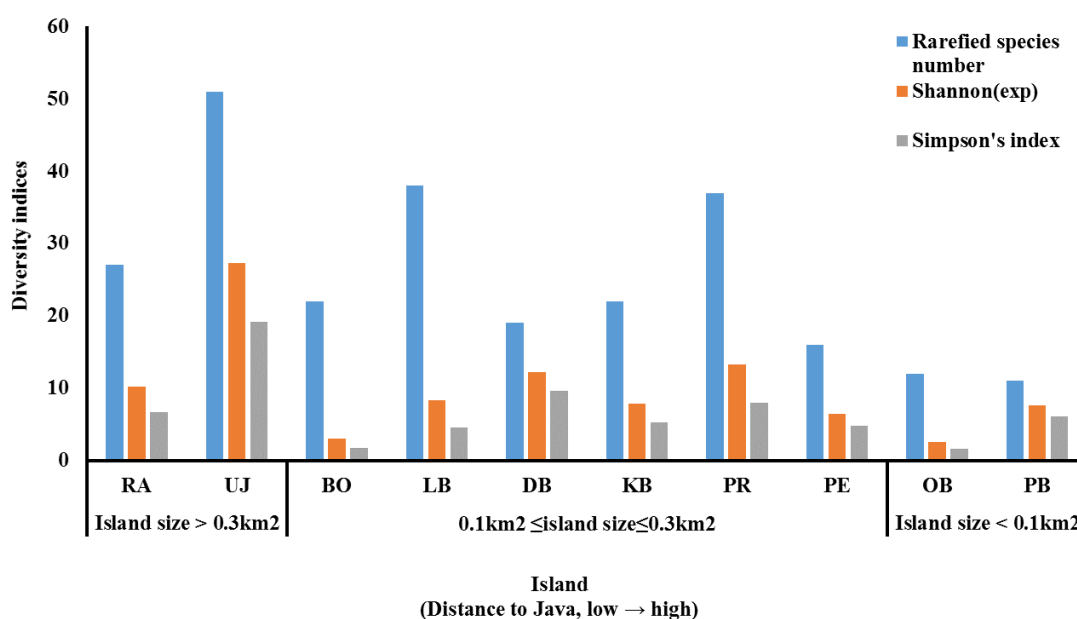
RA=Rambut; UJ=Untung Jawa; BO=Bokor; LB=Lancang Besar; DB=Damar Besar; KB=Kotok Besar; PR=Pramuka; PE=Pemagaran; OB=Opak Besar; PB=Putri Barat

Figure 31 Comparisons of beetle species diversity indices on islands from pitfall traps
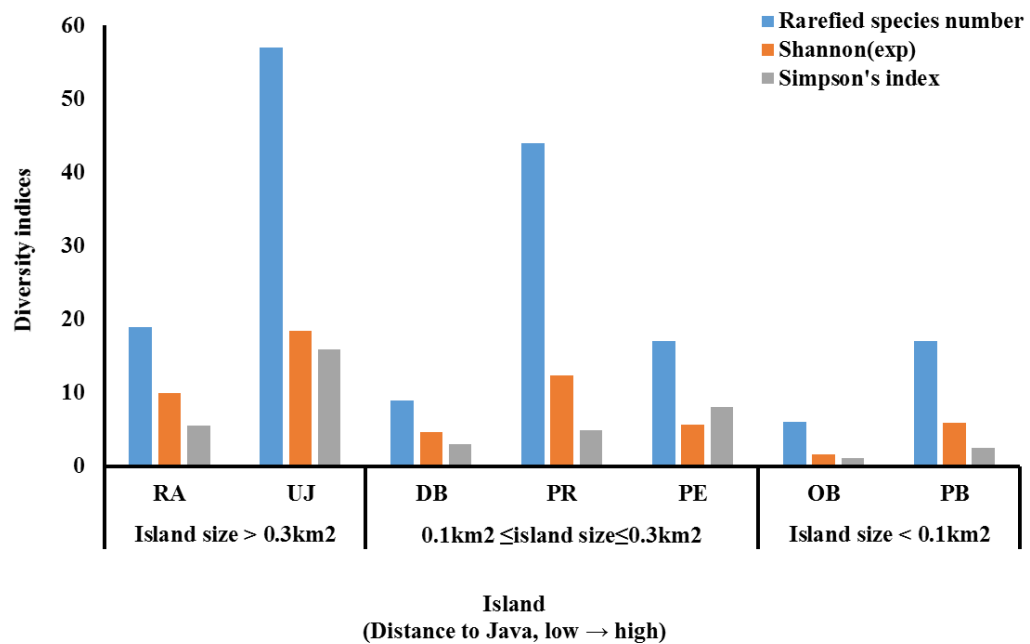
RA=Rambut; UJ=Untung Jawa; DB=Damar Besar; PR=Pramuka; PE=Pemagaran; OB=Opak Besar; PB=Putri Barat

Figure 32 Comparisons of beetle species diversity indices of small islands from FITs

4.3.2 Linear regression analysis: Beetle species richness response to island area and island distance measurements

Based on the results from ground-dwelling beetles recorded from pitfall traps, the correlation between rarefied species number and log-transformed island area was significantly positive (P = 0.028, R^2 = 0.474) (Figure 33a). Meanwhile, the rarefied species number was negatively correlated with all three isolation metrics, most significantly with distance to Java (P = 0.035, R^2 = 0.446) (Figure 33b). There were no significant impacts (linear regression analyses, $P > 0.05$) of distance to nearest island (P = 0.497, R^2 = 0.060) (Figure 33c) and mean distance to islands within a radius of 5km (P = 0.096, R^2 = 0.307) (Figure 33d) towards ground-dwelling beetle species richness on the studied islands.

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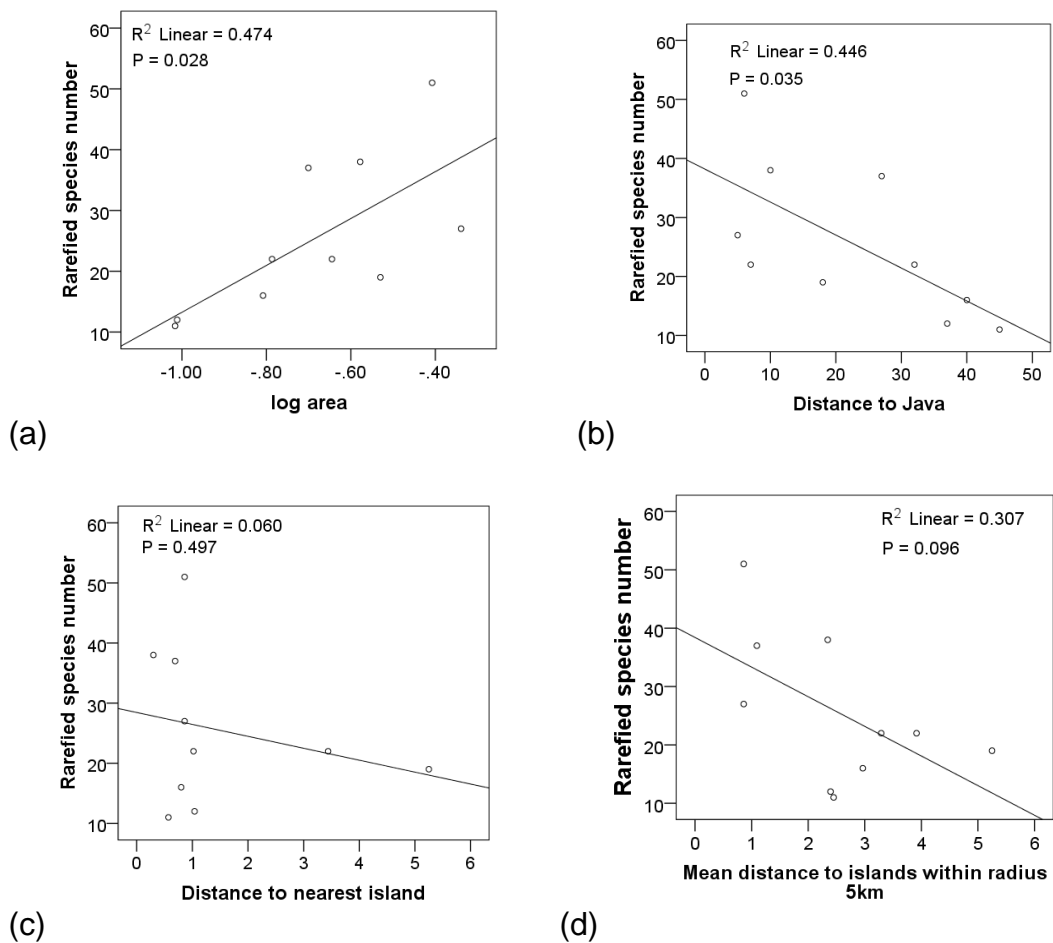
Figure 33 Linear regressions between rarefied species number from pitfall traps and (a) the log-transformed island area, (b) distance to Java, (c) distance to nearest island, and (d) mean distance to islands within radius 5km.

From FITs, all parameters were much weaker correlates and had no significant impacts (linear regression analyses, $P > 0.05$) towards rarefied species number for dispersive beetles. Island area (log-transformed) (P = 0.32, R^2 = 0.196) (Figure 34a), distance to Java (P = 0.304, R^2 = 0.474) (Figure 34b) and distance to the nearest island (P = 0. 417, R^2 = 0.135) (Figure 34c) were still relatively important correlate of rarefied species number from actively dispersed beetles from FIT. Mean distance to islands within radius 5km was the most important metric for dispersive beetle species richness (P = 0.114, R^2 = 0.422) (Figure 34d).
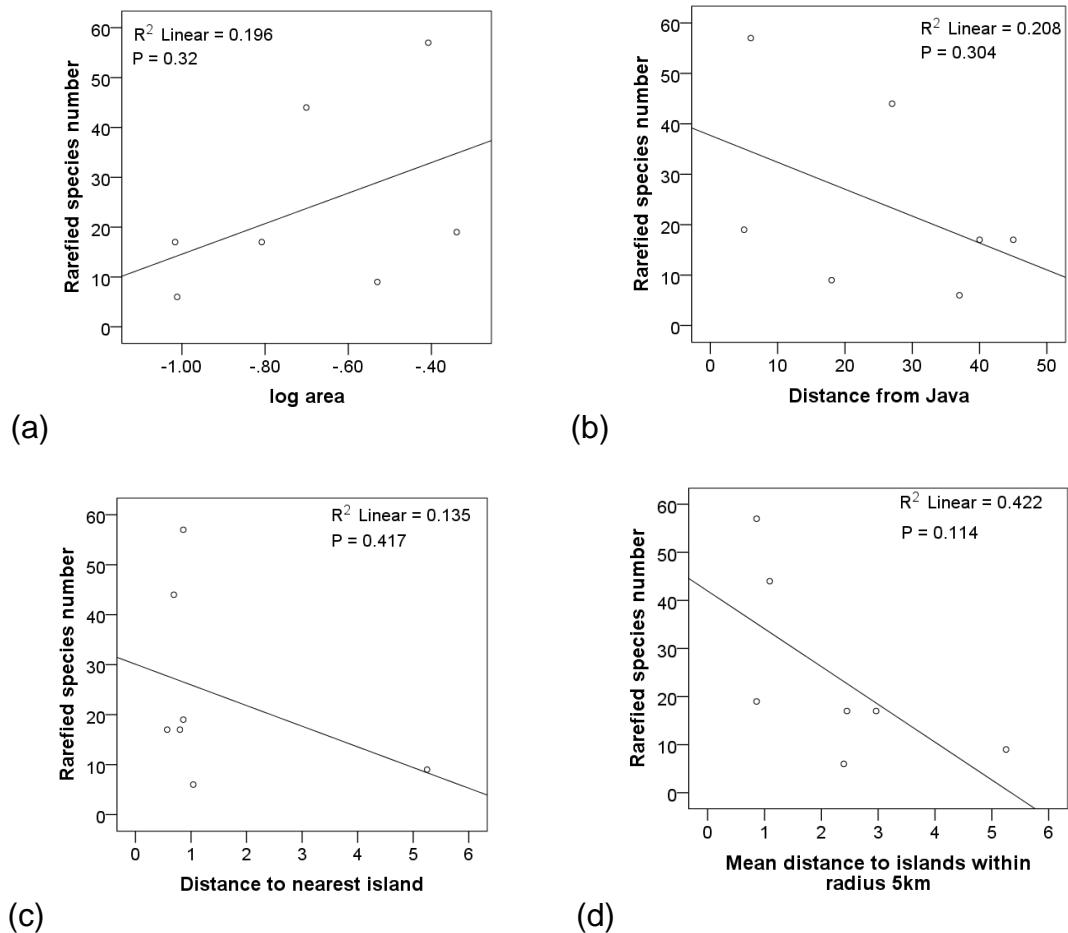
Figure 34 Selected relationships between rarefied species number from FITs and (a) the log-transformed island area, (b) distance to Java, (c) distance to nearest island, and (d) mean distance to islands within radius 5km.

4.3.3 Principal components analysis of island environmental data

The PCA based on the island area and distance measurements yielded only two PCs (island principal components: IPCs) with eigenvalues > 1 (Table 4). These IPCs explained 92.26% of the overall variance. The first IPC (IPC1) accounted for 48.47% and was closely linked to island area, but also to the two isolation measures, distance to Java and mean distance to islands within a radius of 5km. The second IPC (IPC2), explaining 43.79% of the variance, was most strongly linked to the distance to the nearest island, and also to distance to Java.

Table 4 Loading of area and distance measurements of the ten islands on two principal components extracted by principal components analysis (unrotated island principal components, IPCs). Only PCs with eigenvalues > 1 are shown.

Environmental variables	Factor 1 (IPC1)	Factor 2 (IPC2)
Distance to Java	0.692	-0.648
Distance to nearest island	0.41	0.885
Mean distance to islands within radius of 5km	0.773	0.592
Area	-0.833	0.446
Eigenvalue	1.94	1.75
Explained variance (%)	48.47	43.79
Cumulative explained variance (%)	48.47	92.26

4.3.4. Multiple linear regressions: predicting beetles species number and diversity from island area and distance parameters

In the MLRs, observed species number, Shannon diversity, and Simpson's index of beetle assemblages were taken as the dependent variables. When the island principal components (IPCs) served as independent variables, the results from pitfall traps (Table 5) indicated that neither of the two IPCs was significant predictors of Shannon diversity and Simpson's index. For the observed species number (adjusted R^2= 0.572, $F1,8$ = 13.023, P = 0.007), IPC1 was a significant predictor (β = -0.787, P = 0.007). These results further explained that the increase of island area and the decrease of distance to Java increased the number of ground-dwelling beetles on the studied islands.

Table 5 Stepwise linear regression from pitfall traps using observed species number, Shannon diversity and Simpson's index of beetles as the dependent variables. The island principal components (IPCs) served as independent variables.

Dependent variable	Adjusted R2	F	P-value	d.f	Selected independent variable	β	Std. Error of β	t	P-value
Observed species number	0.572	13.023	0.007	1,8	IPC1	-0.787	2.804	-3.609	0.007

The results from FITs also showed that only 1 model with the significant input was explained. Shannon diversity (adjusted R^2= 0.559, $F_{1,5}$ = 8.612, P = 0.032) showed significant link with IPC1 (β = -0.795, P = 0.032), explaining that increasing area significantly linked with increasing dispersive beetle diversity (Table 6). As IPC1 was negatively linked to island area and positively to distance to Java, these results showed that larger islands and islands closer to Java had higher Shannon diversity of dispersive beetles.

Table 6 Stepwise linear regression from FITs using rarefied species number, Shannon diversity and Simpson's index of beetles as the dependent variables. The island principal components served, and all individual predictors associated with IPCs served as independent variables.

Dependent variable	Adjusted R^2	F	P-value	d.f	Selected independent variable	β	Std. Error of β	t	P-value
Shannon diversity	0.559	8.612	0.032	1,5	IPC1	-0.795	1.315	-2.935	0.032

4.3.5. Redundancy analysis and canonical correspondence analysis: beetle species composition and island area and island distance parameters

The first canonical correspondence analysis of beetle species from pitfall traps including two IPCs. These two axes explained only a small proportion of 14 and 6.9% of the total variance in the dataset. Hence, the IPCs investigated, although small, still, a significant correlation with the composition of beetle assemblages.

In the ordination (Figure 35a), the distribution of ground-dwelling beetle assemblages from pitfall traps along the first axis was significantly correlated with IPC1, that was negatively correlated with island area and positively correlated with distance to Java. Several species from family Scarabaeidae, Carabidae, Scolytidae, Curculionidae, and Scydmaenidae, were positioned far on the positive side. Their positions were negatively associated with increases in the value of IPC1, hence occurring on larger and less isolated islands. However, other species from the families above, as well as species from the family Anthribidae, were also found on smaller and isolated islands, which were positively associated with increases in the value of IPC1.

The second canonical axis was strongly correlated with IPC2. This PC positively linked to the distance to the nearest island and also negatively associated with distance to Java. One species from the family Nitidulidae, Nitidulidae sp.14 (Nit14), and, to a lesser degree, representative species from the family of Carabidae, Anthribidae, Tenebrionidae, Curculionidae, and Chrysomelidae, all had positive species scores. Hence, these species occurred on islands located remotely from other islands but closer to Java. The rest of the species were negatively associated with increases in the value of IPC2, showing their occurrence on islands positioned close to neighbouring islands but further away from Java (Figure 35a).

The canonical correspondence analysis of dispersive beetle assemblages from FIT also including two IPCs, with the two axes, explained 17.8 and 15.2% of the total variance in the dataset. The IPCs have strong correlation with the composition of beetle assemblages. The distribution of beetle assemblages along the first axis was significantly correlated with IPC1. Species on small and isolated islands, which were positively associated with increases in the value of IPC1, were representatives from almost all of the families including Nitidulidae, Scolytidae, and Scarabaeidae. However, other Scolytidae species (*Xyleborus perforans* (Sco6) and *Xyleborus affinis* (Sco7)) were found on large islands and located closer to Java. Meanwhile, some species from family Scydmaenidae (Scydmaenidae sp.1 (Scy1)), Curculionidae (Curculionidae sp.8 (Cur8)), and Scarabaeidae (*Onthophagus trituber* (Sca24)) had negative species score, hence occurring on large and less isolated islands (Figure 35b).

Meanwhile, the second canonical axis was closely linked to IPC2, which is associated with distance to the nearest island and distance to Java. Species occurring on islands close to Java and far from neighbouring islands were showed clearly by species representative from the family Curculionidae (Curculionidae sp.14 (Cur14) and Curculionidae sp.10 (Cur10)), Scolytidae (*Xylosandrus compactus* (Sco3)) Nitidulidae (Nitidulidae sp.11 (Nit11)). Some species from family Scolytidae also had positive scores, hence found on more isolated islands and close to other neighbouring islands. Species positioned in the middle between IPC1 and IPC2 were representatives from the family of Carabidae, Scarabaeidae, and Scydmaenidae. This position indicates that those species occurred on islands with intermediate isolation.
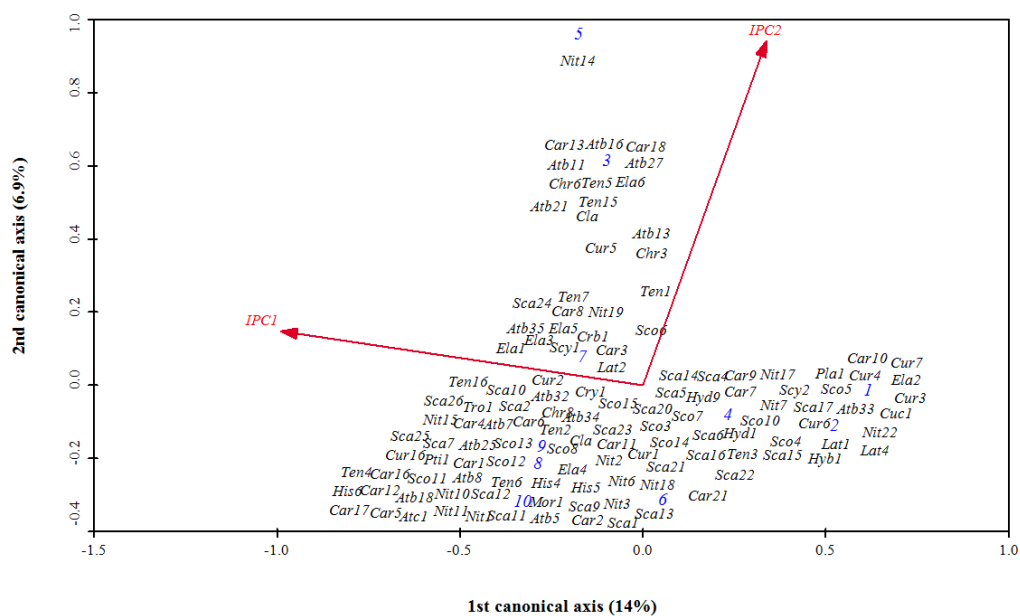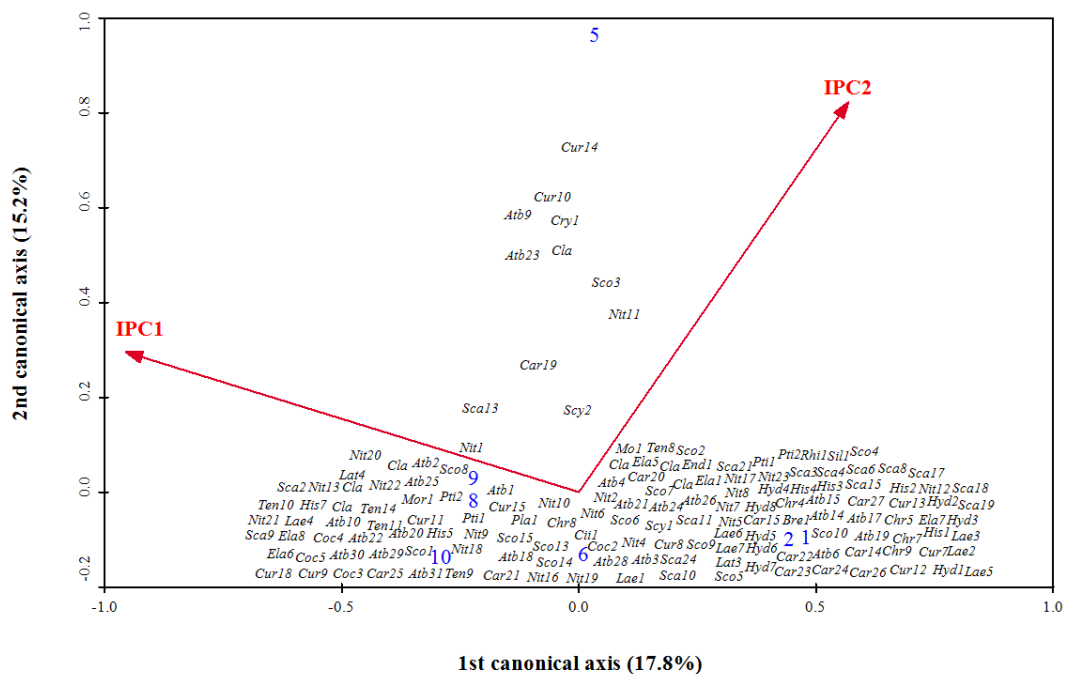
Figure 35 CCA ordination plots for the influence of island characteristics on the beetle species composition on small islands from (a) pitfall traps, and (b) FITs. Blue numbers indicate the studied islands.

More detailed analyse were conducted based on members from the three beetle families Carabidae, Scarabaeidae, and Scolytidae collected in the pitfall traps (see Chapter 2 on Sampling Methods). The results showed that the species composition of ground-dwelling Carabidae appeared to be strongly influenced by both IPC1 and IPC2. Both IPCs were more strongly associated with the first axis, with an overall explained variance of 18.3%, compare to the second axis, which only contributed an additional 0.5% towards the explained variance. Three carabid species (*Cyindidina* sp.1 (Car10) and, to a lesser degree, Cicindelini sp.1 (Car9) and *Brachinini* sp.1 (Car7)) were negatively associated with the increase in the value of IPC1, hence occurring on larger, less isolated islands. One species, *Pterostichinae* sp.1 (Car18), was positioned in the middle between IPC1 and IPC2, potentially occurred on islands with intermediate size and isolation. Meanwhile, one carabid species, Carabidae sp.21 (Car21), occurred on a more isolated island with neighbouring islands. The rest of the carabid species occurred on smaller and more isolated islands. The three smallest islands, Opak Besar (8), Pemagaran (9), and Putri Barat (10), were grouped together while the larger islands were more heterogeneous in their carabid assemblage compositions (Figure 36a).

The CCA analysis of Scarabaeidae species composition from pitfall traps generated two canonical axes, where IPC1 and IPC2 contributed 32.1% and 5.7% towards the original variance, respectively. Scarabid species compositions from pitfall traps clustered towards the centre of the CCA plot, indicating that the distribution patterns of these species might not be as strongly influenced by the environmental predictors. However, *Onthophagus trituber* (Sca24) showed a slightly clear preference for less isolated and no neighbouring islands (Figure 36b).

For ground dwelling Scolytidae species composition from pitfall traps, the overall explained variance was 13.3%, towards which IPC1 contributed 8.6% and IPC2 an additional 4.7%. Hence, the principal components showed only a small, nonetheless significant correlation with the composition of island scolytid beetle assemblages. *Xylosandrus morigerus* (Blandford, 1894) (Sco4), *Xylonsandrus crassiusculus* (Sco5) and *Xyleborinus perminutissimus* (Sco10) were negatively associated with IPC1, hence occurring on islands with large and less isolated

islands. On the other hand, *Xylosandrus compactus* (Sco3) *Xyleborus affinis* (Sco7), *Cryphalus* spp. (Sco14) and *Coccotrypes* spp. (Sco15) showed a preference for more isolated islands and with close neighbouring islands (Figure 36c).

(a)
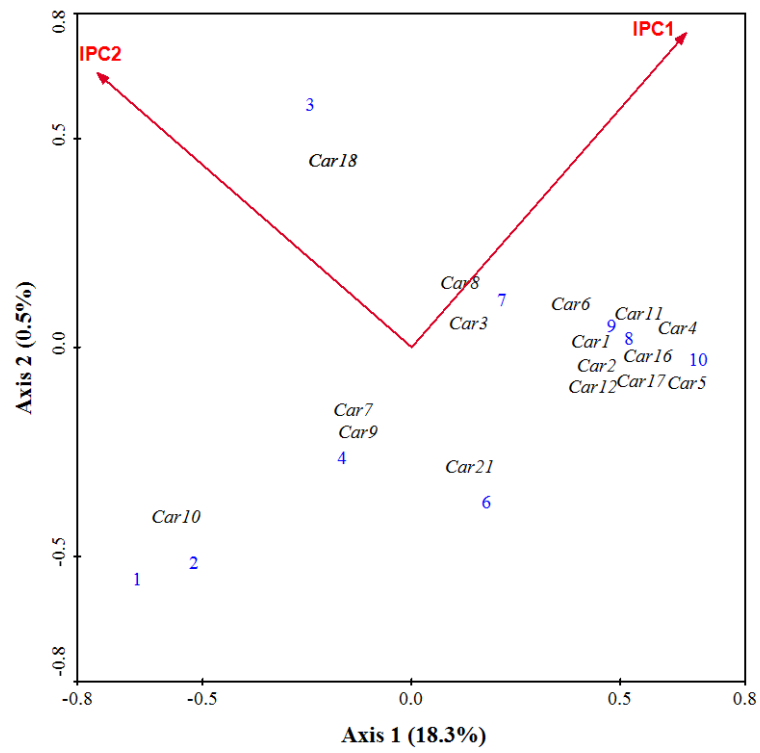
(b)
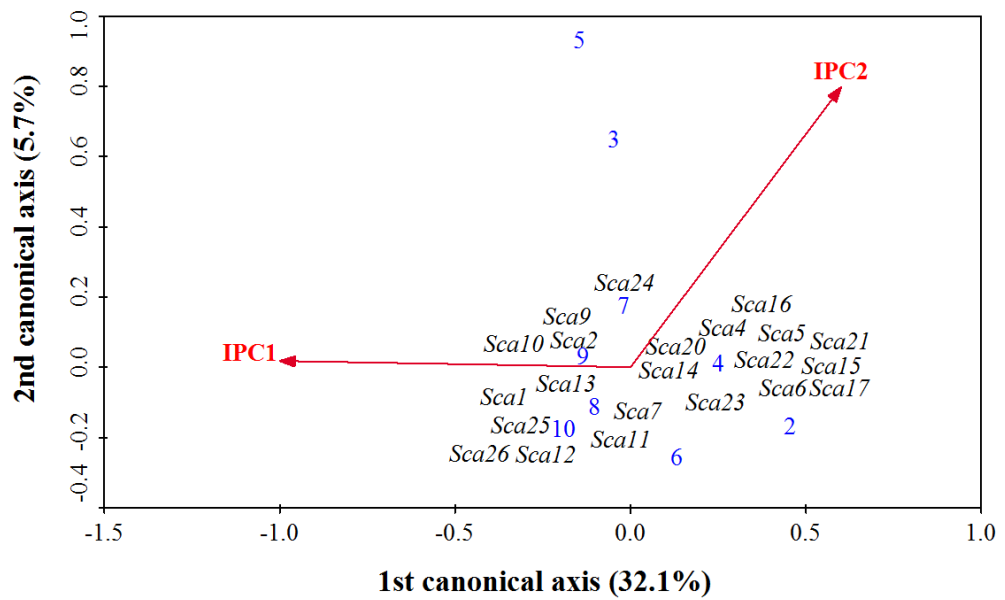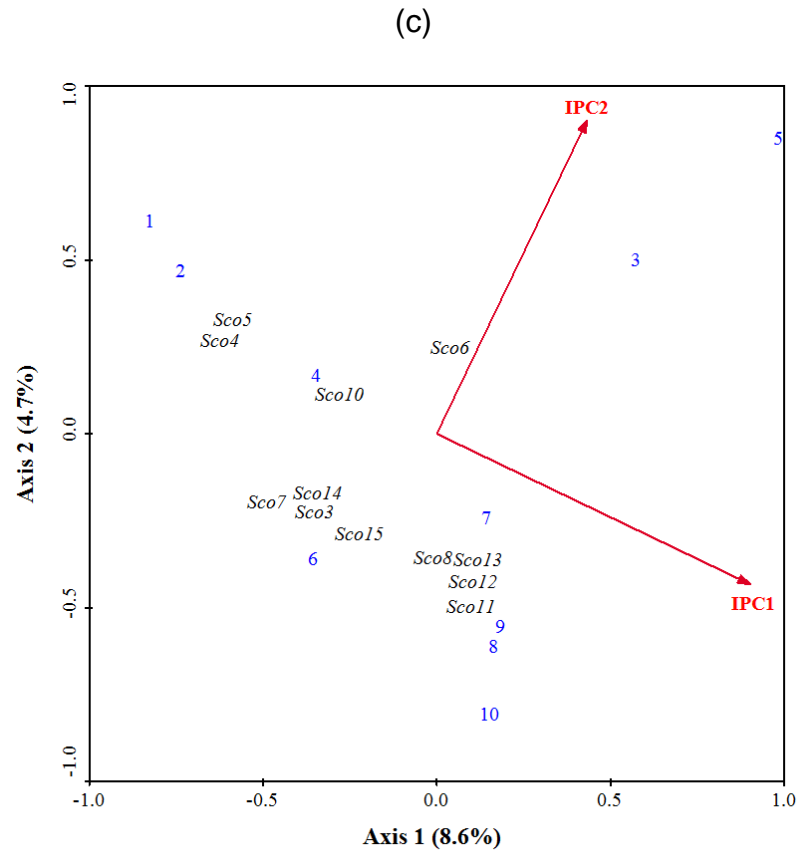
Figure 36 Ordination plots for the influence of island characteristics on beetle species composition on small islands of (a) Carabidae, (b) Scarabaeidae, and (c) Scolytidae from pitfall traps. Blue numbers indicate the studied islands.

From actively dispersed carabid species from FITs, with an overall explained variance of 52.7%, IPC1 contributed 41.4%, and IPC2 contributed 11.3%. *Tachyina* sp.2 (Car20), *Tachyina* sp.3 (Car21), and *Tachyina* sp.7 (Car25) were negatively associated with increases in the value of IPC2, hence occurring on more isolated islands. *Tachyina* sp.1 (Car19), on the other hand, was positioned in the middle between IPC1 and IPC2, indicating that the distribution patterns of these species might not strongly influenced by the environmental predictors. The rest of the carabid species showed a clear preference for larger but more isolated islands. (Figure 37a).

The distribution of dispersive scarabid beetle assemblages from FITs along the first axis was significantly correlated with IPC1 (33.2% explained variance). The second canonical axis was strongly correlated with IPC2 (17.1% explained

variance). Most Scarabaeidae species from FITs were negatively associated with increases in the value of IPC1, hence occurring on larger and less isolated islands. *Dynastinae* sp.1 (Sca2) and *Onthophagus* sp.3 (Sca11), however, showed a negative correlation with IPC2, hence occurring on more isolated islands and with neighbouring islands. Meanwhile, *Onthophagus* sp.1 and *Onthophagus* sp.5 (Sca9 and Sca13, respectively) were positioned in the middle between IPC1 and IPC2, indicating the distribution patterns of these species might not as strongly influenced by both IPCs (Figure 37b)

(a)
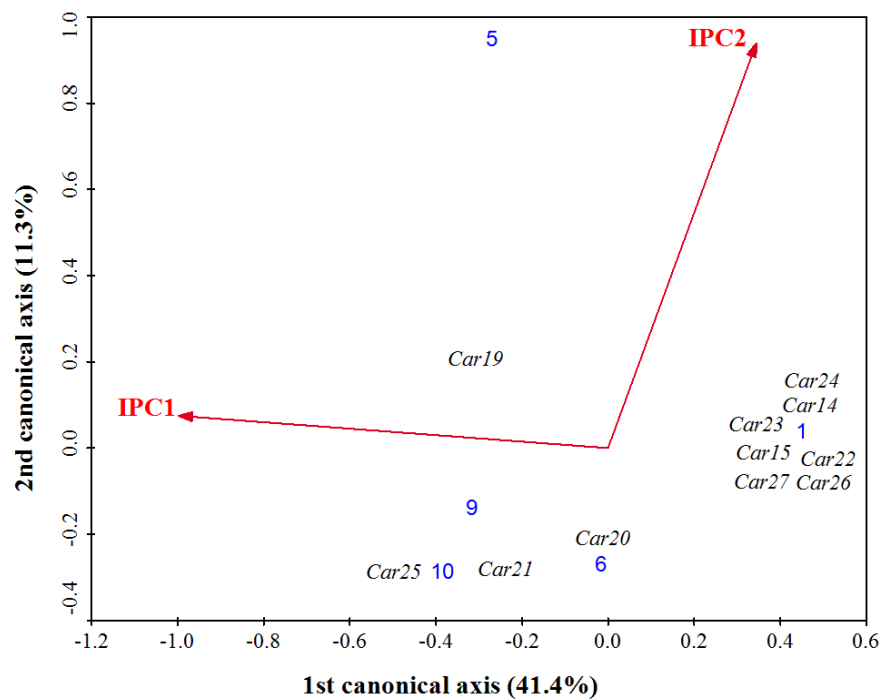
(b)
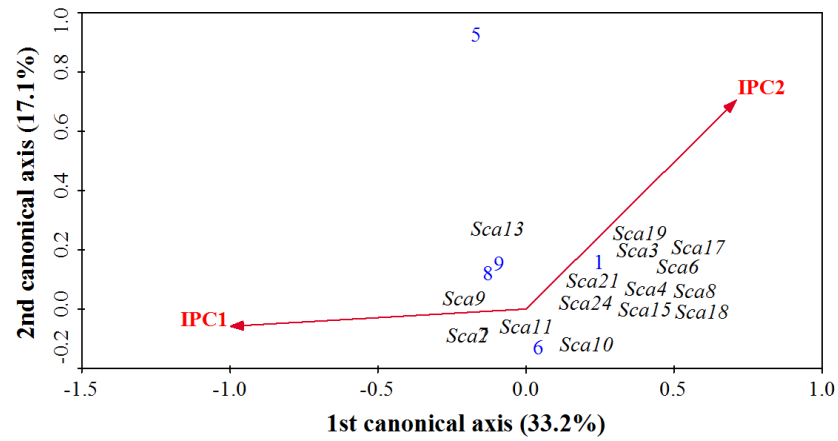
(c)
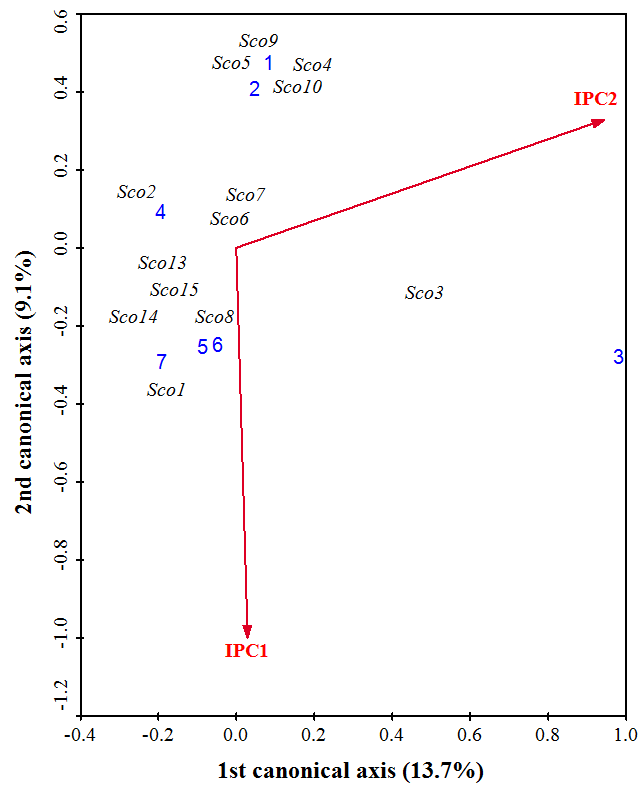
Figure 37 Ordination plots for the influence of island characteristics on beetle species composition on small islands of (a) Carabidae, (b) Scarabaeidae, and (c) Scolytidae) from FITs. Blue numbers indicate the studied islands.

The canonical correspondence analysis of actively dispersed scolytid species from FITs also included two IPCs. The two axes explained 13.7 and 10.1% of the total variance in the dataset. The IPCs have strong correlation with the composition of scolytid beetle assemblages. The first axis was correlated with IPC2, which was associated with distance to the nearest island and distance to Java. The second canonical axis was strongly correlated with IPC1. Scolytidae sp.1 (Sco1), *Xyleborus similis* (Sco8), *Hypothenemus* spp. (Sco13), *Cryphalus* spp. (Sco14), and *Coccotrypes* spp. (Sco15), showed a preference for small and more isolated islands. On the other hand, *Xylosandrus morigerus* (Sco4), *Xylosandrus crassiusculus* (Sco5), *Dryocoetiops coffeae* (Sco9), *Xyleborus perminutissimus* (Sco10), and to a lesser degree, *Xyleborus perforans* (Sco6), and Xyleborus affinis (Sco7) were negatively associated with IPC1, hence occurred on larger islands and positioned closer to Java. Meanwhile, *Xylosandrus compactus* (Sco3) was positioned in the middle between IPC1 and IPC2, indicating less influenced by both principal components (Figure 37c).

4.4 Discussion

4.4.1 The response of beetle diversity to variations in island size

Accordance to my hypothesis, island area proved to have a significant effect on the diversity of ground-dwelling beetles on the studied islands in Kepulauan Seribu Marine National Park. In models predicting beetle diversity based on the IPCs and individual parameters, this factor is also important in influencing the diversity of beetles. These results are also consistent with findings from previous studies that similarly revealed a significant link of species diversity patterns with island area for ants (Rizali et al., 2010), tenebrionid beetles (Fattorini, 2002; Fattorini and Fowles, 2005; Fattorini, 2011), terrestrial isopods (Sfenthourakis, 1996), centipedes (Simaiakis, 2006) and land snails (Mylonas, 1982; Triantis et al., 2005; Triantis, 2006).

The main, and most debated, explanation for the positive correlation between island size and species richness is that large islands generally contain more habitat diversity (Fox & Fox, 2000; Gillespie & Roderick, 2002; Triantis et al., 2005) compare to small islands. This theory is difficult to prove in the field

because habitat diversity and island size are strongly correlated (Yu and Lei, 2001), making it nearly impossible to distinguish the two. However, some of the largest islands in this study are dominated by single habitat (see Chapter 2 on Study Area). Thus, the results suggest that the correlation between island size and beetle diversity on the studied islands followed the classic island biogeography theory.

However, a study by Lomolino & Weiser (2001), which analysed a large number of studies on island faunas, including ants, beetles, and butterflies found that species richness tended to vary independently of the area for islands up to approximately 1 km^2. All islands surveyed during my study in Kepulauan Seribu Marine National Park are indeed much smaller (Table 1). On the other hand, Dengler (2009) argued that most studies, including Lomolino & Weiser (2001), which claimed to have detected a small island effect, used a statistically flawed approach. He further explained that deviating results reported in the literature can mostly be attributed either to methodological shortcomings or to the fact that authors actually studied area based SSRs (species sampling relationships) rather than real SARs (species-area relationships).

Whereas a SAR arises from several plots or geographic units (e.g. islands) of different sizes whose species richness is known with sufficient precision, a SSR yields only one value for a single plot with defined area but unknown species richness, from which random samples are drawn to achieve this goal (Dengler, 2009). Analysis of SARs aims to elucidate the relationship between area and species richness, and thus addresses a more fundamental question than that of SSRs (Gray et al., 2004a). SARs are more widely applicable, such as for extrapolation, establishing a common spatial gain for analyses, deriving β-diversity measures, and hypothesis testing (Scheiner, 2003). SSRs, on the other hand, really only address species richness in a precisely delimited area (total plot), a property that may be extremely costly or even impossible to measure directly in certain taxa that are difficult to observe (e.g. insects, soil microbes or marine benthos). Hence, the misinterpretations and terminological confusion around different types of SARs and their delimitation from species sampling relationships SSRs might therefore show that fundamentally different shapes of

species–area relationships for small islands are not proven and seem improbable.

Most studies concluded that the species richness of a region or area is the result of many processes acting across space and time. Island area has proved to be an important variable in explaining variation in island beetle species numbers in Kepulauan Seribu Marine National Park. However, it is clear that quantification of other factors, such as climate, habitat diversity, evolutionary history, that partially co-vary with the area, is necessary to model reliably and predict species number variations across insular systems on this archipelago.

4.4.2 Influence of different island isolation measurements on beetle assemblages

This study comprises of multiple island isolation metrics, not only because it cannot be captured in a single metric (McMaster, 2005; Borges & Hortal, 2009, Cardoso et al., 2010, Weigelt & Kreft, 2012), but also because different island isolation influence beetle diversity differently on islands in Kepulauan Seribu Marine National Park. This study also emphasizes that a variety of facets of isolations affect island colonization. Although the ordinary distance to Java or main source area in this study is an adequate and simple measure (Weigelt & Kreft, 2012), accounting for distance to the nearest island and mean distance to other islands has increased the explanatory power of isolation for beetle richness on the studied islands.

The results indicate that distance to Java and mean distance to islands within the radius of 5km were strongly linked to 1st IPC. Distance to the nearest island and, again, distance to Java were linked to 2nd IPC. Contradicting my hypothesis and previous studies (Johnson and Simberloff, 1974; McMaster, 2005; Cardoso et al., 2010; Weigelt & Kreft, 2012) which identified the important influence of distance to the nearest islands, this distance parameter is a poor predictor of beetle species richness in Kepulauan Seribu Marine National Park. In models predicting beetle diversity based on the IPCs and distance to the nearest island as an individual parameter, this factor is not significant in influencing the diversity of beetles.

Contradicting a study by Whittaker and Fernández-Palacios (2007) and Fattorini (2011), the results suggest that no 'stepping stone' processes were involved in determining beetle species richness on the studied islands and that islands between target and source areas did not decrease isolation. Direct dispersal and other mechanisms were probably the relevant immigration mechanism. The studied islands have different habitat (see Chapter 2 on Study Area), and species colonization depends on the favourability of island environmental conditions and suitable source areas (Steinbauer et al. 2012). Hence, the immigration process to the nearest islands might be more successful if this study used the nearest island with analogous habitats. The variations in distance of nearest-island might have affected the results, especially for beetle species with restricted long-distance dispersal abilities, for which the chance of immigration depends on the maximum distance to cross. A study by Weigelt and Kreft (2012) showed that the size of these neighbouring islands can be an important driver of island species richness as well. They found that large islands, as well as the mainland, serve as major sources for colonization and maintenance of species richness. The same study also showed that the absolute area of a potential source is more important than its size relative to the target island. All islands in this study are all less than 1km^2, hence can be classified as small islands (Lomolino and Weiser, 2001). Therefore, these results might also explain that small islands are less important sources of immigration, even for small target islands.

On the other hand, in models predicting beetle diversity based on the IPCs, both mean distance to islands within a radius of 5km and distance to Java are important in influencing the diversity of beetles. Distance to Java was also a significant predictor when a linear regression predicting beetle diversity was calculated based on this parameter as a predictor. The results indicate that the more remote the island is from Java, the more severe the sweepstakes route and the smaller the number of species that would successfully colonize and become established on the island. The validity of this isolation metric has been tested in the vast majority of studies (Case, 1975; Abbott, 1978; Chown, 1998; Alsos et al., 2007; Harbaugh and Baldwin 2007). Successful colonization over large bodies of water, however, is potentially easier for plants than for animals (Yu and Lei, 2001). Without having a mate to reproduce with, plants only require one fertile seed or spore to colonize a remote island. Also, some plants can withstand long

periods of seawater immersion (Yu and Lei, 2001) and successfully colonize remote islands. On the other hand, as beetles have, in general, limited ability to actively disperse over the sea (Qie et al. 2001; Lomolino, 2000b), immigration rates are expected to be very low. This results can also indicate that most beetle species have probably colonized the studied islands by other means, such as anthropogenic activities on the islands, or dispersal by birds. In Kepulauan Seribu Marine National Park, anthropogenic activities are mainly in the forms of permanent settlement on islands and tourism. As humans travel in and out these islands, different species might have been intentionally and inadvertently introduced into new ecosystems. Many island species are particularly vulnerable to biological invasions due to their isolation and limited space. Moreover, some islands of this archipelago have been the target for habitat loss, fragmentation, and degradation primarily for settlement and tourism reasons (S. Puspitasari, pers. obs.). Such habitat destruction not only directly damages the island flora but also reduces the faunal biodiversity. As forested areas are diminishing, suitable habitats and food resources for fauna, such as beetles, also disappearing.

The significance of mean distance to islands within a radius of 5km shows that clustered island groups make dispersal possible for species, which are not capable of extraordinary long-distance dispersal. This is an indication of successful migration among islands within island groups was high. This result partly contradicts the prediction by Hanski & Gyllenberg (1997) and Nieminen & Hanski (1998) where scattered islands accumulated actively dispersing species quicker than islands close to each other. The proportion of large islands or landmass within the island cluster is also important. A study by Diver (2008) suggested that the optimal buffer radius for measuring isolation depended on the spatial scale of the study. For this study, mean distance within the defined radius of 5km around the target island can thus be quantified as an important factor to influence beetle species diversity.

Another factor to consider in interpreting these results is that isolation effects interact with species-specific dispersal properties (Lomolino, 1982; Weigelt and Kreft, 2012). Species differ strongly in their immigration and extinction rates (Yu and Lei, 2001). My analysis did not specifically integrate dispersal or population traits of the individual beetle species, not least since this information is widely

lacking for many species. Smaller beetle species, which are bad competitors but good colonizers due to high dispersal abilities, might also have difficulties establishing themselves on islands close to the coast characterized by a higher proportion of larger species, which are better competitors but are not able to colonize more isolated islands due to their low dispersal abilities. Some beetle taxa might also be poor island colonizers and, therefore, are often totally absent even on islands located in close vicinity of nearby larger landmasses, where they can occur in high abundances. For example, no hydrophilid beetles were recorded in Kepulauan Seribu Marine National Park in this study, although several species occurred in Java (see Appendix 1, Chapter 3). This result might be explained by the lack of fresh ground water sources, such as rivers, streams or lakes, on the studied islands (S. Puspitasari, pers. obs). Several beetle species from the genus *Onthophagus* (Scarabaeidae) were also only recorded in Java. Low dispersal abilities of these dung beetle species (Da Silva and Hernandez, 2014), and resource availability (Simmons and Ridsdill-Smith, 2011) might have caused difficulties in establishing persisting populations of these beetles on small islands. Their close association with specific habitat types – the number of some dung beetle species and their abundance was significantly higher in primary forest than another habitat (Gardner et al., 2008; Hernandez and Vaz-de-Mello, 2009; Da Silva et al., 2013) might as well explain their lack of appearance on small islands such as the ones investigated in Kepulauan Seribu Marine National Park.

Although they are part of Kepulauan Seribu Marine National Park, some of the studied islands were also a tourist destination, including the furthest island, Putri Barat. Busy and continuous traffic and visitors hopping from one island to another might have dampened the effects of island isolation. Finally, with no comparative studies on beetles in this area, and with limited information on beetles in Indonesia, only a portion of the information on specimens is available up to species level. Hence, there is limited information on activities, immigration ability, and habitat preferences of beetles on the studied islands.

4.4.3 Biogeographic patterns of beetles in Kepulauan Seribu Marine National Park

A positive relationship exists between island size and island beetle species richness in Kepulauan Seribu Marine National Park. The observed trends have also been reported by Fattorini (2011), who found that island area was important for the beetle composition on a given island. Within the ground-dwelling beetles that were chiefly recorded in the pitfall traps, IPC1 and therefore Island area were strongly influenced the actual composition of beetles from the family of Scarabaeidae, Carabidae, Scolytidae, Curculionidae, and Scydmaenidae. For Carabidae beetles, this pattern might be explained because most carabid species are generalist predators (Lovei and Sunderland 1996). Hence, they are more active in their foraging. Moreover, carabids are, in general, poor fliers and the direction of airborne dispersal is highly influenced by wind direction (Lindroth 1985; As 1984). Therefore, the flight may not be needed for carabids, and instead may be able to use energy reserves directly, and immediately, for survival and reproduction (Kotze, 2008) once an island is reached. At the same time, species representative from the family Nitidulidae, Carabidae, Anthribidae, Tenebrionidae, Curculionidae, and Chrysomelidae occurred on islands located remotely from other islands but closer to Java. Although these species occurred on islands near Java, where anthropogenic gene flow can be a significant risk (Davies et al., 2007; Grobler et al., 2011), they were not recorded in Java (see Appendix 1). Hence, they are unlikely to be introduced species. Moreover, beetle habitat preference may lead to different faunal composition, such as the absence of natural predators, affecting the overall beetle compositions. Some islands near Java, such as Rambut Island, have a very different habitat. For some of the flightless beetles, habitat preference can also explain the way they migrate. For example, beetles that occur mainly on vegetation (Chown 1998), such as Curculionidae and Chrysomelidae, are more likely to be transported by birds than beetles on rock surfaces that hide in crevices in the rocks (Grobler et al., 2001).

Meanwhile, the dominance occurrence of actively dispersing beetle species from family Nitidulidae, Scolytidae, and Scarabaeidae, recorded in the FITs on small and isolated islands, shows their adaptive and successful approach in colonising remote islands. For bark beetles, their habitat consists mostly of dead wood and

similar materials, and the "area" they can use as habitats are strongly bound by the available dead wood material suitable for feeding and reproduction (Stevens et al., 2006). Moreover, logs and dead trees, which mainly came from Java, but potentially also from other islands, might drift and land on some of the remote islands in the archipelago.

When focusing on carabid beetles, ground-dwelling carabids had a wide distribution on the studied islands. Most carabid beetles are generalist predators (Lovei and Sunderland 1996), although they can be classified into specialisation (Kotze and O'Hara 2003), and habitat association categories (Lindroth 1985, 1986). Poor disperser carabids may also be relatively good survivors (Kotze et al., 2000; Zalewski and Ulrich 2006), as flightlessness is often a trait selected for on islands. Moreover, this characteristic might have been influenced by different breeding type and fecundity (Niemela, 1988a, 1988b; Desender, 2000; Zalewski and Ulrich, 2006) that are of considerable importance in explaining the distribution of carabid species on islands. Actively dispersed carabids from FIT, however showed a higher occurrence on more isolated islands, and most of these species, such as *Tachyina* sp.2 (Car20), Tachyina sp.3 (Car21), and *Tachyina* sp.7 (Car25), were not recorded in Java (see Appendix 2). With strong selection for dispersal ability in island populations and selection against dispersal in Java, one can presume that island population dynamics of dispersive carabid beetles is more dependent on migrants originating from islands rather than Java. Nieminen and Hanski (1998) and Hanski et al., (2006) favoured a similar argument in explaining regional distributions of moths and butterflies. Moreover, species from higher trophic level, such as carabids, are often more sensitive to environmental changes (Zou et al., 2015). It is possible that islands closer to Java experiencing higher environmental disturbances than isolated islands, hence affecting the carabids species assemblages on islands.

On Scarabaeidae beetles, the result was in line with study from dung beetle studies in fragmented tropical forests where species richness is positively correlated with area (Klein, 1989; Andresen, 2003; Feer & Hingrat, 2005; Qie et al., 2011). However, Qie at al. (2011) found that, below 35.8 ha, area became unimportant for scarabids and isolation, and the relative amount of forest edge had a strong positive effect on species richness. It is possible that other

geographical and environmental characters, including dung burial and nutrient recycling (Horgan, 2005; Slade et al., 2007; Yamada et al., 2007), secondary seed dispersal (Feer, 1999; Andresen, 2003), biological control (Fincher, 1973; Gronvold et al., 1992; Nichols et al., 2008), and the absence of mammals on the islands (S. Puspitasari pers. obs.) might have also affected the outcomes of this study.

The influences of IPC2, which is strongly linked to the distance to the nearest island, are not strong for scarabids distribution patterns from both pitfall traps and FITs. The relative flight abilities of different dung beetle species are poorly known. It was suggested that there are two forage-flight patterns in dung beetles: large-bodied dung beetles tended to fly rapidly and continuously for long distance, while small-bodied species perched on leaves (Qie at al., 2011) and occasionally fly for short distances (Larsen et al., 2008). The question here was, however, not only whether the dung beetles can, but also whether they will fly across the open water between the islands. In a study by Qie et al. (2011), floating pitfall traps were used and found that dung beetle captures declined significantly and sharply from exposed soil bank to water. On the other hand, this study found less isolated islands harbour more species, which provides indirect evidence for differences in the dispersal ability among dung beetle species. Hence, source–sink dynamics may exist between neighbouring sites for species that cross the water barrier.

The significance of both IPCs was also found in scolytid beetle assemblages, especially for actively dispersed Scolytidae beetles collected from FITs. In general, most scolytids live in temporary habitats and are more dispersive than species occupying permanent habitats. Hence, migration is essential to their success (Langelotto and Denno, 2001). Most of the studied islands in Kepulauan Seribu Marine National Park have been swamped by dead wood or dying materials from Java (S. Puspitasari, pers. obs.). Scolytids normally use these materials for their reproduction (Johansson, 1994) and they fly over large areas in their search for host materials. Hence, the size of the island is an important factor affecting scolytid beetles.

Some ground-dwelling scolyid species recorded from pitfall traps occurred on the smaller island. This finding contradicted study by Rigby and Lawton (1981) who

found that for bark insects and some other herbivore insect taxa, the island area was not a significant factor in influencing the species assemblages. In this study, *Hypothenemus* spp. was one of the species occurred on the smaller island. This species is usually associated with disturbed habitats (Wood and Pullin, 2002) and often able to breed in a variety of microhabitats, under bark, in the pith of twigs, in seeds and fruits. This species is also able to do so in a wider range of hosts and range of environmental conditions than most Scolytidae beetles. These characters help to explain the wide distribution of some of the species in the tropics, and the ease with which they can be introduced into new areas (Beaver & Maddison, 1990). Thus, the preferences of this species to live on the smaller island is probably also related to other factors, such as anthropogenic disturbance and introduced species.

4.4.4 Synthesis

Overall, results in this chapter clearly indicate that island area and distance to Java proved to have significant effects on the diversity of beetles on islands in Kepulauan Seribu Marine National Park. To substantiate these conclusions and establish if these explanations follow the classical Island Biogeography Theory, further quantification of other factors, such as climate, habitat diversity, evolutionary history, that partially co-vary with the area, is necessary to model reliably and predict species number variations across insular systems on this archipelago. Additional analysis of anthropogenic activities on islands could explain whether they can influence the effects of island isolation. More studies on beetles on islands in Indonesia would also allow a better understanding of information on activities, immigration ability, and habitat preferences of beetles on the studied islands with different size and isolation.

Chapter 5. Influence of settlements and human activities on small island beetle biota

5.1. <u>Introduction</u>

The negative impacts of large-scale, anthropogenic habitat alteration on islands have long been known (Soulé and Orians, 2001; Brooks et al., 2002; Chown et al., 2005). Fragmentation, alteration, and destruction of habitat caused by human activity have resulted in the extinctions of native species on many islands (Chown et al., 2005; Brooks et al., 2002). Humans also alter island diversity by introducing non-native species (Lonsdale, 1999; McKinney, 2002). Most of the introduced plant and especially insect species appear to have reached islands accidentally (Chown et al., 1998). It is widely assumed that at global scales, these species introductions will ultimately exacerbate the reduction in diversity precipitated largely by other human activities (Sax et al., 2002).

However, at local and regional scales, the impacts of exotic species on diversity varies with both taxon and region McKinney, 2002; Sax et al., 2002; Duncan et al., 2013). In many cases, it appears that diversity increases with the introduction of non-indigenous species (Rosenzweig, 1995; Davis, 2003; Chown et al., 2005). It's also found that both indigenous and exotic species respond similarly to environmental heterogeneity (Stohlgren *et al*., 2003; Hawkins *et al*., 1999), and high diversities of native and non-native plant species were compatible with one another (Thomas and Palmer, 2015). There is empirical evidence that widespread non-native species can play an important role in maintaining ecosystem functions, such as pollination (Pattemore and Wilcove, 2012**),** with such roles needing to be assessed when planning invasive species control or eradication programmes.

At Kepulauan Seribu Marine National Park, most of the islands are now forming the focus of an intense debate. There are considerable grounds for their conservation, as the preceding observations indicate. However, there is high demand for tourism on these islands, with associated land use changes and the associated potential for targeted and accidental new alien species introductions

(Rizali, 2010). This study identified three main habitats on the studied islands, undisturbed forest on uninhabited islands, disturbed forest on islands with mixed forest and human settlement, and settlement areas themselves. This chapter therefore looks at how anthropogenic disturbances and altered habitats link to the composition of the beetle assemblages on small islands. With the impacts of introduced non-native species, and environmental heterogeneity, it was hypothesised accordingly that islands with settlements are expected to have higher species richness.

Beetles can serve as powerful and reliable ecological indicators, as they present characteristics such as rapid response to environmental changes, short life-cycles, high abundances and wide distributions in a broad range of habitats, they fulfil numerous and highly diverse ecological functions, and can be easily, and cost-effectively sampled (Brown 1997; McGeoch 1998; Pearce & Venier 2006; Barlow et al. 2007; Gardner et al. 2008; Uehara-Prado et al. 2009). On islands, beetles have also been used to see the effects of human and habitat fragmentation caused by anthropogenic activities (Davis, 1994; Fox et al., 2006; Davidson et al., 2011). A study on carabid beetles (Coleoptera, Carabidae) on the Aland Islands, SW Finland found that most of the species were found in low numbers outside each preferred environmental type. The number of species and species diversity was highest in cultivated habitat and lowest in forests, suggested that forest habitat on the islands do not support a high diversity of adult carabids (Niemela and Halme, 1992). Another study showed how the New Zealand dung beetles have evolved a generalist diet of dung and carrion to persist in indigenous ecosystems despite the decline of native birds and the introduction of many mammal species (Stavert et al., 2014).

However, while overall species richness is often increased following invasions by alien species, habitat specialists often suffer as a result. In their study in Kepulauan Seribu Marine National Park, Rizali et al. (2010) found that there were ant species that did not seem to tolerate any form of human disturbance. Some ant species for example were found only on Rambut Island, the largest undisturbed forested island. This underscores the problematic role of human disturbances and highlights the importance of protected areas in preserving the diversity of species-rich invertebrate faunas. Accordingly, I hypothesize that

forest habitats on undisturbed forested islands will harbour more unique and distinct beetle faunas, containing species that only occur in this particular island setting.

When potential food is scarce and habitat areas are shrinking, generalist traits are likely to be advantageous. Highly varying degrees of specialisation to both food and habitat has been documented in beetles (Wirta et al., 2008; 2010). This has been studied on dung beetles (Hanski, 1991; Davies et al., 2005). In this group, although mammal dung comprises the major food source for many dung beetle species, diverse arrays of non-mammalian dung and non-dung-based diets have been recorded. Feeding trials confirmed that *Saphobuis edwardsi* (Scarabaeidae: Scarabaeinae) was generalist dung and carrion feeder (Stavert et al., 2014) and displayed preferences for avian omnivore dung, mammal carnivore and omnivore dung and avian carrion. The study by Stavert et al. (2014) also suggested that some *Saphobius* species were trophic generalists, with nitrogen isotope enrichment values that span several trophic guilds. In marine carrion feeding trials, *S. edwardsi* were found in decomposing squid indicated the consumption of squid and suggested that dung beetles may have been involved in the flow of nutrients from marine to terrestrial forest ecosystems.

In addition to generalists, some species commonly encountered in open habitats often seem to occur in a wide range of other habitats, too, albeit in low numbers (Niemela and Halme, 1992). The same pattern was also reflected by a study of Warren-Thomas et al. (2014), who found low number of habitat generalist carabid species in forest ecosystems. The reverse patterns have also been observed for some forest species' occurrence in open habitats. Some forest species for example appear able to breed in shaded overgrown cultivations, but many specimens found in fields and pastures were possibly only transients from surrounding forest (Niemela and Halme, 1992). Generalist species on islands have been introduced by human (Vitousek et al., 1996; Thompson, 1998; Fox et al., 2006). These species will be very likely to increase on islands with human settlements. Therefore, I hypothesize that when comparing disturbed forest habitats in mixed forest and settlement habitat islands with undisturbed forest habitats, the former will contain a larger proportion of generalists.

The ecological and evolutionary processes that influence host range evolution, facilitating host shifts in some species but preventing host shifts in others, are poorly understood. The top insect predators, including beetles, were often seen as generalists that will prey on nearly all other invertebrates, including each other (Bay, 1974; Batzer and Wissinger, 1996; Klecka and Boukal, 2012). However, this traditional view must be revised, because diets of predatory beetles in different habitats might vary from highly specialized to broadly general (Klecka and Boukal, 2012). Human activities have caused many species to expand their ranges (Pitelka, 1997; Fox et al., 2006), and humans have introduced organisms into many new and often novel environments (Vitousek et al., 1996) that influence host ranges (Thompson, 1998). For example, plants introduced to new localities are often colonized by local herbivores, providing an opportunity for diet expansion and shifts onto new hosts (Tabashnik, 1983; Thomas et al., 1987; Bowers et al., 1992; Carroll and Boyd, 1992; Fraser and Lawton, 1994; Leclaire and Brandl, 1994; Fox et al., 1996; Fox and Fox, 2000).

However, the high dependence of herbivorous insects on their host plants implies that plant invaders can affect these insects directly, by not providing a suitable habitat, or indirectly, by altering host plant availability (Almeida-Neto et al., 2011). The same study also found negative effects of land use intensity on the species richness and taxonomic diversity of the insect herbivore assemblages. These effects were mediated by an increase in the proportion of exotic host plant species. A likely implication of such reduction in the species richness and taxonomic diversity of the insect herbivore assemblages is the accelerated loss of specialized plant-herbivore interactions, thus favouring interactions among generalist species and the biotic homogenization of species interactions across human-disturbed habitats. My final hypothesis is therefore that human settlements on islands will affect different beetle feeding guilds differently. However, herbivorous beetles will be more strongly affected because of the presence of human settlements

5.2   <u>Methods and data analysis</u>

This chapter was based on the entire set of study plots. As indicated in chapter 3, this represented a total of 70 pitfall sampling plots and 11 flight interception plots located on the 10 islands in Kepulauan Seribu Marine National Park. The islands' dominant land covers were classed into three types of habitat, widely undisturbed forest encountered on uninhabited islands, disturbed forest on islands with human settlements and settlement areas themselves.

This study used forest cover as one of the environmental parameters to reflect the level of habitat changes on the studied islands, which were originally shrub forest and lowland forest, before human arrivals (FWI/GWF, 2002). The information on the size of forest cover were generated using Google Earth-Pro measurements. Data on human populations were provided by the authorities of Kepulauan Seribu Marine National Park. (Table 7).

Table 7 Island habitat characteristics, human population and forest cover of the 10 studied islands of the Kepulauan Seribu Marine National Park, Indonesia.

Island	Human Population	Forest cover (ha)	Habitat		
			Settlement	Disturbed Forest	Mature forest
Rambut	1	44.72			X
Untung Jawa	1698	0	X		
Bokor	1	15.74			X
Lancang Besar	1554	6.11	X	X	
Damar Besar	3	25.21			X
Pramuka	1004	0	X		
Kotok Besar	50	17.01	X	X	
Opak Besar	0	9.74			X
Pemagaran	11	13.99			X
Putri Barat	2	8.84			X

As mentioned in chapter 4, the abundance of all beetle species were pooled based on the type of trap. Specimens from baited and non-baited pitfall traps on

each island were combined and represented island's pitfall trap specimens (PT). Specimens collected by flight interception traps on each island were combined to represent island's flight interception trap specimens (FIT). All specimens that were identified to species and morphospecies level will be called "species" in the following. Beetle species encountered in settlement habitats and in both or either undisturbed forest and disturbed forest habitats, were classed as generalists. Settlement specialists were beetles species found only in settlement habitats. Meanwhile, beetle species found in either or both undisturbed and disturbed forest habitats were classed as forest specialists. Individual-based rarefaction was use to compare the α-diversity of beetle species on each island. This was further underpinned by measures of exponential Shannon diversity (Jost, 2006) and Simpson's diversity indices (Simpson, 1949).

For the analysis of species turnover patterns between sites and habitat, chord-normalized expected species shared (CNESS) dissimilarity matrices (Trueblood et al., 1994) were calculated. The CNESS matrices can be calculated for different sample sizes via changes of the sample size parameter m. The resulting matrix either puts a strong focus on dominant species when low figures are selected for m or on the composition of the entire community for large numbers of m. The matrix for $m=1$ as well as for $m=$number of individuals in the least well-sampled plot (m=30 for beetles in this study) as the largest common sample size were calculated. Non-metric multidimensional scaling (NMDS) of the CNESS matrices was subsequently used to visualize the species turnover patterns between islands with different habitat. To evaluate how well the particular configuration reproduces the distance matrix, a stress value is provided. The smaller the stress value, the better is the fit of the ordination plot to the observed distance matrix (Clarke, 1993). Practical experience suggests the following rule of thumb for interpreting Kruskal's (Kruskal and Wish, 1978) stress (formula 1): stress <0.05 gives an excellent representation with no prospect of misinterpretation; stress <0.1 corresponds to a good ordination with no real risk of drawing false inferences; stress <0.2 can still lead to usable representations, although for values at the upper end of this range there is potential to misleading impressions; stress >0.2 is likely to yield plots which could be dangerous to interpret (Clarke, 1993).

Multiple linear regression models with stepwise forward selection were employed to measure the influence of forest cover and human population on beetle diversity. Beetle variables included the rarefied number of beetle species, Exponential Shannon diversity index, and Simpson's diversity index.

Multiple linear regression models with stepwise forward selection and nonmetric multidimensional scaling (NMDS) were calculated using SPSS version 22. I calculated a dissimilarity matrix based on CNESS (chord-normalized expected species shared) indices using the COMPAH (Combinatorial Polythetic Agglomerative Hierarchical Clustering) program. All other calculations and statistical analyses were carried out in R language version 3.1.2 (R Development Core Team, 2011) with the use of 'vegan' and 'gplots' packages (Oksanen et al., 2012).

The identification of beetle feeding guilds was conducted at the Museum of Natural History in Oxford. Species were compared and evaluated with help and assistance by Darren J. Mann, Head of Life Collection at the museum. Beetle species were placed in different feeding guilds of herbivores, predators, fungivores, saprophages and coprophages, necrophages and saproxylic species. Beetle species that could not be assigned to a feeding guild because of a lack of definitive data or a broad range of feeding guilds were identified based on dominant feeding guilds on family level.

5.3. Result

5.3.1. α-diversity

In general, islands with settlements harboured the highest number of observed beetle species. In pitfall trap samples, the highest number of beetle species was observed on Untung Jawa, Pramuka, and Lancang Besar settlements, with 51, 37, and 32 species, respectively. On the other hand, Putri Barat has the lowest number with only 11 observed beetle species. Rarefaction curves showed a similar pattern to the observed specie richness for pitfall traps, with Untung Jawa being more diverse in the number of beetle species (Figure 38a).

Similar results were also recorded from FITs, with Untung Jawa and Pramuka harbouring the highest number of species at 56 and 43, respectively. The lowest number from FIT samples was recorded on island dominated by undisturbed forest, Opak Besar, with only 5 species. The similar patterns were also showed by rarefaction curves (Figure 38b)

(a)

(b)
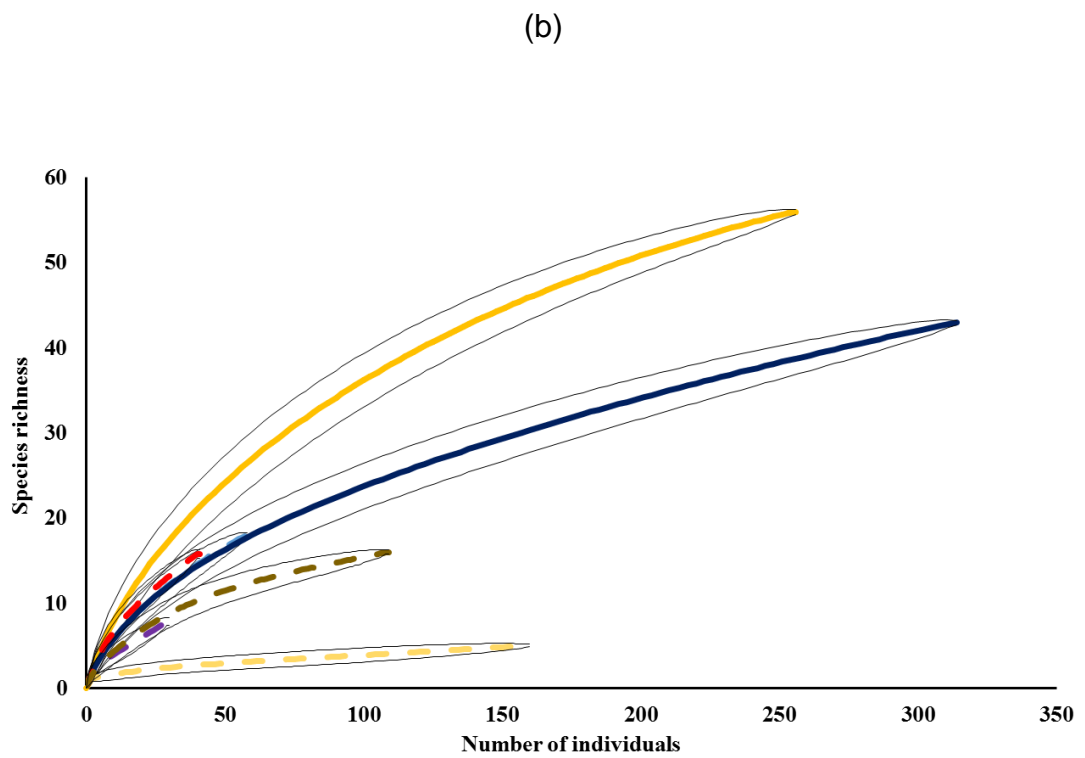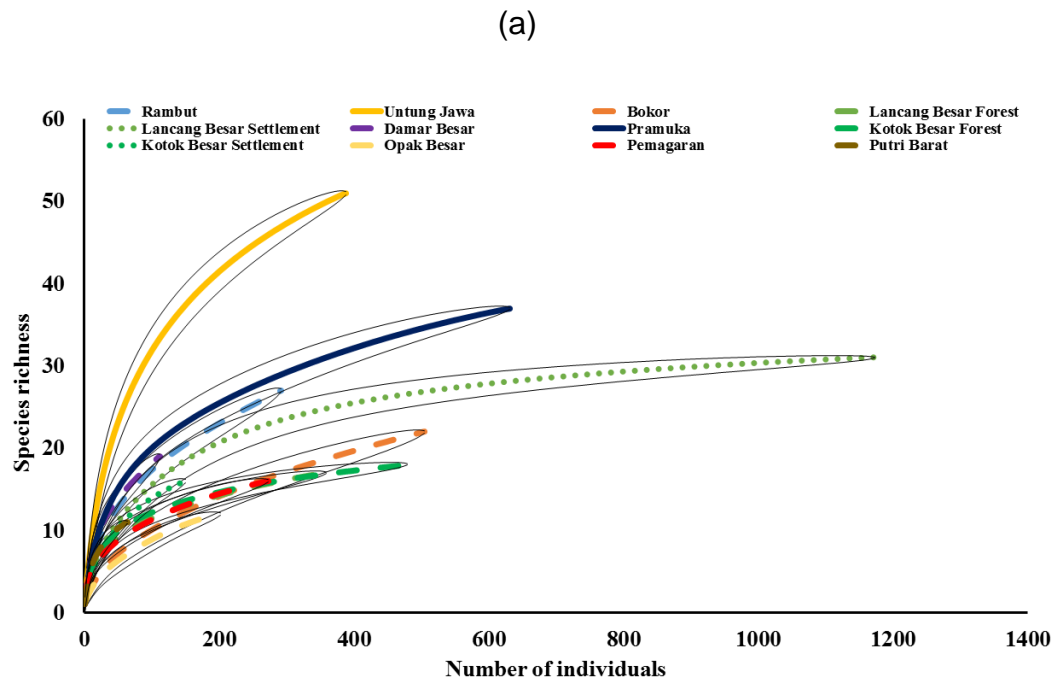
Figure 38 Rarefaction curves of beetle species richness on the studied islands from (a) pitfall traps and (b) FITs (black lines represent 95% confidence intervals)

On the number of recorded generalist beetle species from pitfall traps, settlement dominated islands, Untung Jawa and Pramuka, and settlement habitat on mixed habitat island of Lancang Besar, harboured the highest number of 22 generalist species. This was followed by 2 forest-dominated islands, Rambut and Bokor, with 17 and 15 generalist species, respectively. Islands with undisturbed forest habitat, Putri Barat and Opak Besar, harboured the lowest recorded number of generalist species, with 5 and 9 species, respectively. Rarefaction curves again showed a similar trend to the observed species richness (Figure 39a).

Similar patterns were also found from FITs, where settlement-dominated island of Untung Jawa and Pramuka harboured the highest observed generalist beetle species, with 15 species. The lowest number was observed on Opak Besar, with 4 generalist beetle species. Similar trends were shown by rarefaction curves (Figure 39b).

(a)

(b)
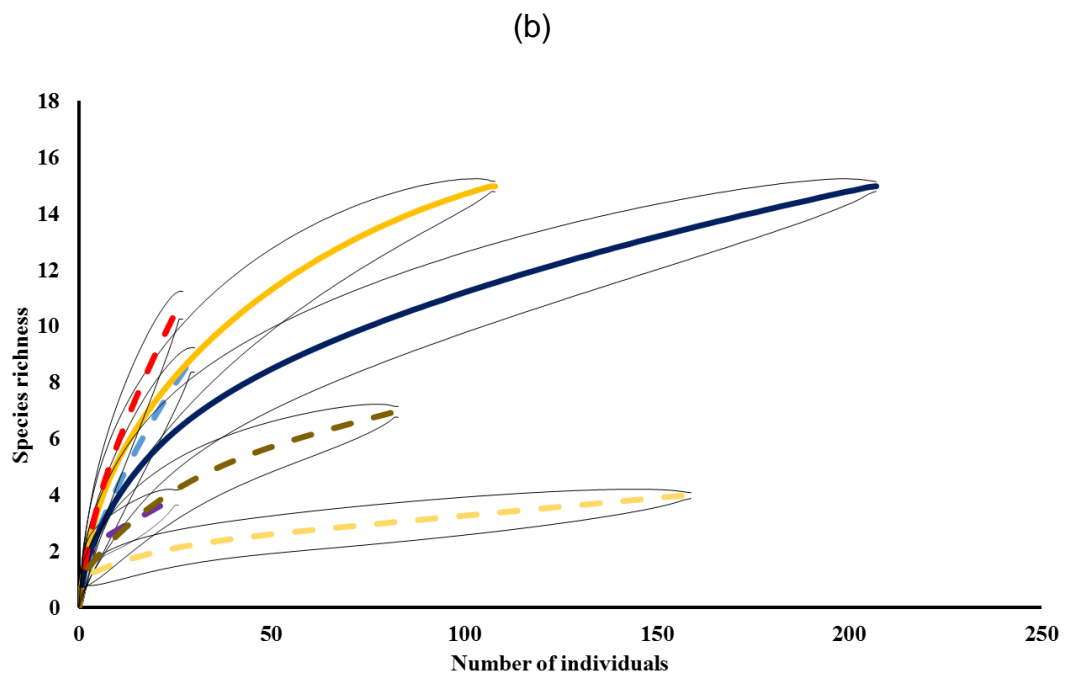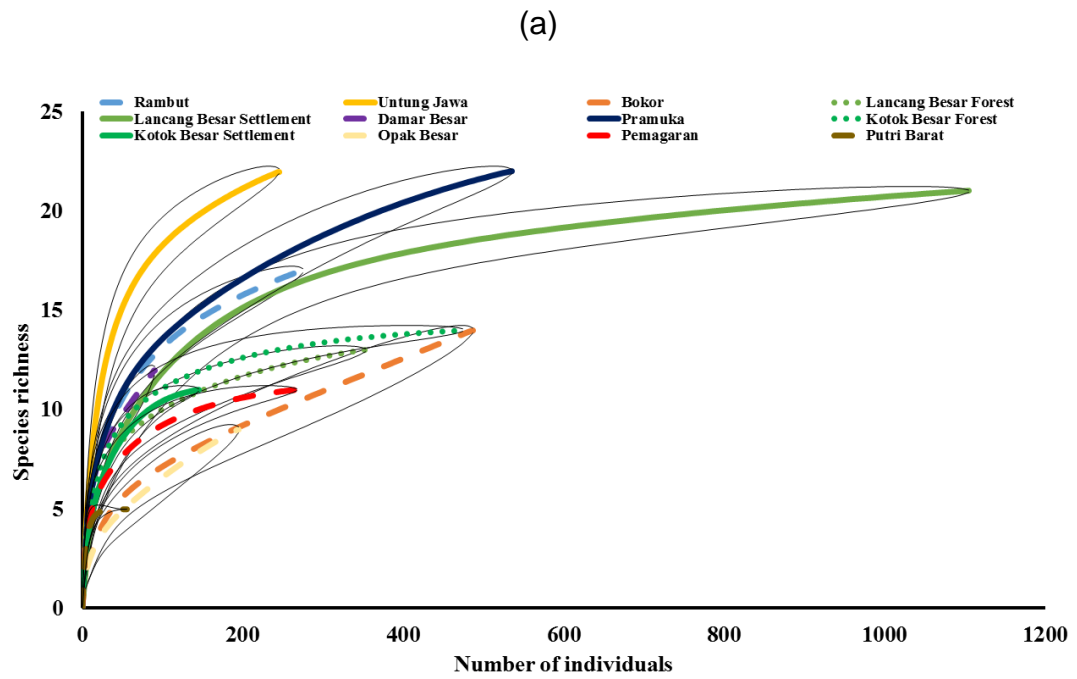
Figure 39 Rarefaction curves of generalist beetle species richness on the studied islands from (a) pitfall trap and (b) FITs (black lines represent 95% confidence intervals)

For the observed forest specialist beetle species from pitfall traps, the island with undisturbed forest habitat, Rambut, harboured the highest number of forest specialist species, with 10 species. It is followed by Bokor and Damar Besar, with 7 forest specialist species on each island. Rarefaction curves showed a slightly higher number of forest specialist species on Rambut and Bokor Island (Figure 40a). Meanwhile, the results from FITs also showed that the highest number of forest specialist species was recorded on islands with undisturbed forest habitat, Rambut and Putri Barat, with 9 species on each island. On the other hand, only 1 forest specialist species was recorded on Opak Besar Island. Rarefaction curves showed marginally lower number on the three islands above (Figure 40b).

(a)

(b)
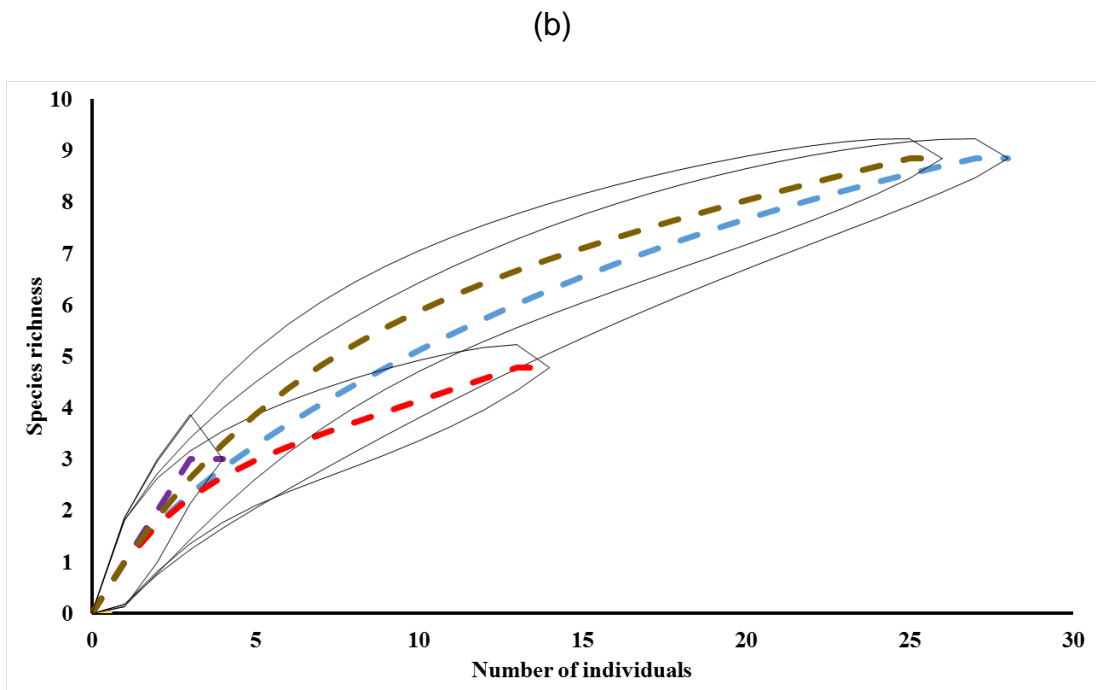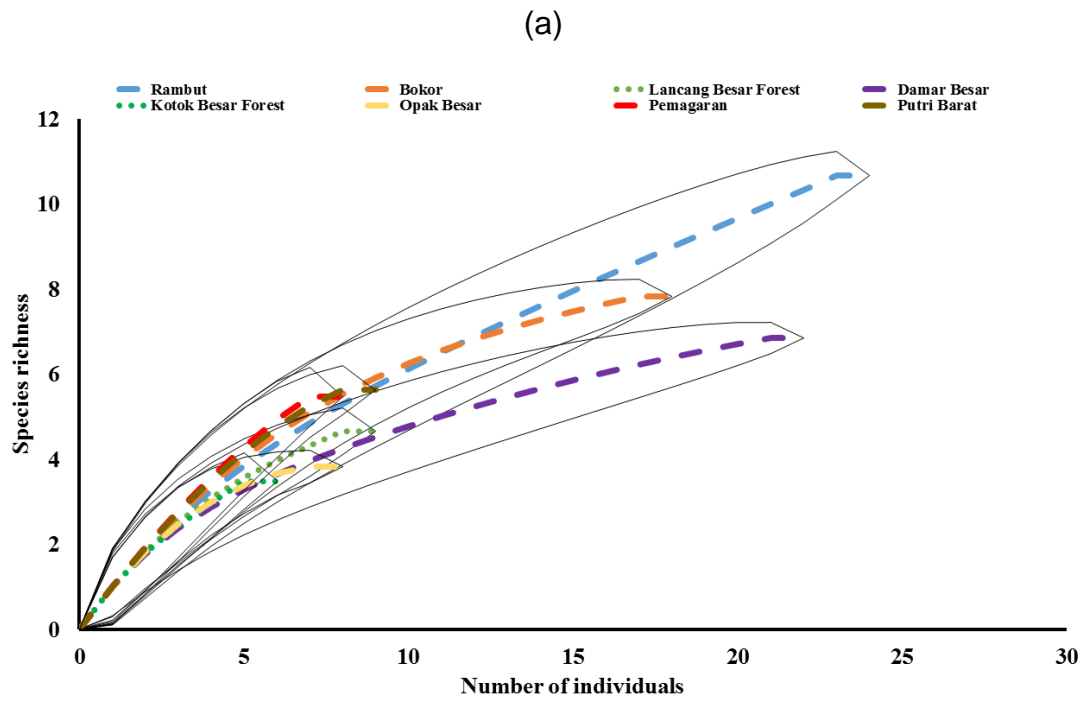
Figure 40 Rarefaction curves of forest specialist beetle species richness on the studied islands from (a) pitfall traps and (b) FITs (black lines represent 95% confidence intervals)

Among the settlement-dominated islands from pitfall traps, Untung Jawa harboured the highest settlement specialist with 29 species. The lowest number was recorded on a mixed habitat island, Kotok Besar, on its settlement habitat with only 3 species. Rarefaction curves showed a slightly higher number on Untung Jawa and Kotok Besar Island (Figure 41a). From FITs, Untung Jawa and Pramuka harboured 41 and 28 settlement specialist species, respectively. Similar trends were shown by rarefaction curves (Figure 41b).
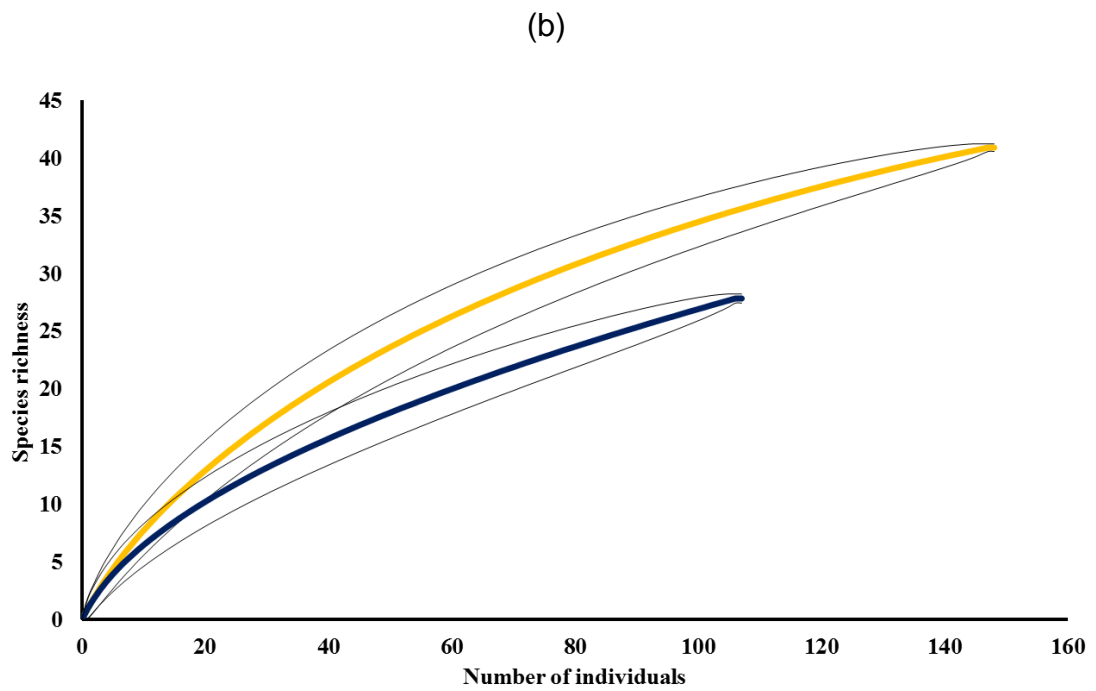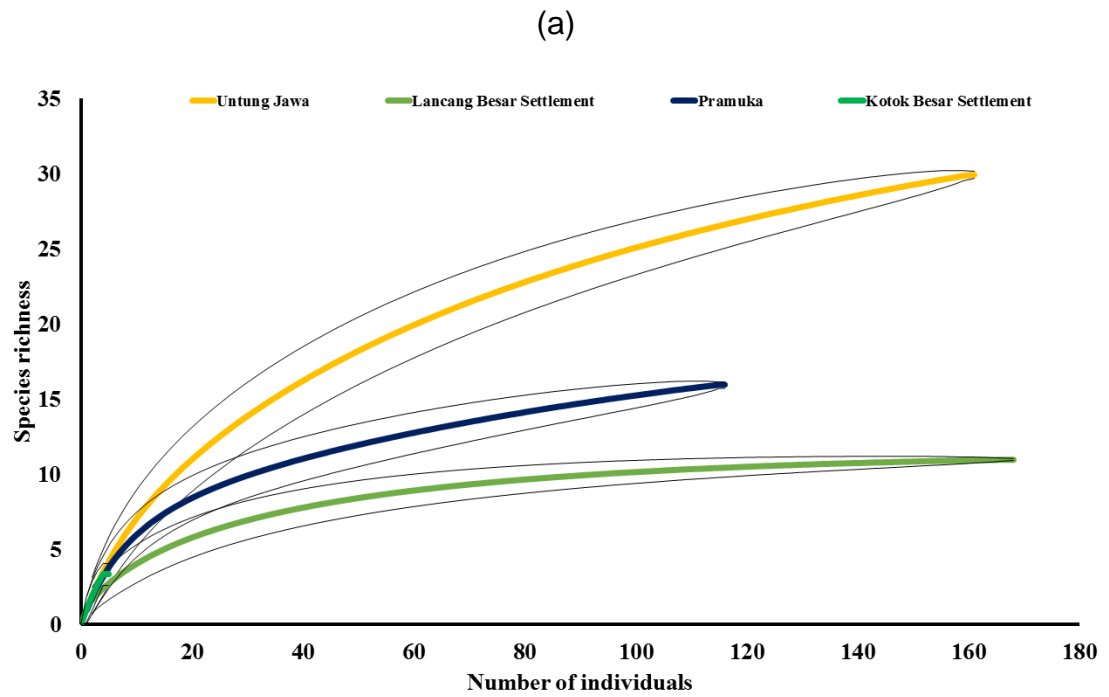
Figure 41 Rarefaction curves of settlement specialist beetle species richness on the studied islands from (a) pitfall traps and (b) FITs (black lines represent 95% confidence intervals)

Beetle species diversity from pitfall traps, assessed both by the Shannon and Simpson's index, was highest on settlement island of Untung Jawa (h_{exp} = 27.29 and D_S=19.2). The lowest for both exponential Shannon and Simpson's index was on island with undisturbed forest, Opak Besar (h_{exp} = 2.61 and D_S = 1.64). On islands with mixed habitat, both diversity index on Lancang Besar settlement (h_{exp} = 6.44 and D_S = 3.25) and Lancang Besar forest (h_{exp} = 6.02 and D_S = 3.65) showed similar level of diversity. Meanwhile, Kotok Besar settlement (h_{exp} = 6.11 and D_S = 3.47) and Kotok Besar forest (h_{exp} = 7.58 and D_S = 3.58) showed that exponential Shannon index was slightly higher on forest habitat than settlement (Figure 42a). When islands with the same habitat combined, the results from pitfall traps showed that settlement habitat on the studied islands had a higher mean rarefied species, exponential Shannon and Simpson's index than undisturbed and disturbed forest habitats (Figure 43a).

FIT samples showed similar patterns to pitfall trap. Untung Jawa (h_{exp} = 18.48, D_S = 15.89), again, showed the highest diversity measured using the exponential Shannon and Simpson's index. Opak Besar, on the other hand, hold the lowest exponential Shannon index (h_{exp} = 1.63) and Simpson's index (D_S = 1.16) (Figure 42b). When comparing mean diversity indices on each habitat, the results from FITs followed similar patterns to pitfall traps. Overall, settlement habitats showed higher mean rarefied species, exponential Shannon and Simpson's index than undisturbed forest habitats (Figure 43b).

The high α-diversity on Untung Jawa Island from pitfall traps was partly related to the low level of dominance of species. On Untung Jawa Island, the three most specimen-rich species Elateridae sp.1, *Onthophagus* sp.3, and *Xyleborus perforans* accounted for only 26.5% of the overall individuals. On Opak Besar Island, the most dominant species *Xyleborus affinis, Xyleborus perforans, and Xylosandrus compactus* represented more than 92% of sampled specimens. From FITs samples, the most dominant species on Untung Jawa Island, *Hypothenemus* spp., *Onthophagus* sp.3, and *Onthophagus* sp.1, accounted for only 25.5%. On the other hand, the number of individuals of *Xyleborus perforans* and *Xyleborus affinis* on Opak Besar Island represented 94% (see Appendix 1).
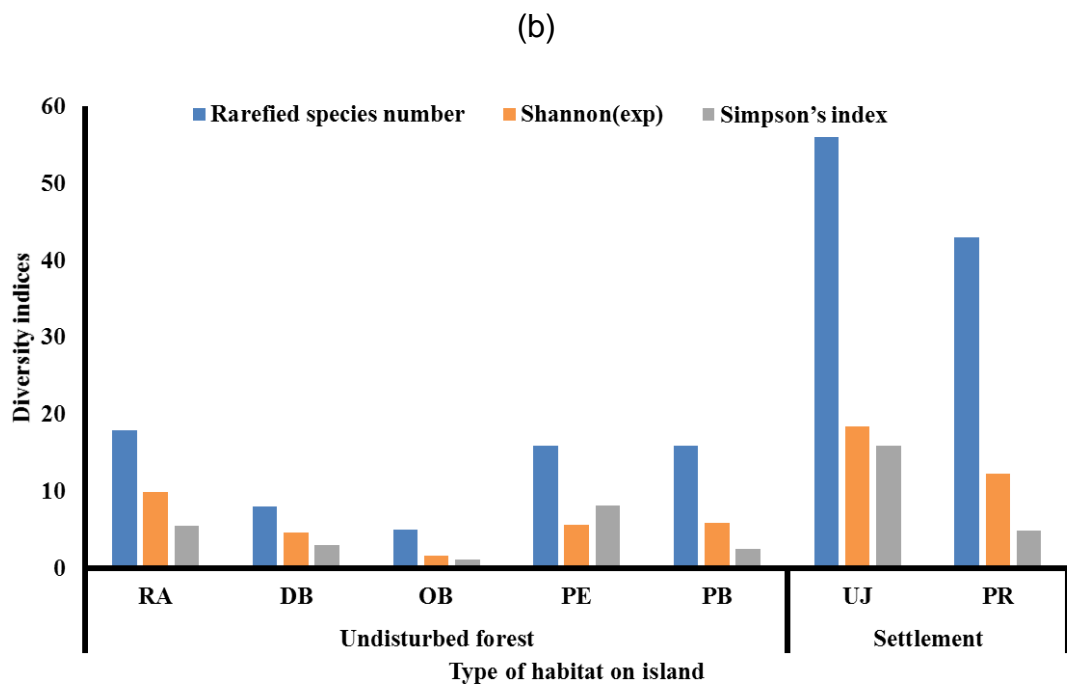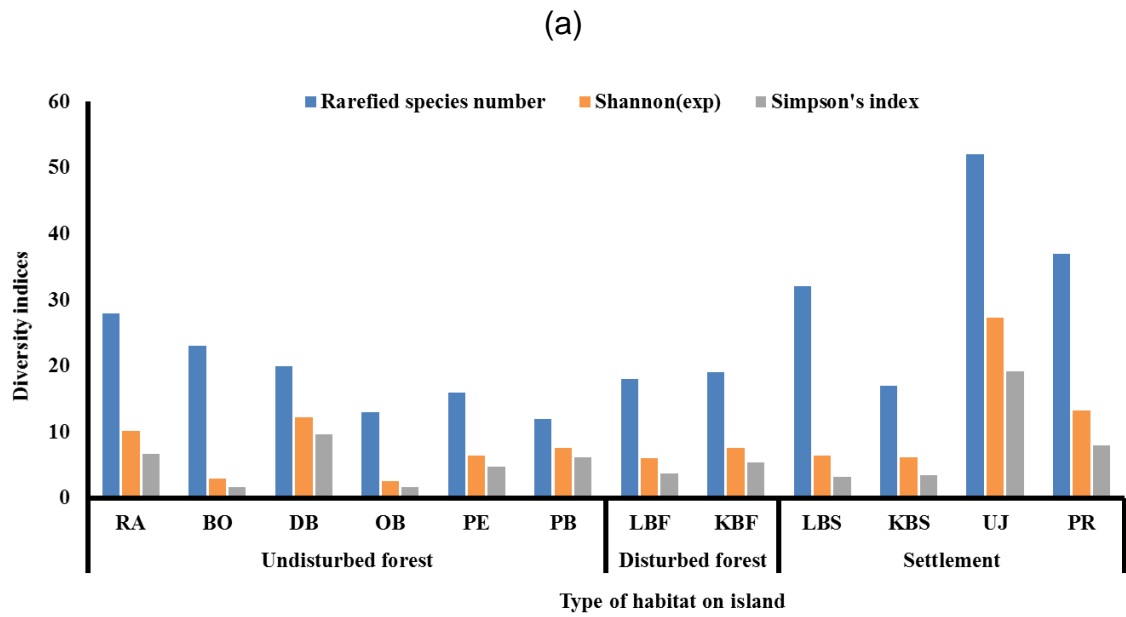
(a)

(b)

RA=Rambut; BO=Bokor; DB=Damar Besar; OB=Opak Besar; PE=Pemagaran; PB=Putri Barat
LBF=Lancang Besar Forest; KBF=Kotok Besar Forest; LBS=Lancang Besar Settlement;
KBS=Kotok Besar Settlement; PR=Pramuka; UJ=Untung Jawa

Figure 42 Comparison of beetle diversity indices on different type of habitat on
island from (a) pitfall traps, and (b) FITs

(a)

(b)
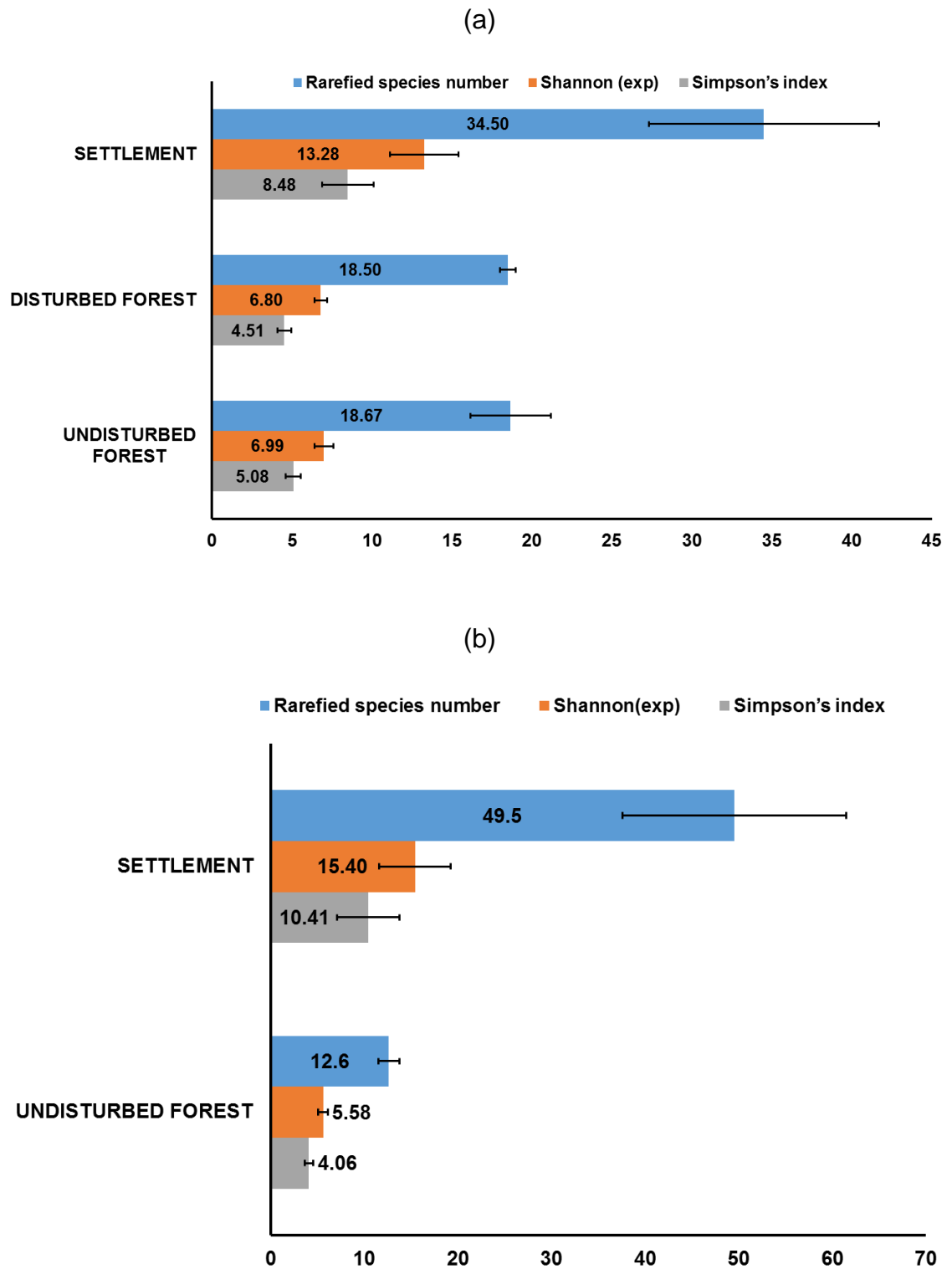
Figure 43 Mean beetle diversity indices on different type of habitat on island from (a) pitfall traps, and (b) FITs. From both traps, means not significantly different ($p<0.05$).

5.3.2. The effects of human population and forest cover on the diversity of beetle species on islands

In the MLRs, rarefied species number, Shannon diversity, and Simpson's index of beetle assemblages were taken as the dependent variables. The results from pitfall traps (Table 8) indicated that forest cover was not a significant predictor for all the dependent variables. While neither of human population and forest covers were significant for Simpson's index. For the rarefied species number (adjusted R^2= 0.743, $F_{1,10}$ = 32.863, P = <0.001), human population was a very significant predictor (β = 0.876, P = <0.001), with increasing number of humans on an island linked significantly with higher rarefied species number. Increasing human population ((β = 0.651, P = 0.022) was also linked, but less significant, with increasing Shannon diversity (adjusted R^2= 0.367, $F_{1,10}$ = 7.369, P = 0.022).

Table 8 Stepwise linear regression from pitfall traps using rarefied species number, Shannon diversity and Simpson's index of beetles as the dependent variables. Human population and forest cover on islands served as independent variables.

Dependent variable	Adjusted R^2	F	P-value	d.f	Selected independent variable	β	Std. Error of β	t	P-value
Rarefied species number	0.743	32.863	<0.001	1,10	Human population	0.876	0.003	5.733	<0.001
Shannon diversity	0.367	7.369	0.022	1,10	Human population	0.651	0.002	2.715	0.022

The result from FITs showed slightly different patterns (Table 9). While forest cover was linked to none of the dependent variables, the effects of human population can be detected on all of them. Increasing size of human population was very significantly linked to increasing rarefied number of beetle species (adjusted R^2 = 0.919, $F_{1,5}$ = 69.086, P < 0.001) and Shannon diversity (adjusted R^2 = 0.776, $F_{1,5}$ = 21.766, P = 0.006), and least significantly on Simpson diversity (adjusted R^2 = 0.537, $F_{1,5}$ = 7.953, P = 0.037).

Table 9 Stepwise linear regression from FITs using rarefied species number, Shannon diversity and Simpson's index of beetles as the dependent variables. Human population and forest cover on islands served as independent variables.

Dependent variable	Adjusted R^2	F	P-value	d.f	Selected independent variable	β	Std. Error of β	t	P-value
Rarefied species number	0.919	69.086	<0.001	1,5	Human population	0.966	0.003	8.312	<0.001
Shannon diversity	0.776	21.766	0.006	1,5	Human population	0.902	0.002	4.665	0.006
Simpson's index	0.537	7.953	0.037	1,5	Human population	0.784	0.002	2.82	0.037

5.3.3. Feeding guilds composition on beetle assemblages on islands

In relation to feeding guilds on beetle species composition, saproxylics was the most abundant feeding guild from pitfall traps. It accounted for 33.4% of the total number of individuals caught on all islands. This feeding guild was also significantly abundant on 6 studied islands, with 7 species representing 89.7% of all sampled individuals on Kotok Besar forest, 4 species (93.6%) on Opak Besar, 6 species (74.8%) on Pemagaran, 6 species (83%) on Putri Barat, 8 species (38.5%) on Pramuka, and 6 species (80.5%) on Kotok Besar settlement. (Figure 44a). Nonetheless, on both Untung Jawa (16 species) and Pramuka (11), saprophages were the most species-rich group (Figure 44b). For herbivores, Damar Besar and Lancang Besar settlement harboured 7 species, each, accounting for 27.4% and 19.8% of the total number of individuals, respectively, while this number was much higher on Lancang Besar forest. Here, 5 herbivore species accounted for 58.6% of all individuals (Figure 44).

(a)
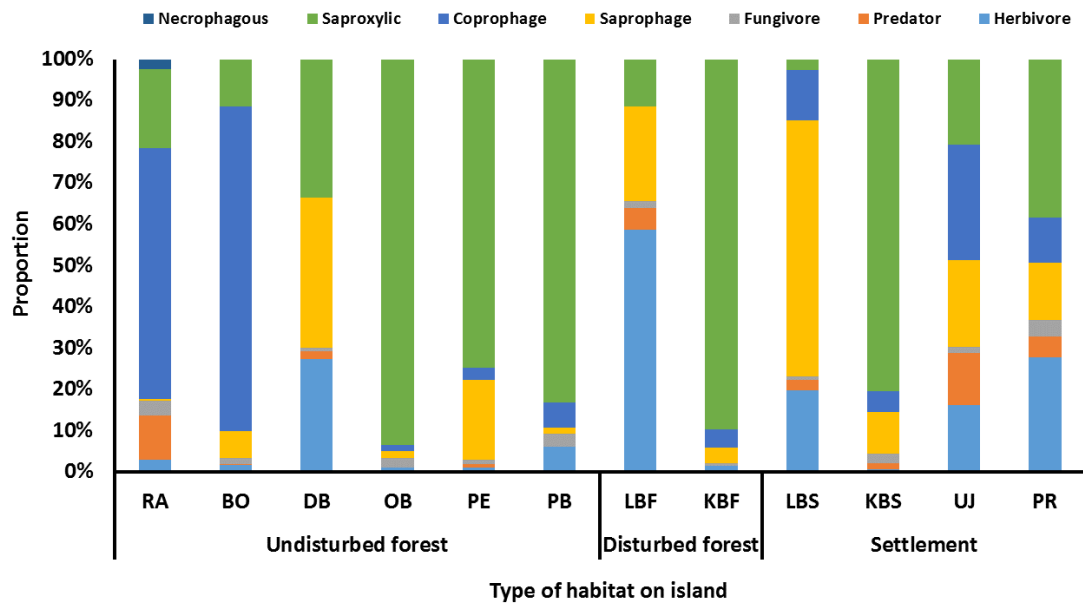
(b)
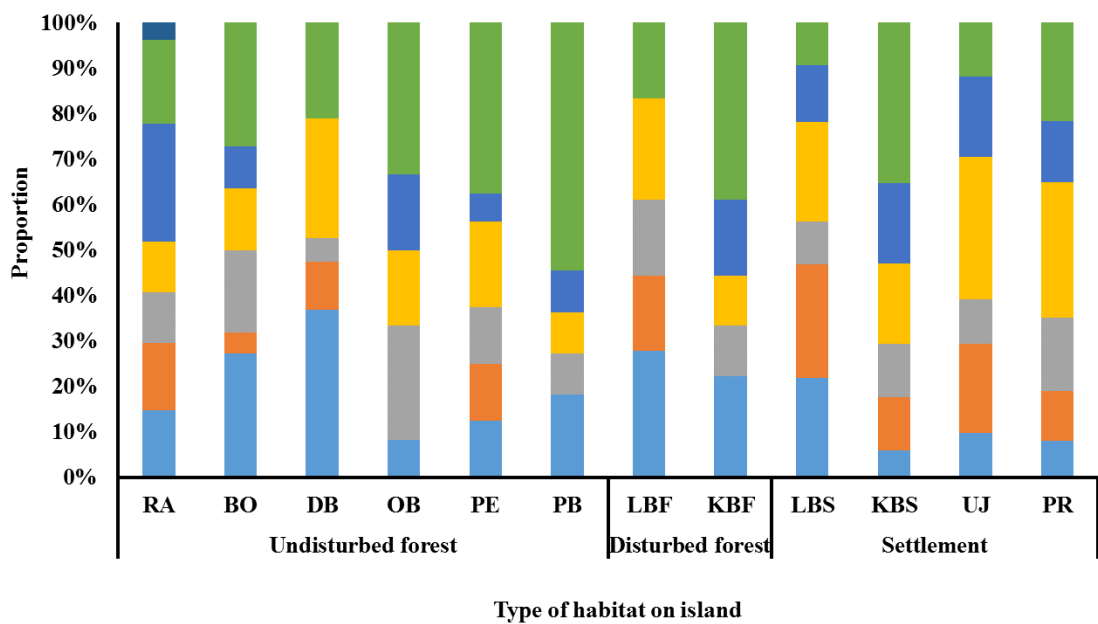
RA=Rambut; BO=Bokor; DB=Damar Besar; OB=Opak Besar; PE=Pemagaran; PB=Putri Barat
LBF=Lancang Besar Forest; KBF=Kotok Besar Forest; LBS=Lancang Besar Settlement;
KBS=Kotok Besar Settlement; PR=Pramuka; UJ=Untung Jawa

Figure 44 Beetle feeding guilds composition from pitfall traps in relation to (a)
abundance and (b) species richness on the studied islands

From FITs, saproxylic again was the most abundant feeding guild, accounted for 54.5% of all sampled individuals. The most abundant saproxylics was recorded on Opak Besar with 4 species representing 99.4% of all sampled individuals (Figure 45a). The highest number of saproxylic species was recorded on Untung Jawa and Pramuka with 7 species, each. However, the most species-rich group was saprophagous beetles. It was recorded on the same islands, Untung Jawa and Pramuka, with 15 species, each (Figure 45b). The most abundant herbivorous beetles were found on Damar Besar, with 4 species representing 56.7% of total sampled individuals. Nonetheless, Untung Jawa harboured the highest number of herbivore beetle species (6 species) (Figure 45b).
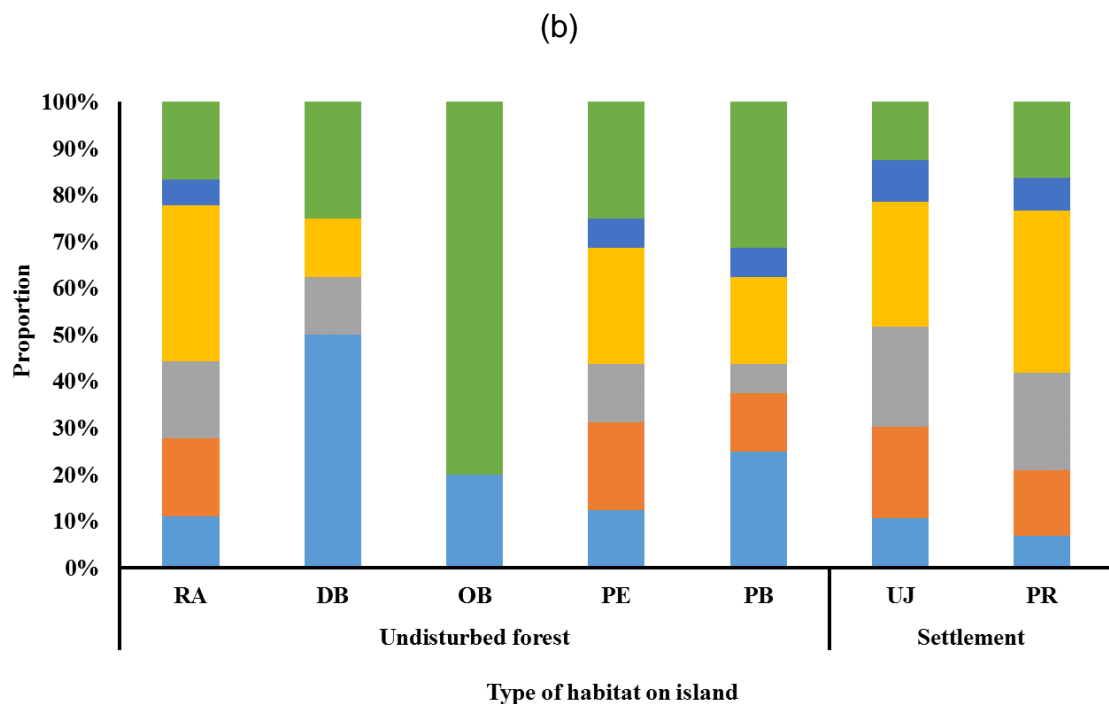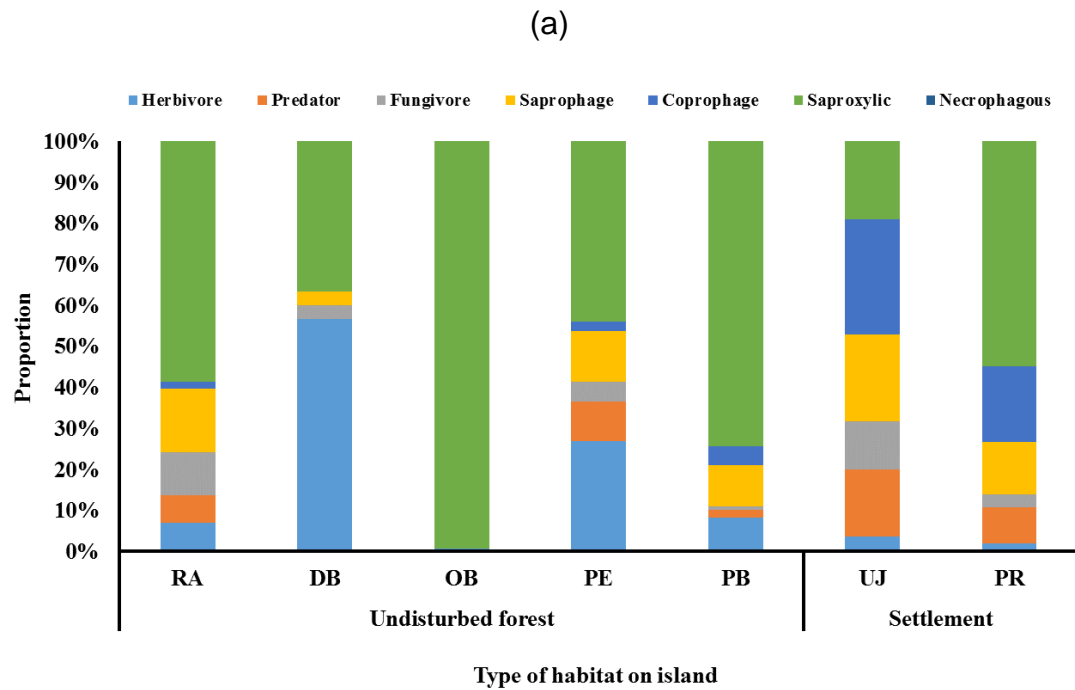
(a)

(b)

RA=Rambut; BO=Bokor; DB=Damar Besar; OB=Opak Besar; PE=Pemagaran; PB=Putri Barat
LBF=Lancang Besar Forest; KBF=Kotok Besar Forest; LBS=Lancang Besar Settlement;
KBS=Kotok Besar Settlement; PR=Pramuka; UJ=Untung Jawa

Figure 45 Beetle feeding guilds composition from FITs in relation to (a)
abundance and (b) species richness on the studied islands

5.3.4. The effects of human population and forest cover on different beetle feeding guilds on islands

The results from pitfall traps indicated that the effect of forest cover only affected herbivorous and necrophagous beetle diversity on islands (Table 10). With the increasing forest cover, the Shannon diversity (adjusted R^2= 0.288, $F_{1,10}$ = 5.451, P = 0.042) and Simpson's index (adjusted R^2= 0.351, $F_{1,10}$ = 6.941, P = 0.025) of herbivorous beetles increased significantly. The same independent variable was more significant on necrophagous beetles, both on rarefied species number (adjusted R^2= 0.581, $F_{1,10}$ = 16.222, P = 0.002) and Simpson's index (adjusted R^2= 0.581, $F_{1,10}$ = 16.222, P = 0.002). On the other hand, human population appeared to be a significant predictor for the other feeding guilds, most significantly on rarefied species number (adjusted R^2= 0.792, $F_{1,10}$ = 42.963, P = <0.001), Shannon diversity (adjusted R^2= 0.861, $F_{1,10}$ = 69.175, P = <0.001), and Simpson's index (adjusted R^2= 0.766, $F_{1,10}$ = 37.066, P = <0.001) of beetle predators. None of the dependent variables were significant predictors for saproxylic beetles.

Meanwhile, the results from FITs (Table 11) showed that forest cover was not a significant predictor for all the dependent variables. Increasing human population, on the other hand, was linked to all beetle feeding guilds, most significantly on coprophagous and fungivore beetles. Both rarefied species number (adjusted R^2= 0.926, $F_{1,10}$ = 76.500, P = <0.001) and Shannon diversity (adjusted R^2= 0.992, $F_{1,10}$ = 712.206, P = <0.001) of coprophagous beetle, and rarefied species number of fungivore beetle (adjusted R^2= 0.940, $F_{1,10}$ = 94.637, P = <0.001) increased with higher number of human settled on the islands.

Table 10 Stepwise linear regression from pitfall traps using species number, Shannon diversity and Simpson's index of beetles based on different feeding guilds as the dependent variables. Human population and forest cover on islands served as independent variables.

Feeding guild	Dependent variable	Adjusted R^2	F	P value	d.f	Selected independent variable	β	Std. Error of β	t	P value
Coprophagous	Species number	0.387	7.931	0.018	1,10	Human population	0.665	0.001	2.816	0.018
	Shannon diversity	0.545	14.171	0.004	1,10	Human population	0.766	0.001	3.764	0.004
	Simpson's index	0.448	9.926	0.01	1,10	Human population	0.706	0.001	3.151	0.01
Fungivore	Species number	0.317	6.104	0.033	1,10	Human population	0.616	0.001	2.471	0.003
	Shannon diversity	0.452	10.084	0.01	1,10	Human population	0.709	<0.001	3.176	0.01
	Simpson's index	0.510	12.450	0.005	1,10	Human population	0.745	<0.001	3.528	0.005
Herbivore	Shannon diversity	0.288	5.451	0.042	1,10	Forest cover	0.594	0.029	2.335	0.042
	Simpson's index	0.351	6.941	0.025	1,10	Forest cover	0.640	0.024	2.634	0.025
Necrophage	Species number	0.581	16.222	0.002	1,10	Forest cover	0.787	0.004	4.028	0.002
	Simpson's index	0.581	16.222	0.002	1,10	Forest cover	0.787	0.004	4.028	0.002
Predator	Species number	0.792	42.963	<0.001	1,10	Human population	0.901	0.001	6.555	<0.001
	Shannon diversity	0.861	69.175	<0.001	1,10	Human population	0.935	<0.001	8.317	<0.001

Feeding guild	Dependent variable	Adjusted R^2	F	P value	d.f	Selected independent variable	β	Std. Error of β	t	P value
	Simpson's index	0.766	37.066	<0.001	1,10	Human population	0.887	<0.001	6.088	<0.001
Saprophage	Species number	0.737	31.758	<0.001	1,10	Human population	0.872	0.001	5.635	<0.001
	Shannon diversity	0.463	10.474	0.009	1,10	Human population	0.715	0.001	3.236	0.009
	Simpson's index	0.399	8.299	0.016	1,10	Human population	0.673	0.001	2.881	0.016

Table 11 Stepwise linear regression from FITs using species number, Shannon diversity and Simpson's index of beetles based on different feeding guilds as the dependent variables. Human population and forest cover on islands served as independent variables.

Feeding guilds	Dependent variable	Adjusted R^2	F	P value	d.f	Selected independent variable	β	Std. Error of β	t	P value
Coprophagous	Species number	0.926	76.500	<0.001	1,5	Human population	0.969	<0.001	8.746	<0.001
	Shannon diversity	0.992	712.206	<0.001	1,5	Human population	0.997	<0.001	26.687	<0.001
	Simpson's index	0.758	19.749	0.007	1,5	Human population	0.893	<0.001	4.444	0.007
Fungivore	Species number	0.940	94.637	<0.001	1,5	Human population	0.975	0.001	9.728	<0.001
	Shannon diversity	0.851	35.199	0.002	1,5	Human population	0.936	0.001	5.933	0.002
	Simpson's index	0.691	14.426	0.013	1,5	Human population	0.862	0.001	3.798	0.013
Herbivore	Shannon diversity	0.670	13.157	0.015	1,5	Human population	0.851	0.001	3.627	0.015
	Simpson's index	0.743	18.348	0.008	1,5	Human population	0.886	0.008	4.283	0.008
Predator	Species number	0.866	39.750	0.001	1,5	Human population	0.942	0.001	6.305	0.001
	Shannon diversity	0.543	8.116	0.036	1,5	Human population	0.787	0.001	2.849	0.036
Saprophage	Species number	0.793	23.939	0.005	1,5	Human population	0.910	0.002	4.893	0.005
	Shannon diversity	0.726	16.936	0.009	1,5	Human population	0.879	0.001	4.115	0.009

Feeding guilds	Dependent variable	Adjusted R^2	F	P value	d.f	Selected independent variable	β	Std. Error of β	t	P value
	Simpson's index	0.609	10.336	0.024	1,5	Human population	0.821	0.001	3.215	0.024
Saproxylic	Species number	0.636	11.463	0.020	1,5	Human population	0.834	0.001	3.386	0.020
	Shannon diversity	0.518	7.436	0.041	1,5	Human population	0.773	<0.001	2.727	0.041
	Simpson's index	0.399	8.299	0.016	1,10	Human population	0.673	0.001	2.881	0.016

5.3.5. Species turnover and similarities

The NMDS ordination plots based on the CNESS dissimilarity matrices from pitfall traps showed that, for dominant beetle species (minimum shared sample size, m=1) the islands formed four distinctive clusters. Settlement islands, Untung Jawa and Pramuka, and islands with undisturbed forest, Rambut and Bokor, formed two tight clusters. The two habitats on mixed habitat island of Lancang Besar formed another tight cluster, with the other islands forming the last close cluster (Figure 46a). This pattern was different for more rare species (sample size m=30), where Untung Jawa and Pramuka still formed a close cluster, while the other islands were more spread out. On mixed habitat islands, Lancang Besar forest and Lancang Besar settlement were more spread out than Kotok Besar forest and Kotok Besar settlement, indicating a higher β-diversity on Lancang Besar Island (Figure 47a). Overall, settlement-dominated islands, Untung Jawa and Pramuka, showed lower β-diversity in both dominant and rare beetle species than islands with forest-dominated habitat and mixed habitat.

From FITs, Untung Jawa had a very distinctive composition of dominant beetle species (sample size m=1) compare to the other islands, which formed a loose cluster (Figure 46b). For more rare species (sample size m=30), two islands with undisturbed forest habitat, Opak Besar and Pemagaran, formed a very tight cluster. The other islands were more spread out (Figure 47b).

(a)
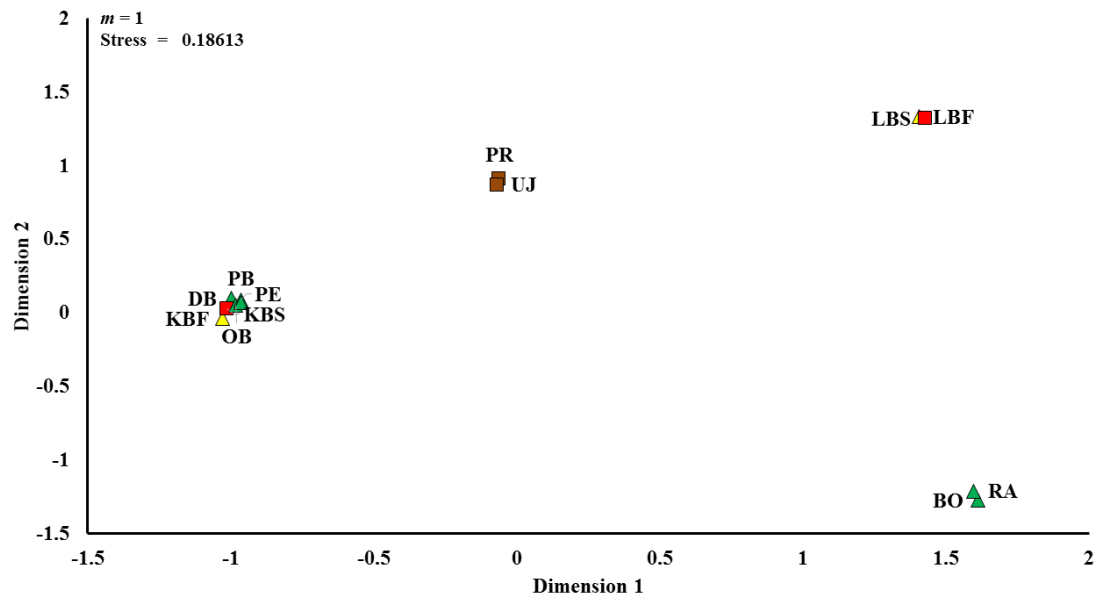
(b)
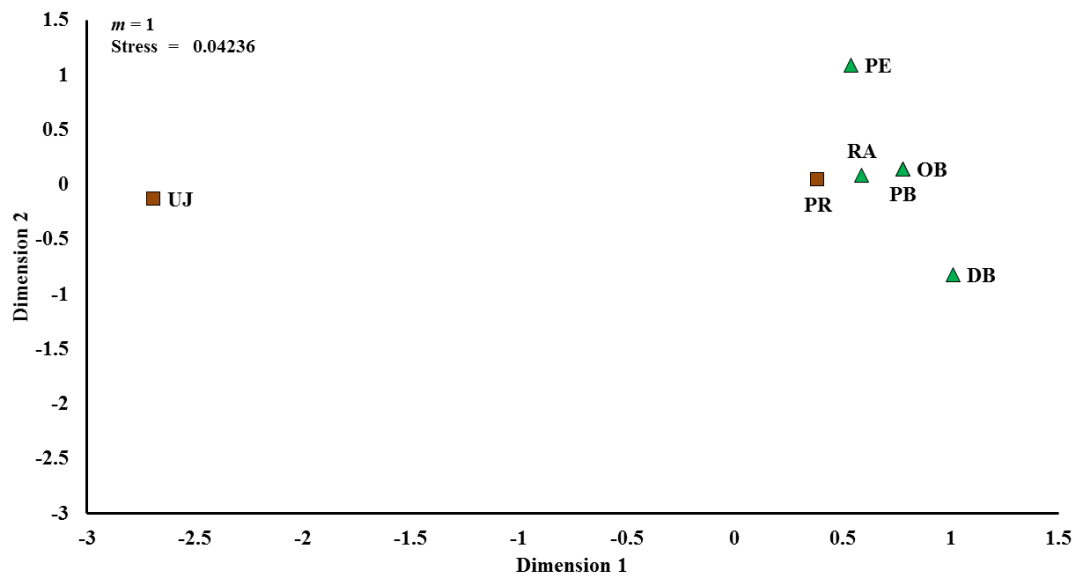
RA=Rambut; UJ=Untung Jawa; BO=Bokor; LBF=Lancang Besar Forest; LBS=Lancang Besar Settlement; DB=Damar Besar; PR=Pramuka; KBF=Kotok Besar Forest; KBS=Kotok Besar Settlement; OB=Opak Besar; PE=Pemagaran; PB=Putri Barat

Figure 46 NMDS ordination plot based on the CNESS distance matrix of beetle species composition on islands for sample sizes at m=1 from (a) pitfall traps and (b) FITs.
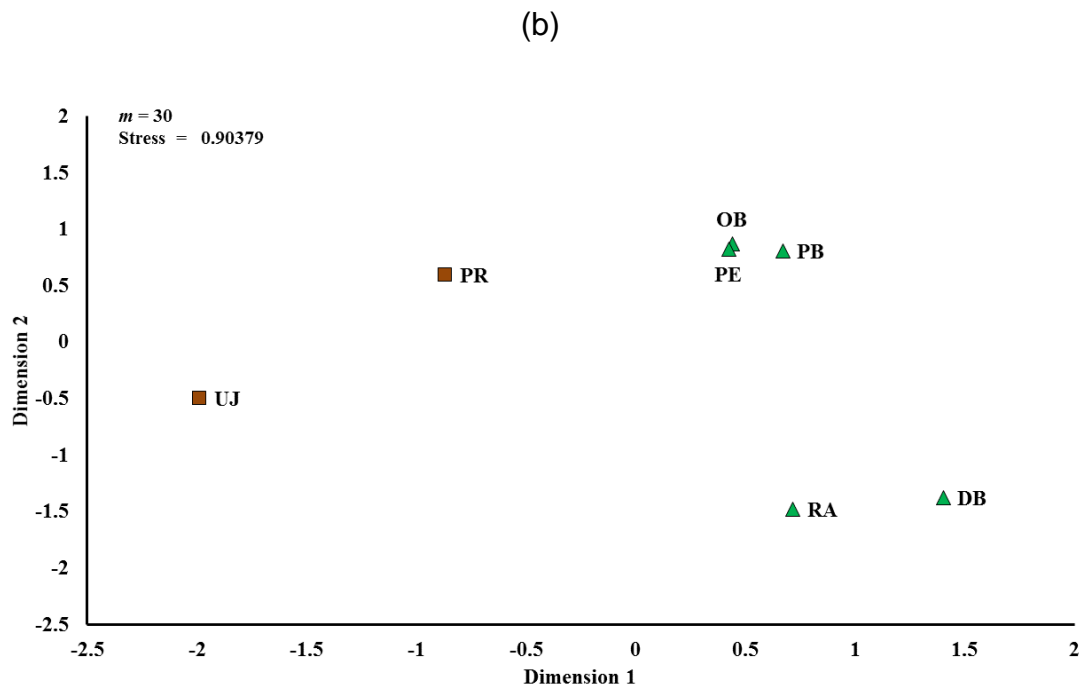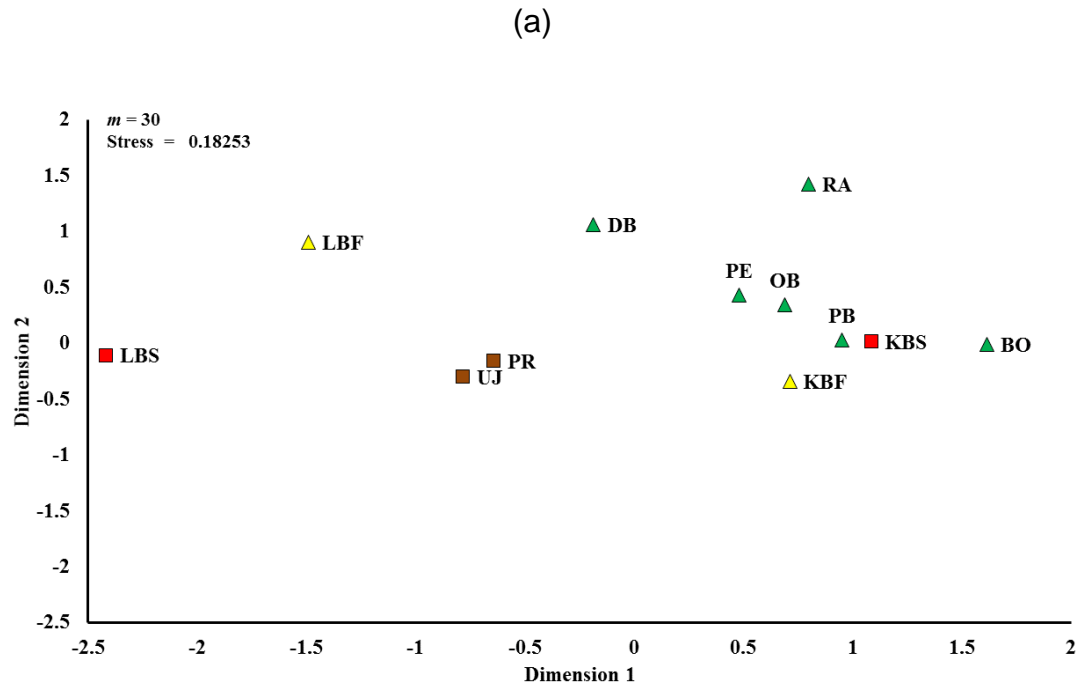
(a)

(b)

RA=Rambut; UJ=Untung Jawa; BO=Bokor; LBF=Lancang Besar Forest; LBS=Lancang Besar Settlement; DB=Damar Besar; PR=Pramuka; KBF=Kotok Besar Forest; KBS=Kotok Besar Settlement; OB=Opak Besar; PE=Pemagaran; PB=Putri Barat

Figure 47 NMDS ordination plot based on the CNESS distance matrix of beetle species composition on islands with forest habitat for sample sizes at m=30 from (a) pitfall traps and (b) FITs.

5.3.6. Unique and shared species on islands with different habitats

When islands with the same type of habitat were combined, the results from pitfall traps showed by both islands dominated by undisturbed forest (FF) and settlements (SS) had a high number of unique species of beetles (29 species). Meanwhile, disturbed forest habitat (FSF) and settlement habitat on mixed habitat islands (SSF) only have 3 unique beetle species, each. However, the structure of the assemblages was quite different. In total, the unique species accounted for 45% of total beetle species in FF, while this number decreased to 43%, 17.6% and 9.7% in SS, FSF and SSF, respectively. Also, FF shared more beetle species with SS (27 species) than with FSF (9 species). Meanwhile, SS shared less beetle species with SSF (21 species) than with FF (27 species). The results also showed that, when FF and FSF combined, in total there were 34 forest species. While when SS and SSF combined, there were 39 settlement species. FF, SS, FSF, and SSF shared only 3 beetle species among them (Figure 48).
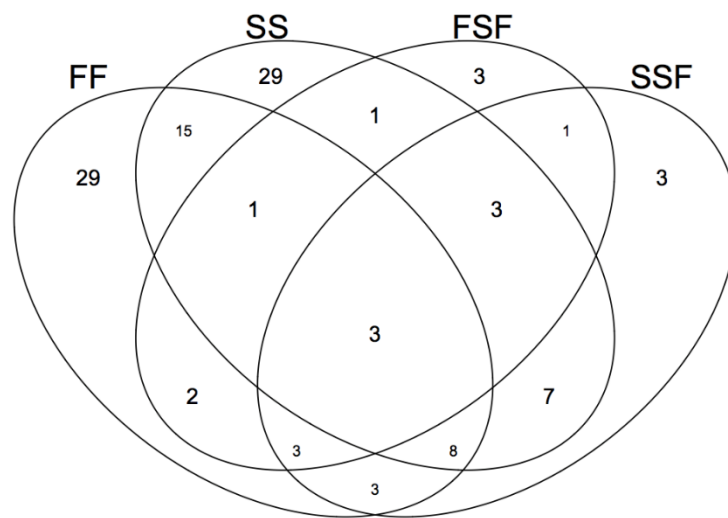
Figure 48 Proportion of shared and unique species between the four different habitats on the studied islands from pitfall traps

From FITs, 58 out 78 beetle species in SS were unique (74%), while the proportion of unique species for beetles in FF was much lower (48.7%) (Figure 49). In total, SS and FF shared 20 beetle species between them, which was accounted for 20.6% of total species number caught from FITs.

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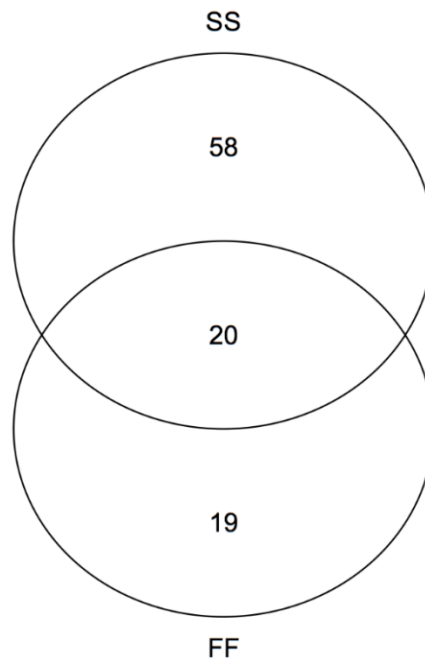
Figure 49 Proportion of shared and unique species between the two different habitats on the studied islands from FITs

5.4.   Discussion

5.4.1. Human impacts on beetle diversity on islands

In accordance with my first hypothesis, beetle diversity from both pitfall traps and FITs peaked on islands dominated by settlements. A positive shift in beetle diversity in disturbed sites on patched habitats and islands has also been observed by other authors (Driscoll & Weir, 2005; Ganho & Marinoni 2005; Marinoni & Ganho 2006). Moreover, the results from MLR showed human population significantly increased beetle species richness. These trends can be related to proximity to Java and island size. With frequent public and private boat traffic to and from the island, visitors and island settlers potentially alter diversity by introducing beetle species into the island (see discussion in chapter 4). As Untung Jawa is the largest and the earliest settlement island in the Kepulauan Seribu Marine National Park, it has attracted more human occupants and increased the risk of continuous propagule transfer into the island. In addition, island settlers often bring back seeds, fruit trees, herbs, or ornamental plants to the island for cooking or gardening (S.Puspitasari, personal interview). The age

of the settlement habitat and the heterogeneity in the introduced tree and plant species on Untung Jawa and Pramuka can also be expected to relate to the high species richness on both islands, as high plant diversity will potentially provide more food resources for herbivore species (Haddad and Baum, 1999; Lewinsohn et al. 2005; Novotny & Basset 2005; Scherer & Romanowski 2005; Barton et al. 2012).

Species compositions of ground-dwelling beetles between Untung Jawa and Pramuka Islands were very similar. This might be explained because these settlement islands shared the same trends, where the original beetle community was replaced by one more adapted to open habitats. Studies on beetles showed that in highly urbanized areas, native specialist species are replaced by native generalist and introduced species that reach very high abundances, which may result in an increase in total species abundance or density with urbanization (Germaine et al. 1998, Crooks et al. 2004, Donnelly and Marzluff 2004, Lim and Sodhi 2004, Donnelly and Marzluff 2006, Shochat et al. 2006, Tratalos et al. 2007, Pennington et al. 2008, Catterall 2009). Previous studies also found that species composition in different urban areas were more similar to one another than are compositions in different natural areas (McKinney 2002, Sorace and Güstin 2008), which was also found in this study.

Island settlements in the study area have also created a variety of open microhabitats for beetles, such as lawns, bare soil, moss and gravel ground covers, and plant litter-covered ground, providing different food resources and prey for ground-dwelling beetles and resulting in the increase in open-habitat beetle species richness in Untung Jawa and Pramuka Island. A study by Holland et al. (2007) showed the possibility of the effect of urbanization in the increase in slug abundance, a common prey of the carabid beetle species *P. melanarius* (Symondson et al. 2002), which was an open-habitat beetle species collected in their study. More food and prey in settlement areas is likely to increase the abundance of some settlement beetle species, possibly contributing to the increased species richness of this group.

The positive effects of human population on ground-dwelling and dispersive beetle diversity was supported by another finding in this study, where in total there

were more settlement beetle species than forest species found on the islands. However, McMaster (2005) argued that present-day human population density may serve as a surrogate for a complex of other factors affecting species richness on islands. For Kepulauan Seribu Marine National Park, identification and evaluation of other potential measures of anthropogenic impact such as total day visitors per year, or percentage of island area under development might be essential for a more complete understanding of overall species richness.

5.4.2. The effect of different forest habitat on beetle species on islands

Very little information is currently available about the ecological preferences of individual beetle species on islands with different habitats in Indonesia. However, the results of this study have identified some patterns in habitat preferences for beetle species on the studied islands. The occurrence of a high number of generalist beetle species on Lancang Besar Island (Figure 38a) might be explained by two underlying mechanisms. Lancang Besar is a mixed habitat island. It may be explained either by the movement of individuals between habitats or by a broad habitat requirements of the species, either for reproduction or hibernation, which enables them to maintain their populations (Pielou 1979). With a combination of forest and settlement habitats, this island made it possible for generalist beetles to conduct a small-scale dispersal. These results were also supported by Niemela (1988a, 1988b), who found that beetle assemblages on Baltic Sea islands were more similar within islands than between them. His study, furthermore, found that most carabid species were found outside their preferred habitat, albeit in small numbers, and it appeared that carabids on small islands used a wide variety of vegetation types, i.e. they were generalists. In a different study, Niemela et al. (1993) found that the majority of dominant carabid species on the islands were found in almost all vegetation types. Habitat modification from undisturbed to selectively logged forests has little impact on beetle species richness, biomass and abundance (Davis, 2000; Davis and Philips, 2005; Nichols et al., 2007; Shahabuddin et al., 2010; Slade et al., 2011). On the other hand, beetle species with specific niche requirements do occur on islands. For example, shore environments on Baltic Sea islands were mainly occupied by hygrophilous

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species, typical of open and moist habitats, and some field and forest carabids were strictly associated only with these environments (Niemela and Halme, 1992, Kotze, 2008). Although my data does not allow me to definitely determine whether specimens found in both habitat were actually members of a breeding population, transient individuals from the favoured environmental type, or specimens deliberately dispersing from one patch to another, it could be suggested that some beetle forest specialists on islands were likely to survive and reproduce well even when the forest habitat has been disturbed.

However, when all islands with the same habitat were looked at together, there was a substantial overlap in beetle species between islands dominated by undisturbed forest and islands dominated by settlement. Thus, contradicting my hypothesis, the overall results show that islands dominated by undisturbed forest (FF) harboured more generalist species than disturbed forest habitats on mixed habitat islands (FSF). One potential explanation would be because of the close proximity of some of the forest dominated islands to settlement islands. The largest island dominated by undisturbed forest, Rambut, was located next to the largest settlement island, Untung Jawa. Although traffic between these islands is not as frequent as the other tourist islands, the national park's staff commute from Untung Jawa to Rambut Island every day. Researchers, who conducted studies on Rambut Island, had to stay on Untung Jawa Island. This traffic might have created propagule transfers. Vacant niches on Rambut Island were potentially filled by generalist beetle species from adjacent settlement islands. These generalist species might have been competing with settlement specialists on Untung Jawa Island. This notion of the 'semipermeable island' has been applied in other taxa and regions (Herzog & Kessler, 2006) and is a promising model for gaining new insights into the regulation of species diversity on islands.

My results for unique species show that, in line with my hypothesis, undisturbed forests harboured more unique species than disturbed forests (Figure 40a and 40b). Beetles, like other insects, are often highly associated with microhabitats (Barton et al. 2012) and sometimes with resources derived from particular plant genera (Lewinsohn et al. 2005; Novotny & Basset 2005; Scherer & Romanowski 2005). Assuming that undisturbed forests on the studied islands still maintain their original habitat, it could be predicted that they have more pristine vegetation and

distinct plant species than disturbed forests. This also shows the significance of vegetation complexity on unique forest species on the studied islands. Interestingly, settlement habitats and undisturbed forest habitats have a similar number of unique species. The number of unique species as a proportion of overall species richness is also similar between settlement habitats and undisturbed forest habitats. It can therefore be speculated that both habitats can sustain their specialist beetle species populations. The high number of settlement specialist beetle species captured from FITs suggests that unique species from settlements generally have a higher mobility.

Further studies, especially those based on comparison of habitat types, are needed to reveal more accurately the habitat requirements of different species and the relative species diversity of beetle assemblages in different habitats on islands. This knowledge is imperative in assessing, for instance, the relative importance of environmental factors and species interactions in structuring species assemblages in different island habitats.

5.4.3. Different beetle feeding guilds on islands

As hypothesised, the diversity of herbivorous beetles on islands was strongly affected by different levels of forest cover. One potential explanation would be that herbivores are closely linked with changes in forest size. Different vegetation compositions, which can be reflected by undisturbed and disturbed forest types, might also affect the diversity of herbivorous beetles on these islands. This argument is supported by Arnold and Asquith (2002), who found that measures of herbivory increased markedly with interactions with rich plant species. However, other theories predicted that species at the top end of food chains were more prone to extinction than species at lower levels because the former tended to have more unstable population dynamics and were less likely to persist in a fluctuating environment (Pimm and Lawton 1977, Lawton 1995, Holt 1996). A study by Davies et al. (2000 & 2007) contradicted these theories, and asserted that species at higher trophic levels were not affected in habitat fragments more than species at lower trophic levels. Based on my results, this theory might be applicable when human population is used as an environmental parameter.

Predator beetle species from pitfall traps were most significantly affected by human population on islands. Perhaps these results were mixed because other traits also determine extinction risk. For example, species at higher trophic levels are often large in body size, but populations of large species are thought to fluctuate less (Pimm 1991) and therefore, to be less extinction prone. Conversely, species at higher trophic levels are usually the taxa with the lowest population densities (Gard 1984) and, thus, at the highest risk of extinction.

Necrophagous beetle species from pitfall traps were also significantly affected by forest cover. This result might be explained by the fact that Rambut and Bokor Island, the two largest forest dominated islands, are also sanctuaries for birds. The density of bird nests might have had an impact on the rate of supply of material inputs for these beetles. Birds transported aquatic secondary production in the form of fish carcasses to the forest floor beneath their breeding colonies, and the supply of carcasses would increase the densities of necrophagous insects. A study by Ueno et al. (2006) supported this argument, by showing that the density of necrophagous beetles in forests in Japan, where Grey Herons breed and drop many carcasses, was significantly higher.

Another possible explanation for the results on necrophagous beetles might be related to predatory interactions, which could be associated with forest cover. Although many necrophagous beetle species consumed the carrion organic material directly (Campobasso et al. 2001), others used the resource as habitat or as a location to find other prey insects attracted to the carrion as food sources (Gibbs and Stanton 2001). My data did not specify predators for this guild, and studies of these predatory interactions (Gibbs & Stanton, 2001; Centeno et al.2002; Arnaldos et al. 2004; Tabor et al. 2004; Gill, 2005; Sharanowski et al. 2008) have been conducted qualitatively, and with no statistical approach, which made it problematic to see the significant of these interactions.

The other beetle guilds from pitfall traps, including coprophage, fungivore, saprophage, and saproxylic, were significantly affected only by human population. Again, my data did not specify native and introduced species. However, coprophagous beetles have been known to flourish in open areas, and are also known for their ability to diversify their diet (Scholtz and Grebennikov,

2005; Davis and Scholtz 2002). This diversification included the dung of domesticated animals, such as chicken (Fincher, 1973), which were associated with settlements. Some dung beetles also utilised non-dung food resources, and this occurs mostly in resource-rich regions, where carrion, fungi, fruit and plant matter are exploited (Davis et al., 2000).

5.4.4. Synthesis

Overall, the studied islands showed a higher α-diversity of ground-dwelling and dispersive beetles encountered chiefly in settlement areas than forest species. This results suggested that human population and settlement give positive effects on the increase of beetle diversity on islands. My results also indicated that, when all islands with the same habitat were combined, islands dominated by undisturbed forest harboured more generalist species than disturbed forest, which are potentially caused by propagule transfers and vacant niches available for generalist beetles. Islands dominated by undisturbed forests also harboured more unique species than islands with disturbed forests. Undisturbed forest habitats therefore have a high biodiversity conservation importance by maintaining their original habitat, pristine vegetation and distinct plant species. The diversity of herbivorous beetles on islands are also strongly affected by different levels of forest cover, which shows the significance of forest size to this feeding guild. For a comprehensive comparison of the relative importance of environmental factors and species interactions in structuring species assemblages in different island habitats, studies on habitat requirements of different species on islands are required.

Chapter 6. Discussion and Conclusion

6.1. General diversity of beetles in the study areas

Many beetle species have a relatively low dispersal ability compared with other insects and are thus vulnerable to isolation by geographic barriers (Ishitani 1996; Kubota et al. 2000). They have been widely used in studies evaluating the effects of disturbances on grassland (Dennis et al. 1997), agro-ecosystem (Fournier and Loreau 2001; Purtauf et al., 2005; Liu et al., 2007), woodland and coastal area (Kotze and O'Hara, 2003), as they are highly abundant in most areas of the world and show highly varying sensitivities to ecological and environmental change. The overall species richness of beetles on Earth is still widely unknown, and the same is also true for many smaller geographic areas in the tropics like the island ecosystems of Indonesia. The main focus of this research was to investigate and compare beetle diversity patterns on islands in the Kepulauan Seribu Marine National Park and on Java to establish the relationship between different beetle assemblages on islands, and how island isolation and area affect assemblage composition. In addition, my research also aimed to provide insights into the effects of anthropogenic activities on beetle diversity at the studied islands.

This study focuses on ground-dwelling beetles, which were captured mainly by pitfall traps, and dispersive beetles that were collected using flight interception traps (FITs). The collected beetle families represent different feeding guilds, including herbivores, fungivores, predators, saprophagous, necrophagous, coprophagous, and saproxylic beetles. In my thesis, I present the first comprehensive sample of these beetles at ten studied islands in the Kepulauan Seribu Marine National Park. A total of 6370 beetles belonging to 34 families, separated into 236 morphospecies, were caught in the study area that also included sites on Java. Among these, 4929 beetles representing 25 families were captured in pitfall traps. The remaining 1441 individuals representing 27 families were caught in the FITs. On the small islands, 4637 individuals representing 24 families and 111 species were captured in pitfall traps and 968 beetles representing 22 families and 97 species were recorded in the FITs. In Java, 292

beetles representing seven families and 32 species were collected from pitfall traps, and FITs yielded 473 beetles representing 20 families and 94 species.

The comparatively high diversity of beetles on the small islands supports two assumptions. One is that islands harbour high levels of biodiversity in relation to beetle assemblages that also represent a high diversity in ecological traits. Secondly, anthropogenic activities play an important role in affecting the overall beetle population, diversity and composition on islands. Based on these findings, the role and position of the Kepulauan Seribu Marine National Park in regulating land use and habitat changes on the islands are significant and important towards the protection of the islands' biodiversity.

6.2. <u>Main findings and lessons for biodiversity conservation</u>

The substantial number of highly abundant island species and a high number of unique island species found in the study areas are important findings. These results indicate that these islands are potentially important for the global conservation of genetic resources, and future analysis of the phylogenies of some of the specimens collected could allow further insights into the presence of distinct small-island ecotypes and species of beetles in the archipelago investigated.

This work also highlights the highly varied results relating to the use of two different types of traps, pitfall traps and FITs, for sampling beetles. It underscores the need for complementary trapping strategies using multiple methods for beetle community surveys in tropical islands to provide an overview of the species present. Cleary, ground-dwelling beetles mostly captured in pitfall traps and the mostly dispersing beetles caught in FITs provide different results in relation to the species composition on the studied islands. Some beetle families, such as Brentidae, Cerylonidae, Ciidae, Coccinellidae, Endomycidae, Laemophloidae, Monotnidae, Ptilidae, and Silvanidae were exclusively sampled at FITs. On the other hand, members of the families Anthicidae, Cerambycidae, Cucujidae Cryptophagidae, Hyborosidae, Lampyridae, and Trogidae were uniquely encountered in the pitfall traps. Members of the families Scarabaeidae and Scolytidae were both dominating the total captures from pitfall traps and FITs.

FITs is still a key method for the understory trap and considered as one of the most popular sampling strategies by entomologists (Malaise 1937, Southwood, 1978; Leather and Watt, 2005; Fraser et al. 2008). It is well appreciated that capture rates of pitfall traps depend on trapping efficiency, species activity and species density (Curtis 1980). Because of these distortions, many authors concluded that this trapping method is of limited value for quantitative estimations of population sizes or the comparison of communities (Greenslade and Greenslade, 1971). Nonetheless, similar limitations also apply to most other types of traps including FITs. The combination of high numbers of ground-dwelling beetle species recorded in pitfall traps in the study area, coupled with dispersive beetles from FITs in my view provides a highly standardized overview of the overall beetle assemblages on the studied islands, especially given the very short sampling time used here and the substantial diversity of the encountered assemblages.

In my work, I test the equilibrium theory of island biogeography, where species richness on islands forms a dynamic equilibrium between the opposing process of immigration and extinction (MacArthur & Wilson, 1967). Using beetle assemblages on the ten studied islands with different area and three different isolation measurements, i.e. the distance to Java, distance to the nearest island, and mean distance to islands within the radius of 5km, the overall results chiefly support the classic theory of island biogeography. Distance to Java, as the main potential source of immigration, and island area were linked significantly to the species number of beetles on the studied islands. Distance to the nearest island and mean distance to islands within the radius of 5km have been used as additional parameters for species richness on islands in previous studies. However, they are not significant predictors to the beetle assemblages in the archipelago I studied. Continuous traffic between islands and the appearance of visitors hopping from one island to another might have dampened the effects of these isolation parameters.

Consequently, my work also highlights the impacts of anthropogenic activities, because although the islands form part of the Kepulauan Seribu Marine National Park, some of the studied islands are also tourist destinations and experience ongoing settlement expansions. The positive effects of such human activities on

the overall species richness of ground-dwelling and dispersive beetles are clearly reflected in my results. Overall, the studied islands harbour more beetle species encountered chiefly in settlement areas than forest species. However, when comparing the type of forest habitat on the islands, undisturbed forests harbour a higher number of unique species than disturbed forests. The assumption is that undisturbed forests on the studied islands still maintain mature and pristine habitat, with their pristine vegetation containing distinct plant species that are potentially associated with particular beetle species.

With regards to different feeding guilds, the diversity of herbivorous beetles on islands is strongly affected by the different levels of forest cover encountered. This pattern shows the significance of forest size and maturity for this guild. My findings can have important implications for conservation of beetle herbivore assemblages. With the threat of forest habitat reduction for settlement and tourism on these islands, interactions between herbivore beetles and plants can be interrupted. As a consequence of this, the more specialised beetle herbivores can be lost very quickly, which can modify the structure and persistence of trophic interaction networks.

Finally, beetles comprise not only the most diverse group of insects, but they also contribute significantly to vital ecological functions such as decomposition by bark beetles, increased forage, nitrogen recycling, and reduced parasite and fly densities due to dung processing by dung beetles. Although a quantitative formula to determine the optimal level of investment in the conservation of beneficial beetles that provide essential services is still not available, this study will help to pay specific attention to beetles and the role they play in island ecosystems.

Second, this study recommends that ecosystem services performed by beetles be taken into account in land-management decisions and policy by the Kepulauan Seribu Marine National Park. With this goal in mind, specific practices on the islands such as land clearing, land-use changing, waste management and grazing should be tailored to protect beetle and insect biodiversity, in general.

My study is just a beginning. With greater attention, research, and conservation, the importance roles and valuable services that beetles provide on island

ecosystem can not only be sustained but increased in capacity. In less direct but no less important ways, human would benefit from the facilitation of the roles and vital services that beetles provide. Hence, increased investment in the conservation of these services, especially on island ecosystem, should be justified.

6.3. <u>Further work</u>

Very little information is currently available about the ecological preferences of individual beetle species on islands and their different habitats in Indonesia. Moreover, with no comparative studies on beetles in the study area, and with limited information for beetles in Indonesia in its entirety, it is very difficult to analyse the data generated by my study in a wider context. There is very limited information on activity patterns, immigration ability and habitat preferences of beetles on the studied islands, and it can be assumed that not all species I encountered are currently known to science. Although the results of this study have identified some patterns in habitat preferences for a number of beetle species on the islands, further work including sampling over longer sampling periods and using a larger number of traps in a wider range of habitats is required for a better understanding of beetle diversity patterns in small tropical islands of Indonesia, and how these patterns respond to habitat changes and anthropogenic activities.

A larger number of islands in Kepulauan Seribu National Park with different size, isolation, habitat type, and anthropogenic activities should also be included in such further studies. This would allow a better understanding of the general biogeographic patterns of beetle assemblages in the archipelago, and allow a clearer identification of environmental parameters affecting the beetle diversity on the islands.

Secondly, the selection of these taxa should include a wider range of other arthropod taxa with varying dispersal activity, such as butterflies, bees and ants, with additional detailed surveying techniques employed such as caterpillar collection and sweep netting. This could decrease the taxon-specific bias in the information of arthropod diversity patterns. A more detailed information on vegetation composition and changes on the islands would furthermore help to

identify relationships between insects and plants on islands and provide a baseline for the identification of general spatiotemporal patterns, providing key information also for the creation of models allowing for the prediction of future diversity patterns and the identification of key threats.

Finally, studies from other small island archipelagos in Indonesia and Southeastern Asia can provide complementary information to substantiate results from this study. An archipelago of small islands like the Molucca islands in the east of Indonesia, and a group of small islands located in the south of Sulawesi, would be ideal places to study insect biodiversity patterns more generally supported by small tropical islands ecosystems. These groups of islands would also be suitable to test the island biogeography theory with additional parameters, such as distance to the nearest island with similar habitat, distance to the nearest island with similar size, island age, and settlement age, overall allowing for a greater understanding of the ecological underpinnings of the patterns I have established in my thesis.

6.4.   Conclusion

The primary focus of this thesis was to investigate and compare the beetle assemblages on ten small islands in Kepulauan Seribu Marine National Park and on Java. The results of this study support the classic theory of Island Biogeography, where island size and distance to Java as the main source of immigration are linked significantly to beetle diversity on the islands. However, other parameters including habitat type and human population strongly affect the overall islands' beetle population, too. In practice, my work highlights areas that require specific attention for beetle biodiversity conservation on small islands in an Indonesian context. These areas include more attention to be given to human activities and resulting habitat changes on the pristine island that currently harbour unique beetle assemblages, a requirement never acknowledged in previous conservation strategies by the national park. This study will help to inform future conservation strategies for the Kepulauan Seribu Marine National Park. The marine-focus approaches are not sufficient for the conservation of the biota contained within this protected area. Managing the terrestrial habitat on

these islands has to be considered, too. I provide strong indications that the small islands harbour not only a highly abundant beetle fauna, but that widely undisturbed islands also provide habitat for species that were not encountered on islands with human settlements, which underlines the potential value of conserving and maintaining these island ecosystem for terrestrial biodiversity conservation.

References

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Abbott, I. (1974) Numbers of plant, insect and land bird species on nineteen remote islands in the Southern Hemisphere. *Biological Journal of Linnean Society*, 6, 143–152.

Abbott, I. (1978) Factors determining the number of land bird species on islands around south-western Australia. *Oecologia,* 33, 221–233.

Abellan, P., Sanchez-Fernandez, D., Velasco, J., Millan, A. (2005) Conservation of freshwater biodiversity: a comparison of different area selection methods. *Biodiversity and Conservation*, 14, 3457-3474.

Abogast, R. T., Throne, J. E. (1997) Insect infestation of farm stored maize in South Carolina: towards characterization of a habitat. *Journal of Stored Products Research*, 33, 187-198.

Acevedo-Whitehouse, K., Duffus, A. L. J. Effects of environmental change on wildlife health

Ackerman J. D., Trejo-Torres, J. C., Crespo-Chuy, Y. (2007) Orchids of the West Indies: predictability of diversity and endemism. *Journal of Biogeography*, 34, 779–786.

Acorn, J. (2006) The world's biggest bug in a grub. *American Entomologist*, 52, 270-272.

Adams, W. (2003) Nature and the Colonial Mind. In Adams, W. and Mulligan, M. (eds.),Decolonizing Nature: Strategies for Conservation in a Post-colonial Era. Earthscan, London.

Adams, W.M. (2004) Against extinction: The story of conservation. Earthscan, London.

Addicott, J. F., J. Bronstein, and F. Kjellberg. (1990) Evolution of mutualistic life-cycles: yucca moths and fig wasps. Pp. 143–161. In F. Gilbert (ed). Genetics, Evolution and Coordination of Insect Life Cycles. Springer, London.

Adler, P. B., White, E. P., Lauenroth, W. K., Kaufman, D. M., Rassweiler, A. & Rusak, J. A. (2005) Evidence for a general species–time–area relationship. *Ecology*, 86, 2032–2039.

Adsersen, H. (1995) Research on islands: classic, recent, and prospective approaches. In Vitousek, P. M., Loope, L. L., and Adsersen, H. (eds.), Islands: Biological Diversity and Ecosystem Function, pp. 7-21. Berlin: Springer-Verlag.

Agrawal, A. A. (2000) Specificity of induced resistance in wild radish: causes and consequences for two specialist and two generalist caterpillars. *Oikos*, 89, 493–500.

Alamsyah, A.T. (2003) Sealand regionalism: new paradigm for water-based settlement development of the Jakarta metropolitan area. Seventh International Congress of APSA, Hanoi 2003: Planning theory and history. Asian Planning Schools Association (APSA), Hanoi, Vietnam.

Alba, C., Prioreschi, R., and Quintero, C. (2013) Population and leaf-level variation of iridoid glycosides in the invasive weed *Verbascum thapsus* L. (common mullein): implications for herbivory by generalist insects. *Chemoecology*, 23, 83–92.

Ali, J. G., and Agrawal, A. A. (2012) Specificity of plant–enemy interactions specialist versus generalist insect herbivores and plant defense. *Trends in Plant Science,* 17(5), 293-302.

Ali, J. R. and Huber, M. (2010) Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature,* 463, 653–656.

Allen, A. P. et al. (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, 297, 1545–1548.

Allen-Wardell, G., Bernhardt, P., Bitber, R., Burquez, A., Buchmann, S., Cane, J., Cox, P., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., JOnes, C., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G., Pavlik, B., Tepedina, V., Torchio, P., Walker, S. (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology*, 12, 8-17.

Almeida-Neto, M., Prado, P. I., Lewinsohn, T. M. (2011) Phytophagous insect fauna tracks host plant responses to exotic grass invasion. *Oecologia*, 165:1051–1062.

Alroy, J. (2002) How many named species are valid? *Proceedings of the National Academy of Sciences,* 99: 6.

Alsos, I. G. (2007) Frequent long-distance plant colonization in the changing Arctic. *Science,* 316: 1606–1609.

Anderson, D.L. & Trueman, J.H.W. (2000) *Varroa jacobsoni* (Acari: Varroida) is more than one species. *Experimental & Applied Acarology*, 24, 165–189.

Anderson, R. S. (1995) An evolutionary perspective on diversity in Curculionoidea. Memoirs of the *Entomological Society of Washington*, 14:103–118.

Anderson, R. S. (2002) Curculionidae Latreille 1802. Pp.722–815. In R. H. Arnett, Jr., M. C. Thomas, P. E. Skelley, and J. H. Frank (eds). American Beetles, Volume 2. CRC Press, NewYork.

Anderson, R. S. and Ashe, J. S. (2000) Leaf litter inhabiting beetles as surrogates for establishing priorities for conservation of selected tropical montane cloud forests in Honduras, Central America (Coleoptera; Staphylinidae, Curculionidae). *Biodiversity and Conservation*, 9: 617–653.

Andresen, E. (2003) Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography*, 26, 87–97.

Archangelsky, M., Beutel, R. G., and Komarek, A. (2005) Hydrophiloidea. Introduction, Phylogeny. Pp. 157–183. In R. G. Beutel and R. A. B. Leschen (eds). Handbook of Zoology: A Natural History of the Phyla of the Animal Kingdom, Volume IV. Arthropoda: Insecta, Part 38. Coleoptera, Beetles, Volume 1. Morphology and Systematics. Walter de Gruyter,Berlin.

Armes, N. J. (1988) The seasonal activity of Anthrenus sarnicus and some other beetle pests in the museum environment. *Journal of Stored Products Research,* 24, 29-37.

Arnaldos, M. I., Garcia, M. D., Romera, E., Presa, J. J., and Luna, A. (2005) Estimation of postmortem interval in real cases based on experimentally obtained entomological evidence. *Forensic Science International,* 149, 57-65.

Arnaldos, M. I., Romera,, E., Presa, J. J., Luna, A., and Garcia, M. D. (2004) Studies on seasonal arthropod succession on carrion in the southeastern Iberian Peninsula. *International Journal of Legal Medicine,* 118, 197-205.

Arnett,R. H., Jr. and Thomas, M. C. (eds). (2001) American Beetles, Volume 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, New York. 443pp.

Arnett, R. H., Thomas, M. C., Skelley, P. E., and Frank, J. H. (2002) American Beetles, Volume2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL. 861pp.

Arnold, A. E., and Squith, N. M. (2002) Herbivory in a fragmented tropical forest: patterns from islands at Lago Gatun, Panama. *Biodiversity and Conservation,* 11**,** 1663–1680.

As, S. (1984) To fly or not to fly? Colonization of Baltic Islands by winged and wingless Carabid beetles. *Journal of Biogeography*, 11(5), 413-426.

Audino, L. D., Louzada, J., and Comita, L. (2014) Dung beetles as indicators of tropical forest restoration success: Is it possible to recover species and functional diversity? *Biological Conservation*, 169, 248-257.

Aukema B (1991) Fecundity in relation to wing-morph of three closely related species of the *melanocephalus* group of the genus *Calathus* (Coleoptera, Carabidae). *Oecologia*, 87: 118–126.

Aukema B (1995) Flying for life: Wing dimorphism in closely related species of the genus *Calathus* (Coleoptera: Carabidae) Ph.D. thesis, Wageningen University, Ponsen & Loojien, Wageningen, The Netherlands, 168 pp.

Australian Bureau of Statistics. (2005) Australia's beef cattle industry. Year Book Australia, 2005. (www.abs.gov.au/Ausstats/abs@.nsf/ Previousproducts/1301.0Feature%20Article232005?opendocument& tabname=Summary&prodno=1301.0&issue=2005&num=&view=)

Australian Museum. 2010. Invertebrate Collection Manual. Australia.

Axmacher, J. C., Brehm, G., Hemp, A., Tunte, H., Lyaruu, H. V. M., Muller-Hohenstein, K., and Fiedler, K. (2009) Determinants of diversity in Afrotropical herbivorous insects (Lepidoptera: Geometridae): plant diversity, vegetation structure or abiotic factors? *Journal of Biogeography*, 36, 337–349.

Axmacher, J. C., Liu, Y., Wang, C., Li, L., Yu, Z. (2011) Spatial a-diversity patterns of diverse insect taxa in Northern China: Lessons for biodiversity conservation. Biological Conservation, 144, 2362–2368.

Axmacher, J. C., Tünte, H., Schrumpf, M., Müller-Hohenstein, K., Lyaruu, H. V. M., Fiedler, K. (2004) Diverging diversity patterns of vascular plants and geometrid moths during forest regeneration on Mt Kilimanjaro, Tanzania. *Journal of Biogeography*, 31(6), 895-904.

Axmacher, J.C., Kühne, L. & Vohland, K. (2008) Notes on α- and β-diversity pattern of selected moth families. In: Kühne, L. (ed.) Butterflies and Moth Diversity of the Kakamega Forest (Kenya). Brandenburgische Universitätsdruckerei, Potsdam, 35-46.

Baars, M. A. (1979) Catches in pitfall traps in relation to mean densities of carabids beetles. Oecologia, 41, 25-46.

Badan Pusat Statistik Indonesia/The Center of Indonesia-Statistic. (2009) Kepulauan Seribu Dalam Angka (1983 - 2009). Indonesian Government.

Ball, G. E. and Y. Bousquet. (2001) Carabidae Latreille,1810. Pp. 32–132. In R. H.Arnett, Jr. and M. C.Thomas (eds). American Beetles, Volume 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, New York.

Balthasar, V., 1969. Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region (Coleoptera Lamellicornia). Vol. 2. – Tschechoslowakische Akademie der Wissenschaften, Prague, 627 pp

Banks, J. E. (1998) The scale of landscape fragmentation affects herbivore response to vegetation heterogeneity. *Oecologia*, 117, 239-246.

Bappenas. (1993) Biodiversity Action Plan for Indonesia. Jakarta.

Barber, H. S. (1931) Traps for cave inhabiting insects. *Journal of the Elisha Michell Scientific Society*, 46, 259-266.

Barlow, J., Gardner, T. A., Araújo, I. S., Ávila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., Hernández, M. I. M., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. B., Mestre, L. A. M., Miranda-Santos, R., Nunes-Gutjahr, A. L., Overal, W. L., Parry, L., Peter, S. L., Ribeiro-Júnior, M. A., da Silva, M. N. F., da Silva Motta, C., Peres, C. A. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceeding of National Academy of Science*, 104(47): 18555–18560.

Barth, F. B. (1985) Insects and Flowers: The Biology of a Partnership. Princeton University Press, Princeton, NJ.

Barton, P., S. Cunningham, D. Lindenmayer, and A. Manning. (2012) The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia*, 3: 1-12.

Batzer, D. P., Wissinger, S. A. (1996) Ecology of insect communities in nontidal wetlands. *Annual Review of Entomology,* 41: 75–100.

Bay, E. (1974) Predator-prey relationships among aquatic insects. *Annual Review of Entomology,* 19: 441–453.

BCMAF, British Columbia Ministry of Agriculture and Food. (1990) Farm Structures Factsheet: Sizing Dairy Manure Storage Facilities. Abbotsford (Canada).

Beaver, R. A. (1979) Non-equilibrium island communities. A guild of tropical bark beetles. *Journal of Animal Ecology,* 48 (3), 987-1002.

Beaver, R. A., and Liu Y. L. (2010) An annotated synopsis of Taiwanese bark and ambrosia beetles, with new synonymy, new combinations and new records (Coleoptera: Curculionidae: Scolytinae). *Zootaxa*, 2602: 1–47.

Beaver, R. A., and Maddison, P. A. (1990) The bark and ambrosia beetles of the Cook Island and Niue (Coleoptera:Scolytidae and Platypodidae). *Journal of Natural History*, 24, 1365-1375.

Becker, P. (1975) Island Colonization by Carnivorous and Herbivorous Coleoptera. *Journal of Animal Ecology*, 44(3), 893-906.

Bellemain, E., and Ricklefs, R. E (2008) Are islands the end of the colonization road? Trends in Ecology and Evolution, 23(8), 461-468.

Bellini, R., F. Pederzani, R. Pilani, R. Veronesi, and S. Maini. (2000) *Hydroglyphus pusillus* (Fabricius) (Coleoptera Dytiscidae): its role as a mosquito larvae predator in rice fields. *Bollettino dell'Istituto di Entomologia* ''Guido Grandi'' della Universitadegli Studi di Bologna, 54: 155–163.

Benbow, M. E., Lewis, A. J., Tomberlin, J. K., and Pechal, J. L. (2013) Source seasonal necrophagous insect community assembly during vertebrate carrion decomposition. *Journal of Medical Entomology*, 50(2), 440-450.

Berenbaum, M. R. (1995) Bugs in the System. Insects and their Impact on Human Affairs. Addison-Wesley Publishing, Reading, Massachusetts, 377pp.

Bernhardt, P. (2000) Convergent evolution andadaptive radiation of beetle-pollinated angiosperms. *Plant Systematics and Evolution*, 222: 293–320.

Berry, A. (ed.) (2002) Infinite tropics: an Alfred Russel Wallace anthology. Verso, London.

Berry, R. E. (1998) Insects and Mites of Economic Importance in the Northwest 2nd Edition.

Beutel, R. G. (1995) Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. *Journal of Zoological Systematics and Evolutionary Research*, 33: 145–171.

Beutel, R. G. (2005) Myxophaga Crowson, 1955. Pp. 43–52. In R. G. Beutel and R. A. B. Leschen (eds). Handbook of Zoology: A Natural History of the Phyla of the Animal Kingdom, VolumeIV. Arthropoda: Insecta, Part 38. Coleoptera, Beetles, Volume 1. Morphology and Systematics. Walter de Gruyter, Berlin.

Beutel, R. G. and Haas, F. (2000) Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics*, 16: 1–39.

Beutel, R. G. and Komarek, A. (2004) Comparative study of thoracic structures of adults of Hydrophiloidea and Histeroidea with phylogenetic implications (Coleoptera, Polyphaga). *Organisms, Diversity and Evolution,* 4:1–34.

Beutel, R. G., and Leschen, R. A. B. (eds) (2005) Coleoptera, Volume 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter De Gruyter, Berlin.

Beutel, R. G. and Leschen, R. A. B. (2005) Phylogenetic analysis of Staphyliniformia (Coleoptera) based on characters of larvae and adults. *Systematic Entomology*, 30: 510–548.

Beutel, R. G.and Pollock, D. A. (2000) Larval head morphology of *Phycosecis litoralis* (Pascoe) (Coleoptera: Phycosecidae) with phylogenetic implications. *Invertebrate Taxonomy*, 14: 825–835.

Beutel,R. G. and Ribera, I. (2005) Adephaga Schellenberg, 1806. Pp. 53–55. In R. G. Beutel and R. A. B. Leschen (eds). Handbook of Zoology: A Natural History of the Phyla of the Animal Kingdom, Volume IV. Arthropoda: Insecta, Part 38. Coleoptera, Beetles, Volume 1. Morphology and Systematics. Walter de Gruyter, Berlin.

Beutel, R. G., M. Balke, and W. E. Steiner, Jr. (2006) The systematic position of Meruidae (Coleoptera,Adephaga) based on a cladistics analysis of morphological characters. *Cladistics*, 22: 102–131.

Bidart-Bouzat, M. D. and Kliebenstein, D. (2011) An ecological genomic approach challenging the paradigm of differential plant responses to specialist versus generalist insect herbivores. *Oecologia*, 167, 677–689.

Biesevac, L. and Majer, J. (2002) Cost effectiveness and data-yield of biodiversity surveys. *Journal of the Royal Society of Western Australia*, 85,129-132.

Bird, E., Ongkosongo, O., (1980) Environmental Changes on the Coasts of Indonesia. The United Nation University

BirdLife International. (2012) Important Bird Areas fact sheet. Indonesia

Blair, C. P., Abrahamson, W. G., Jackman, J. A., and Tyrrell, L. (2005) Cryptic speciation and host-race formation in a purportedly generalist tumbling flower beetle. *Evolution*, 59(2), 304-316.

Blair, R. B. (1999) Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? *Ecological Applications*, 9, 164-170.

Blair, R. B. (2004) The effects of urban sprawl on birds at multiple levels of biological organization. *Ecology and Society,* 9(5), 2.

Bluthgen, N., and Metzner, A. (2007) Contrasting leaf age preferences of specialist and generalist stick insects (Phasmida). *Oikos*, 116, 1853-1862.

Bodenheimer, F. (1951) Insects as Human Food: a Chapter of the Ecology of Man. Junk, The Hague. 352pp.

Boiteau, G. (2000) Efficiency of flight interception traps for adult Colorado Potato Beetles (Coleoptera: Chrysomelidae). *Ecology and Behaviour*, 93 (3).

Boltà, N. C., Rull, V., Sáez, A., Margalef, O., Bao, R., Rabes, S. P., Blaauw, M., Garcés, B. V., Giralt, S. (2013) Vegetation changes and human settlement of Easter Island during the last millennia: a multiproxy study of the Lake Raraku sediments. *,* 72, 36-48.

Bonada, N., Prat, N., Resh, V. H., and Statzner, B. (2006) Developments in aquatic insect biomonitoring: A comparative analysis of recent approaches. *Annual Review of Entomology*, 51, 495-523.

Bonneil, P., Bouget, C., Brustel, H., and Vallet, A. (2009) Insect sampling methods. In (eds.) Bouget, C., Nageleisen, L. M. Forest Insect Studies: Methods and Techniques, Key Consideration for Standardization. The French Office National des Forêts, Paris.

Borges, P. A. V., and Hortal, J. (2009) Time, area and isolation: factors driving the diversification of Azorean arthropods. *Journal of Biogeography*, 36, 178-191.

Bornemissza, G.F. (1970) Insectary studies on the control of the dung breeding flies by the activity of the dung beetle, *Onthophagus gazella* F. (Coleoptera: Scarabaeidae). *Journal of the Australian Entomological Society*, 9, 31–41.

Bornemissza, G. F. (1976) The Australian dung beetle project 1965–75. *Australian Meat Research Committee Review*, 30: 1–30.

Bornemissa, G. F. and Williams, C. H. (1970) An effect of dung beetle activity on plant yield. *Pedobiologia*, 10: 1–7.

Bouchard, P. (2002) Phylogenetic revision of the flightless Australian genus *Apterotheca* Gebien (Coleoptera:Tenebrionidae: Coelometopinae). *Invertebrate Systematics*, 16: 449–554.

Bouchard, P., Grebennikov, V. V., Smith, A. B. T., and Douglas, H. (2009) Biodiversity of Coleoptera. In: Footit, R. G., Adler, P. H. (eds.) Insect Biodiversity, Science and Society. Wiley-Blackwell, Oxford.

Bouchard, P. Wheeler, T. A., Goulet, H. (2006) Ground beetle (Coleoptera: Carabidae) from alvar habitat in Ontario. *Journal of the Entomological Society of Ontario*, 136, 3-23.

Bousquet, Y. (1990) Beetles Associated with Stored Products in Canada: An Identification Guide. Canada Department of Agriculture Publication, Otawa, Ontario.

Bowden, R. D. (1995) Using natural attributes of islands to examine the influence of biodiversity on ecosystem function. In Vitousek, P., Adsersen, H. and Loope. L. (eds.), Islands: Biological Diversity and Ecosystem Function, Springer Verlag, Heidelberg.

Bowers, M. D., Stamp, N. E., and Collinge, S. K. (1992) Early stage of host range expansion by a specialist herbivore, *Euphydras phaeton* (Nymphalidae). *Ecology*, 73, 526-536.

Boyer, A. G., Jetz, W. (2010) Biogeography of body size in Pacific island birds. *Ecography*, 33, 369-379.

BPPK (Badan Penelitian dan Pengembangan Kehutanan). (2010) Hutan Penelitian Dramaga. Ministry of Forestry, Republic of Indonesia.

Brehm, G., Süßenbach, D. & Fiedler, K. (2003) Unique elevational patterns of geometrid moths in an Andean montane rainforest. *Ecography*, 26, 456–466.

Brockerhoff , E. G., Jones, D. C., Kimberley, M. O., Suckling, D. M., Donaldson, T. (2006) Nationwide survey for invasive wood-boring and bark beetles (Coleoptera) using traps baited with pheromones and kairomones. *Forest Ecology and Management,* 228, 234-240.

Brockerhoff, E. G., Knızek, M., Bain, J., (2003) Checklist of indigenous and adventive bark and ambrosia beetles (Curculionidae: Scolytinae and Platypodinae) of New Zealand and interceptions of exotic species (1952–2000). *New Zealand Entomology*, 26, 29–44.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. & Hilton-Taylor, C. (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology,* 16, 909–923.

Brose, U. (2003) Island biogeography of temporary wetland carabid beetle communities. *Journal of Biogeography*, 30, 879–888.

Brown, E. S. (1954) The biology of the coconut pest *Melittomma insulare* (Col: Lymexylonidae), and its control in the Seychelles. *Bulletin of Entomological Research*, 45:1–66.

Brown, J. H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, 58, 445–449.

Brown, J. H. and Lomolino, M. V. (1998) Biogeography, 2nd eds. Sinauer Associates, Sunderland, MA, USA.

Brown, J. H. and Lomolino, M. V. (2000) Concluding remarks: historical perspective and the future of island biogeography theory. *Global Ecology & Biogeography*, 9, 87–92.

Brown, J., Scholtz, C.H., Janeau, J.L., Grellier, S. And Podwojewski, P. (2010) Dung beeltes (Coleoptera: Scarabaeidae) can improve soil hydrological properties. *Applied Soil Ecology*, 46, 9–16.

Brown, K. S. (1997) Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. *Journal of Insect Conservation*, 1(1): 25–42.

Brown, W. L. and Wilson, E. O. (1956) Character displacement. *Systematical Zoology*, 5, 49-64.

Browne, F.G. (1961) The biology of Malayan Scolytidae and Platypodidae. *Malayan Forest Records*, 22, 1–255.

Bruenig, E. F. (1996) Conservation and Management of Tropical Rainforests. CAB International, Wallingford.

Brues, C. T. (1946) Insect Dietary. An Account of the Food Habits of Insects. Harvard University Press, Cambridge, Massachusetts.466pp.

Brustel, H. (2004) Biological value of French forests assessed with saproxylic beetles: a way to conserve this natural heritage. Proceedings of the 3rd European Symposium and Workshop on the Conservation of Saproxylic Beetles. Riga, Latvia, July 7th-11th 2004.

Bunnefeld, N. and Phillimore, A. B. (2012) Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature's experiments. *Ecography*, 35: 15–22.

Burel, F., Butet, A., Delettre, Y.R. & De La Peña, M.N. (2004) Differential response of selected taxa to landscape context and agricultural intensification. *Landscape and Urban Planning*, 67, 195–204.

Burke, H. R., Clark, W. E., Carte, J. R., and Fryxell, P. A. (1986) Origin and dispersal of the boll weevil. *Bulletin of the Entomological Society of America*, 32: 228–238.

Bussler, H., Bouget, C., Brustel, H., Brändle, M., Riedinger, V., Brandl, R., Müller, J. (2011) Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns. *Forest Ecology and Management,* 262, 1887-1894.

Butterfield, J., Luff, M. L., Babes, M., Eyre, M. D. (1995) Carabid beetle communities as indicators of conservation potential in upland forests. *Forest Ecology andManagement*, 79, 63-77.

Caltagirone, L. E. (1981) Landmark examples in classical biological control. *Annual Review of Entomology,* 26: 213–232.

Caltagirone, L. E. and R. L. Doutt. (1989) The history of the vedalia beetle importation to California and its impact on the development of biological control. *Annual Review of Entomology,* 34: 1–16.

Campbell, J. M., Sarazin, M. J., and Lyons, D. B. (1989) Canadian Beetles (Coleoptera) Injurious to Crops, Ornamental Stored Products, and Buildings. Research Branch Agriculture Canada Publication 1826, Ottawa, Ontario.

Campobasso, C. P., Di Vella, G., and Introna, F. (2001) Factors affecting decomposition and Diptera colonization. *Forensic Science International*, 120, 18-27.

Canning-Clode, J., Bellouc, N., Kaufmann, M. J., Wahl, M. (2009) Local–regional richness relationship in fouling assemblages – Effects of succession. *Basic and Applied Ecology*, 10, 745–753.

Capinera, J. L., Gardener, D. R.,and Stermitz, F. R. (1985) Cantharidin levels in blister beetles (Coloeoptera: Meloidae) associated with alfalfa in Colorado. *Journal of Economic Entomology*, 78: 1052–1055.

Cardoso, P. et al. (2010) Drivers of diversity in Macaronesian spiders and the role of species extinctions. *Journal of biogeography*, 37, 1034–1046.

Carpenter, G. H. (1928) The Biology of Insects. Sidgwick and Jackson,London.473pp.

Carroll, S. P., and Boyd, C. (1992) Host race radiation in the soapberry bug: natural history with the history. *Evolution*, 46, 1053-1069.

Carson, H. L., Hardy, D. E., Spieth, H. T., Stone, W. S. (1970) The evolutionary biology of the Hawaiian Drosophilidae. In: Hecht, M. K., Steere, W. C. (eds.) Essays in evolution and genetics in honour of Theodosius Dobzhansky. Appleton-Century Crofts, New York.

Cartagena, M. C., and Galante, E. (2002) Loss of Iberian island tenebrionids beetles and conservation management recommendations. *Journal of Insect Conservation*, 6, 673-681.

Case, T. J. (1975) Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. *Ecology,* 56, 3–18.

Caterino, M. S., Hunt, T., and Vogler, A. P. (2005) On the constitution and phylogeny of Staphyliniformia (Insecta: Coleoptera). *Molecular Phylogenetics and Evolution*, 34: 655–672.

Catterall, C. P. (2009) Responses of faunal assemblages to urbanisation: global research paradigms and an avian case study. Pages 129-155 in M. J. McDonnell, A. K. Hahs, and J. H. Breuste, editors. Ecology of cities and towns: a comparative approach. Cambridge University Press, New York, New York, USA

Centeno, N., Maldonado, M., and Oliva, A. (2002) Seasonal patterns of arthropods occurring on sheltered and unsheltered pig carcasses in Buenos Aires Province (Argentina). *Forensic Science International*, 126, 63-70.

The Center of Indonesia-Statistic (2009) Kepulauan Seribu Dalam Angka (1983–2009), Indonesian Government.

Chaddick, P. R. and Leek, F. F. (1972) Further specimens of stored product insects found in ancient Egyptian tombs. *Journal of Stored Products Research*, 8: 83–86.

Chao, A., Chiu, C.-H., and Jost, L. (2010) Phylogenetic diversity measures based on Hill numbers. *Philosophical Transactions of the Royal Society B,* 365: 3599–3609.

Chao, A., Nicholas, J. G., Gotelli, J.,Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., Ellison, A. M. (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84: 45–67.

Chape, S., Harrison, J., Spalding, M., and Lysenko, I. (2005) Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 360 : 443.

Chatzimanolis, S., Norris, L. A., Caterino, M. S. (2010) Multi-Island Endemicity: Phylogeography and Conservation of Coelus pacificus (Coleoptera: Tenebrionidae) Darkling Beetles on the California Channel Islands. *Annals of the Entomological Society of America*, 103, 785-795.

Chown, S. L. (1998) Ecological biogeography of Southern Ocean islands: species area relationships, human impacts, and conservation. *American Naturalist,* 152, 562–575.

Chown, S. L., Gremmen, N. J. M., and Gaston, K. J. (1998) Ecological Biogeography of Southern Ocean Islands: Species-Area Relationships, Human Impacts, and Conservation. *The American Naturalist*, 152(4), 562-575.

Chown, S. L., Hull, B., and Gaston, K. J. (2005) Human impacts, energy availability and invasion across Southern Ocean Islands. *Global Ecology and Biogeography,*14, 521–528.

Chown, S. L. and Smoith, V. R. (1993) Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia*, **96**, 508–516

Clarke, G. M., (2000) Inferring demography from genetics: a case study of the endangered golden sun moth, Synemon plans. *Biological Conservation,* 92, 371-381.

Clarke, K. R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18, 117-143.

Clarke, W. H. and Bloom, P. E. (1992) An efficient and inexpensive pitfall trap system. *Entomological News*, 103, 55-59.

Clausen, C. P. (1940) Entomophagous Insects. McGraw-Hill Book Co. NewYork. 688pp.

Clausen, C. P. (1952) Parasites and predators. Pp. 380–388. In Insects. The Yearbook of Agriculture 1952. United States Department of Agriculture, Washington, DC.

Clausen,C.P. (1976) Phoresy among entomophagous insects. *Annual Review of Entomology,* 21: 343–368.

Clausen, C. P. (1978) Scarabaeidae. Pp. 277–292. In C. P. Clausen (ed). Introduced Parasites and Predators of Arthropod Pests and Weeds: A World

Review. United States Department of Agriculture Handbook No. 480. Washington, DC.

Cole, F. R., Medeiros, A. C., Loope, L. L., Zuehlke, W. W. (1992) Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology*, 73, 1313-1322.

Convention on Biological Diversity (CBD). (www.cbd.int/)

Cook, L. G. and Crisp, M. D. (2005) Directional asymmetry of long-distance dispersal and colonization could mislead reconstructions of biogeography. *Journal of Biogeography,* 32: 741–754.

Cooper, J., Hockney, P. A. R., Brooke, R. K. (1985) Introduced mammals in South and South West African islands: history, effects on birds and control. In: Bunning, L. J. (eds.) Proc Birds and Man Symposium. Witwatersrand Bird Club, Johannesburg, 179-203.

Cooter, J. & Barclay, M.V.L. (2006) A Coleopterist's Handbook . Amateur Entomological Society.

Costanza, R. and Mageau, M. (2000) What is a healthy ecosystem? *Aquatic Ecology*, 33, 105-115.

Courtney, S. P., and Kibota, T. T. (1990) Mother doesn't always know best: selection of hosts by ovipositing insects. In: E. A. Bernays, editor. Insect-plant interactions, volume 2. CRC Press, Boca Raton, Florida. Pages 162-188.

Cox, C. B. & Moore, P. D. (1985) Biogeography: an ecological and evolutionary approach. Blackwell Scientific Publications, Oxford.

Crane, E. (1990) Bees and Beekeeping: Science, Practice and World Resources. Ithaca (NY), Comstock.

Crawford, C. S., Mackay, W. P., and Cepeda-Pizarro, J. G. (1993) Detrivores of the Chilean arid zone (27–32S) and the Namib Desert: a preliminary comparison. *Revista Chilenade Historia Natural*, 66: 283–289.

Crepet, W. L. (1979) Insect pollination: a paleontological perspective. *BioScience*, 29: 102–108.

Crepet, W. L. (1983) The role of insect pollination in the evolution of angiosperms. Pp. 31–50. In L. Real (ed). Pollination Biology. Academic Press, New York.

Crews, S. C., Puente-Rolónc, A. R., Rutsteina, E., Gillespie, R. G. (2010) A comparison of populations of island and adjacent mainland species of Caribbean Selenops (Araneae: Selenopidae) spiders. *Molecular Phylogenetics and Evolution,* 54: 970–983.

Crooks, K. R., Suarez, A. V., and Bolger, D. T. (2004) Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biological Conservation,* 115, 451-462.

Curtis, D. J. (1980) Pitfalls in spider community studies (Arachnida: Aranae). *Journal of Arachnology*, 8, 271-280.

Cushman, J. H. (1995) Ecosystem-level consequences of species additions and deletions on islands. In: In Vitousek, P. M., Loope, L. L., and Adsersen, H. (eds.), Islands: Biological Diversity and Ecosystem Function, pp. 7-21. Berlin: Springer-Verlag.

Dacke, M., Nordstrom, P., Scholtz, C. H. (2003) Twilight orientation to polarised light in the crepuscular dung beetle Scarabaeus zambezianus. *Journal of Experimental Biology*, 206, 1535-1545.

Dadour, I., and Allen, J. (2001) Control of bush flies by dung beetles. Department of Agriculture Farm note Series: 1991. (14 February 2006; http://agspsrv34.agric.wa.gov.au/agency/pubns/farmnote/1991/F05891.htm)

Dahl, A. 2004. United Nations Environment Programme Island Directory. (http://islands.unep.ch/isldir.htm).

Darwin, C. 1859. On the Origin of Species by means of Natural Selection. John Murray, London.

Da Silva, P. G., Hernandez, M. I. M (2014) Local and regional effects on community structure of dung beetles in a mainland-island scenario. *PLoS ONE* 9(10).

Da Silva, P. G., Vaz-de-Mello, F. Z., Di Mare, R. A. (2013) Diversity and seasonality of Scarabaeinae (Coleoptera: Scarabaeidae) in forest fragments in

Santa Maria, Rio Grande do Sul, Brazil. *Anais de Academia Brasileira de Ciencias,* 85, 679–697.

Davidson, G. (1974) Genetic Control of Insect Pests. Academic Press, London. 158pp.

Davidson, R. L., Rykken, J., and Farrell, B. (2011) Carabid beetle diversity and distribution in Boston Harbour Islands national park area (Coleoptera, Carabidae). *ZooKeys,* 147, 497-526.

Davies, A. L. V., Philips, T. K. (2005) Effect of deforestation on a southwest Ghana dung beetle assemblage (Coleoptera: Scarabaeidae) at the periphery of Ankasa Conservation Area. *Environmental Entomology*, 34, 1081-1088.

Davies, K. F., and Margules, C. R. (1998) Effects of habitat fragmentation on carabid beetles: experimental evidence. *Journal of Animal Ecology,* 67, 460-471.

Davies, K. F., Margules, C. R., and Lawrence, J. F. (2000) Which traits of species predict population declines in experimental forest fragments? *Ecology*, 81(5), 1450-1461.

Davies, S. J., Chown, S. L., and Joubert, L. J. (2007) Renewed management systems and provisions for South Africa's sub-Antarctic islands. *Papers and Proceedings of the Royal Society of Tasmania*, 141, 115–120.

Davis, A. J., Huijbregts, H., Krikken, J. (2000) The role of local and regional processes in shaping dung beetle communities in tropical forest plantations in Borneo. *Global Ecology and Biogeography*, 9, 281–292.

Davis, A. L. (1994) Habitat fragmentation in southern Africa and distributional response patterns in five specialist or generalist dung beetle families (Coleoptera). *African Journal of Ecology,* 32, 192-207.

Davis, A. L. V. and Philips, T. K. (2005) Effect of Deforestation on a Southwest Ghana Dung Beetle Assemblage (Coleoptera: Scarabaeidae) at the Periphery of Ankasa Conservation Area. *Environmental Entomology*, 34(5), 1081-1088.

Davis, A. L. V., Scholtz, C. H., Philips, T. K. (2002) Historical biogeography of scarabaeine dung beetles. *Journal of Biogeography*, 29, 1217-1256.

Davis, G. A., Havill, N. P., Adelman, Z. N., Caccone, A., Kok, L. T., Salom, S. M. (2011) DNA barcodes and molecular diagnostics to distinguish an introduced and native Laricobius (Coleoptera: Derodontidae) species in eastern North America. *Biological Control*, 58(1), 53-59.

Davis, M. (2003) Biotic globalization: does competition from introduced species threaten biodiversity? *BioScience*, 53(5), 481-489.

Day, R. W., and Quinn, G. P. (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs,* 59, 433-463.

DeBach, P. (1966) The competitive displacement and coexistence principle. *Annual Review of Entomology,* 11: 183–212.

DeBach, P. (1974) Biological Control by Natural Enemies. Cambridge University Press, London. 323pp.

DeBach, P. and O. Rosen. (1991) Biological Control by Natural Enemies, Second Edition. Cambridge University Press, Cambridge. 440pp.

De Clerck-Floate, R. A., Wikeem, B. M., and Bourchier, R. S. 2005. Early establishment and dispersal of the weevil, Mogulones cruciger (Coleoptera: Curculionidae) for biological control of houndstongue (Cynoglossum officinale) in British Columbia, Canada. Biocontrol Science and technology, 15, 173-190.

DeFoliart, G. R. (1989) The human use of insects as food and as animal feed. *Bulletin of the Entomological Society of America*, 35: 22–35.

DeFoliart, G. R. (1992) Insects as human food. *Crop Protection*, 11: 395–399.

DeFoliart, G. R. (1999) Insects as food and why the Western attitude is important. *Annual Review of Entomology*, 44: 21–50.

De La Peña, M.N., Butet, A., Delettre, Y., Morant, P. & Burel, F. (2003) Landscape context and carabid beetle (Coleoptera: Carabidae) communities of hedgerows in western France. *Agriculture, Ecosystems & Environment*, 94, 59–72.

Dembilio, O., Jacas, J. A. (2010) Basic bio-ecological parameters of the invasive Red Palm Weevil, Rhynchophorus ferrugineus (Coleoptera: Curculionidae), in Phoenix canariensis under Mediterranean climate. *Bulletin of Entomological Research*, 101, 153-163.

Den Boer, P. J. (1970) On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). *Oecologia*, 4:1–28.

Den Boer, P. J. (1990) The survival value of dispersal in terrestrial arthropods. *Biological Conservation,* 54:175–192.

Den Boer, P. J., Van Huizen, T. H. P., Den Boer-Daanje, W., Aukema, B., Den Bieman, C. F. M. (1980) Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera, Carabidae). *Entomological Genetics,* 6:107–134.

Dengler, J. (2009) Which function describes the species–area relationship best? A review and empirical evaluation. *Journal of Biogeography*, 36, 728–744.

Dennis, P. Young, M. R., Howard, C. L., and Gordon, I. J. (1997) The response of epigeal beetles (Coleoptera: Carabidae, Staphylinidae) to varied grazing regimes on upland Nardus stricta grasslands. *Journal of Applied Ecology*, 34, 433-443.

Desender, K. (2000) Flight muscle development and dispersal in the life cycle of carabid beetles: patterns and processes. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie*, 70: 13–31.

Desender, K., and Baert, L. (1996) Easter Island revisited: carabid beetles (Coleoptera: Carabidae). *The Coleopterists Bulletin*, 50(4), 343-356.

Diamond, J. M., Bishop, K. D., and van Balen, S. (1987) Bird survival in an isolated Javan woodland: island or mirror? *Conservation Biology*, 1, 132-142.

Didham, R. K., Hammond, P. M., Lawton, J. H., Eggleton, P., and Stork, N. E. (1998) Beetle species responses to tropical forest fragmentation. *Ecological Monographs*, 68, 295-323.

Diffendorfer, J. E., Gaines, M. S., and Holt, R. D. (1995) Habitat fragmentation and movements of three small mammals (Sigmodon, Microtus, and Peromyscus). *Ecology,* 76, 827- 839.

Diver, K. C. (2008) Not as the crow flies: assessing effective isolation for island biogeographical analysis. *Journal of Biogeography,.* 35: 1040–1048.

Dobbs, T. T., Brodel, C. F., (2004) Cargo aircraft as a pathway for the entry of nonindigenous pests into South Florida. *Florida Entomology.* 87, 65–78.

Dodson, C. H. (1975) Coevolution of orchids and bees. Pp.91–99. In L.E. Gilbert and P. H. Raven (eds). Coevolution of Animals and Plants. University of Texas Press, Austin.

Donnelly, R., and Marzluff, J. M. (2004) Importance of reserve size and landscape context to urban bird conservation. *Conservation Biology,* 18, 733-745.

Donnelly, R., and Marzluff, J. M. (2006) Relative importance of habitat quantity, structure, and spatial pattern to birds in an urbanizing region. *Urban Ecosystems,* 9, 99-117.

Dooley, J. L., and Boweres, M. A. (1998) Demographic responses to habitat fragmentation: experimental tests at the landscape and patch scale. *Ecology,* 79, 969-980.

Doube, B. M. (1990) A functional classification for analysis of the structure of dung beetle assemblages. *Ecological Entomology,* 15: 371- 383.

Dowd, P. F. (2000) Dusky sap beetle (Coleoptera: Nitidulidae) and other kernel damaging insects in Bt and non-Bt sweet corn in Illinois. *Journal of Economic Entomology*, 93, 1714-1720.

Doyen, J. T. (1976) Marine beetles (Coleoptera excluding Saphylinidae) In Cheng, L. (ed). Marine Insects. North-Holland Publishing, Amsterdam.

Driscoll, D. A., and Weir, T. (2005) Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. *Conservation Biology*, 19(1), 182-194.

Duan, J. J., M. S. Paradise, J. G. Lundgren, J. T. Bookout, C. J. Jiang, and R. N. Wiedenmann. (2006) Assessing non target impacts of Bt corn resistant to root worms: tier-1 testing with larvae of *Poecilus chalcites* (Coleoptera: Carabidae). *Environmental Entomology,* 35: 135–142.

Duncan, R. P., Boyer, A. G., Blackburn, T. M. (2013) Magnitude and variation of prehistoric bird extinctions in the Pacific. *Proceedings of National Academy of Science USA*, 110(16):6436–6441.

Eggers, H. (1923) Neue indomalayische Borkenkäfer (Ipidae). *Zoologische Mededeelingen*, 7, 129–220.

Eidmann. H. H. (1992) Impact of bark beetle on forests and forestry in Sweden. *Zeitschrift fur Angewandte Entomologie*, 114, 193-200.

Eliasson, U. (1995) Patterns of diversity in island plants. In: Vitousek, P. M., Loope, L. L., Adsersen, H (eds). Islands, Biological Diversity and Ecosystem Function. Springer-Verlag, New York.

Ellers-Kirk, C. and Fleischer, S. J. (2006) Development and life table of Acalyma vittatum (Coleoptera: Chrysomelidae), a vector of Erwinia tracheiphila in cucurbits. *Environmental Entomology* 35, 875-880.

Ellis, E.C. & Ramankutty, N. (2008) Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, 6, 439–447.

Emerson, B. C., Oromi, P. (2005) Diversification of the forest beetle genus Tarphius on the Canary Island, and the evolutionary origins of island endemics. *Evolution*, 59(3), 586-598.

Encyclopaedia Britannica (1997) Encyclopaedia Britannica (UK) Ltd.

Encyclopaedia Britannica (2012) Encyclopaedia Britannica (UK) Ltd.

Erwin, T. L. (1982) Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin*, 36: 74–75.

Erwin, T. L. (1983) Tropical forest canopies, the last biotic frontier. *Bulletin of the Entomological Society of America*, 29: 14–19.

Erwin, T. L. (1988) The tropical forest canopy: the heart of biotic diversity. Pp.123–129. In E. O. Wilson and F. M. Peter (eds). Biodiversity National Academy Press, Washington, DC.

Erwin,T. L. (1991) Natural history of the carabid beetles at the BIOLAT Biological Station, Rio Manu, Pakitza, Peru. *Revista Peruana de Entomologia,*33: 1–85.

Erwin, T. L. (1993) Biodiversity at its utmost: tropical forest beetles. Pp. 27–68. In M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson (eds). Biodiversity II. Understanding and Protecting our Biological Resources. Joseph Henry Press, Washington, DC.

Erwin, T. L. (1997) Biodiversity at its utmost: tropical forest beetles. In: Reaka-Kudla, M. L., Wilson, D. E., Wilson, E. O. (eds). Biodiversity II. Understanding and Protecting Our Biological Resources. Joseph Henry Press, Washington, D. C.

Estrada, A., and Coates-Estrada, R. (2002) Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. *Biodiversity and Conservation,* 11**,** 1903–1918.

Ewl, J. J., Hogberg, P. (1995) Experimental studies on islands. In Vitousek, P. M., Loope, L. L., and Adsersen, H. (eds.), Islands: Biological Diversity and Ecosystem Function, pp. 7-21. Berlin: Springer-Verlag.

Farhan, A. M., and Lim, S. (2012) Vulnerability assessment of ecological conditions in Seribu Islands, Indonesia. *Ocean & Coastal Management*, 65, 1 - 14.

Farhan, A. R., Lim, S. (2011) Resilience assessment on coastline changes and urban settlements: A case study in Seribu Islands, Indonesia. *Ocean and Coastal Management, 5*4, 391-400.

Farrell, B. D. (1998) Inordinate fondness explained: why are there so many beetles. *Science*, 281: 555–559.

Fattorini, S. (2002) Biogeography of the tenebrionid beetles (Coleoptera; Tenebrionidae) on the Aegean Islands (Greece). *Journal of Biogeography*, 29(1), 49-67.

Fattorini, S. (2010) The influence of geographical and ecological factors on island beta diversity patterns. *Journal of Biogeography*, 37, 1061–1070.

Fattorini, S. (2011) Influence of island geography, age and landscape on species composition in different animal groups. *Journal of Biogeography*, 38, 1318-1329.

Fattorini, S. & Fowles, A. P. (2005) A biogeographical analysis of the tenebrionid beetles (Coleoptera, Tenebrionidae) of the island of Thasos in the context of the Aegean Islands (Greece). *Journal of Natural History*, 39:46, 3919-3949

Fauzi, A. & Buchary, E.A. 2002. A socioeconomic perspective of environmental degradation at Kepulauan Seribu Marine National Park, Indonesia. *Coastal Management,* 30, 167–181.

Favila, M. and Halffter, G. (1997) Indicator groups for measuring biodiversity. *Acta Zoologica Mexicana* (n.s.), 72, 1–25.

Feer, F. & Hingrat, Y. (2005) Effects of forest fragmentation on a dung beetle community in French Guiana. *Conservation Biology*, 19, 1103–1112.

Feer, F. (1999) Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest. *Journal of Tropical Ecology*, 15, 129–142.

Fenster, C. B., Ambruster, W. S., Wilson, P., Dudash, M. R., and Thomson, J. D. (2004) Pollination syndrome and floral specialisation. *Annual Review of Ecology, Evolution and Systematics*, 35, 375-403.

Fichter, E. (1941) Apparatus for the comparison of soil surface arthropod population. *Ecology*, 22, 338-339.

Finch, S. 1990. The effectiveness of traps used currently for monitoring population of the cabbage root fly (*Delia radicum*). *Annals of Applied Biology,* 116, 447-454.

Fincher, G.T. (1973) Dung beetles as biological control agents for gastrointestinal parasites of livestock. *Journal of Parasitology*, 59, 396–399.

Fincher, G. T. (1981) The potential value of dung beetles in pasture ecosystems. *Journal of Georgia Entomological Society*, 16, 301-316.

Fincher, G. T. (1986) Importation, colorization, and release of dung-burying scarabs. Miscellaneous Publications of the Entomological Society of America, 62: 69–76.

Fisher, B. L. (1998) Insect behavior and ecology in conservation: preserving functional species interactions. *Annals of the Entomological Society of America*, 91: 155–158.

Fisher, R. C. (1988) An inordinate fondness for beetles. *Biological Journal of the Linnean Society*, 35: 313–319.

Fisher, R.A., Corbet, A. & Williams, C.B. (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology*, 12, 42–58.

Fitter R. (1974) Most endangered mammals: an action programme. Oryx, 12 (436).

Fonseca, C. R. (2009) The silent mass extinction of insect herbivores in biodiversity hotspots. *Conservation Biology,* 23:1507–1515.

Food and Agriculture Organization of the United Nations (FAO). (www.fao.org)

Footit, R. G., Adler, P. H. (eds.) Insect Biodiversity, Science and Society. Wiley-Blackwell, Oxford

Foufopoulos, J., Ives, A. R. (1999) Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. *The American Naturalist*,153:1–25.

Fournier, E., Loreau, M. (2001) Respective roles of recent hedges and forest patch remnants in the maintenance of ground-beetle (Coleoptera: Carabidae) diversity in an agricultural landscape. *Landscape Ecology*,16: 17–32.

Fox, B. J. & Fox, M. D. (2000) Factors determining mammal species richness on habitat islands and isolates: habitat diversity, disturbance species interactions and guild assembly rules. *Global Ecology & Biogeography*, 9, 19–37.

Fox, C. W. (2006) Colonization of a new host by a seed feeding beetle: genetic variation, maternal experience, and the effect of an alternate host. *Annales Zoologici Fennici* 43:239-247.

Fox, C. W., Czesak, M. E., and Fox, R. W. (2001) Consequences of plant resistance for herbivore survivorship, growth, and selection on egg size. *Ecology*, 82, 2790-2804.

Fox, C. W., Gordon, D. M., Bojang, P. (2006) Genetic and environmental sources of variation in survival on non-native host species in the generalist seed beetle, *Stator limbatus. The Southwestern Naturalist*, 51(4), 490-501.

Fox, C. W., Harbin, A. D., and Mousseau, T. A. (1996) Suitability of a non-host palo verde for development of *Stator limbatus* (Coleoptera; Bruchidae) larvae. *Pan-Pacific Entomologist,* 72, 31-36.

Frantsevich, L., Dai, Z., Wang, W. Y., Zhang, Y. (2005) Geometry of elytra opening and closing in some beetles (Coleoptera, Polyphaga). *Journal of Experimental Biology*, 208, 3145-3158.

Fraser, S. M., and Lawton, J. H. (1994) Host range expansion by British moths onto introduced con ifers. *Ecological Entomology,* 19, 127-137.

Freitag, R. (1979) Carabid beetles and pollution. Pp.485–506. In T. L. Erwin, G. E. Ball, D. R. Whitehead, and A. L. Halpern (eds). Carabid Beetles: Their Evolution, Natural History, and Classification. Junk, The Hague.

French, S. S., DeNardo, D. F., Greives, T. J., Strand, C. R., Demas, G. E. (2010) Human disturbance alters endocrine and immune responses in the Galapagos marine iguana (*Amblyrhynchus cristatus*). Hormon Behaviour, 58(5), 792-799.

Frenot, Y., Gloaguen, J. C., Masse, L. and Lebouvier, M. (2001) Human activities, ecosystem disturbance and plant invasions in subantarctic Crozet, Kerguelen and Amsterdam Islands. *Biological Conservation*, 101, 33-50.

Freuler, J., G. Blandenier, H. Meyer, and P. Pignon. (2001) Epigeal fauna in a vegetable agroecosystem. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 74: 17–42.

Frolov, A.V., Akhmetova, L.A. & Scholtz, C.H. (2008) Revision of the obligate mushroom-feeding African "dung beetle" genus *Coptorhina* Hope (Coleoptera: Scarabaeidae: Scarabaeinae). *Journal of Natural History*, 42, 1477–1508

Fullard, J. H. Barclay, R. M. R., and Thomas, D. W. (2010) Observations on the behavioural ecology of the Atiu Swiftlet *Aerodramus sawtelli*. *Bird Conservation International*, 20 (4), 385-391.

FWI/GFW. (2002) The State of the Forest: Indonesia. Bogor, Indonesia: Forest Watch Indonesia, and Washington DC: Global Forest Watch.

Gadeberg, R. M. E. and Boomsma, J. J. (1997) Genetic population structure of the large blue butterfly Maculinea arcon in Denmark. *Journal of Insect Conservation,* 1, 99-111.

Gagné, S. A., and Fahrig, L. (2010) The trade-off between housing density and sprawl area: minimizing impacts to forest breeding birds. *Basic and Applied Ecology,* 1(1), 723-733.

Gallagher, E.D. (1998) Compah96, http://www.es.umb.edu/faculty/edg/files/pub/COMPAH.EXE (15.05.2004).

Ganho, N. G., Marinoni, R. C. (2005) A diversidade inventarial de Coleoptera (Insecta) em uma paisagem antropizada do Bioma Araucária. *Revista Brasileira De Entomologia*, 49(4):535–543.

Ganzhorn, J. U., Lowry, P. P., Schatz, G. E., Sommer, S. The biodiversity of Madagascar: one of the world's hottest hotspots on its way out. Oryx, 35, 346 - 348.

Garcia-Salazar, C. G., Gildow, F. E., Fleischer, S. J., Cox-Foster, D., and Lukezic, F. L. (2000) ELISA versus immunolocalization to determine the association of *Erwinia tracheiphila* in *Acalymma vittatum* (F.) (Coleoptera: Chrysomelidae). *Environmental Entomology*, 29: 542–550.

Gard, T. C. (1984) Persistence in food webs. Pages 208-219 *in* S. A. Levin and T G. Hallam, editors. *Mathematical ecology*. Springer Verlag, Berlin, Germany.

Gardner, T. A., Barlow, J., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B. (2008) The cost-effectiveness of biodiversity surveys in tropical forests. *Ecological Letter,* 11, 139–150.

Gardner, T. A., Hernndez, M. I. M., Barlow, J., Peres, C. A. (2008) Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *Journal of Applied Ecology,* 45, 883–893.

Gaston, K. J. (1991) The magnitude of global insect species richness. *Conservation Biology*, 5: 283–296.

Gaston, K. J. (2000) Global patterns in biodiversity. *Nature,* 405, 220-227.

Gaston, K. J., and Fuller, R. A. (2008) Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution*, 23:14–19.

Gentile, G., Argano, R. 2005. Island biogeography of the Mediterranean sea: the species–area relationship for terrestrial isopods. Journal of Biogeography, 32, 1715–1726.

Germaine, S. S., Rosenstock, S. S., Schweinsburg, R. E. and Richardson, W. S. (1998) Relationships among breeding birds, habitat, and residential development in Greater Tucson, Arizona. *Ecological Applications*, 8:680-69

Gibbs, G.W. (2010) Do New Zealand invertebrates reflect the dominance of birds in their evolutionary history? *New Zealand Journal of Ecology*, 34, 152–157.

Gibbs, J. P., and Stanton, E. J. (2001) Habitat fragmentation and arthropod community change: carrion beetles, phoretic mites, and flies. *Ecological Applications*, 11, 79-85.

Giblin-Davis, R. M., Pena, J. M., and Duncan, R. E. (1994) Lethal pitfall trap for the evaluation of semiochemical-mediated attraction of Metamasius hemipterus sericues (Coleoptera: Curculionidae). *Florida Entomologist*, 77, 247-255.

Gilbert, F. S. (1980) The equilibrium theory of island biogeography: fact or fiction? *Journal of Biogeography*, 7, 209–235.

Gill, G. J. (2005) Decomposition and arthropod succession on above ground pig carrion in rural Manitoba.University of Manitoba, Winnipeg, Manitoba, Canada.

Gillard, P. (1967) Coprophagous beetles in pasture ecosystems. *Journal of the Australian Institute of Agricultural Science*, 33: 30–34.

Gillespie, R. G., and Roderick, G. K. (2002) Arthropods on islands: colonization, speciation, and conservation. *Annual Review of Entomology,* 47:595-632.

Gilpin, M. E. & Hanski, I. (1991) Metapopulation dynamics: empirical and theoretical investigations. Cambridge University Press, Cambridge.

Goldberg, L. (1996) A history of pest control measures in the anthropology collections, National Museum of natural History, Smithsonian Institution. *Journal of the American Institute of Conservation,* 35, 23-43.

Goldstein, P. Z., Simmons, T. (2002) A checklist and commentary on the scarabaeid fauna of the Massavhusetts offshore islands (Coleoptera: Scarabaeidae*). Journal of the New York Entomological Society*, 110(3), 389-401.

Göltenboth, F., Timotius, K. H., Milan, P. P., and Margraf, J. (2006) Ecology of Insular Southeast Asia: The Indonesian Archipelago. Elsevier.

Gómez, A. S. (2010) Activity density versus biomass distribution patterns among ground-beetle species as bioindicator for conservation planning over a wide range of altitudes in Tenerife (Canary Islands). *Ecological Indicators*, 10, 1213-1217.

Gotelli, N. J., and Chao, A. (2013) Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. Pages 195–211 in S. A. Levin, editor. The encyclopaedia of biodiversity. Second edition, volume 5. Academic Press, Waltham, Massachusetts, USA.

Gotelli, N. J., and Collwell, R. K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters,* 4: 379–391.

Grassle, J.F., and Smith, W. (1976) Similarity measure sensitive to contribution of rare species and its use in investigation of variation in marine benthic communities. *Oecologia*, 25,13-22.

Gray, J. S., Ugland, K. I. & Lambshead, J. (2004a) Species accumulation and species area curves – a comment on Scheiner (2003). *Global Ecology and Biogeography*, 13, 469– 476.

Gray, J. S., Ugland, K. I. & Lambshead, J. (2004b) On species accumulation and species–area curves. *Global Ecology and Biogeography*, 13, 567–568.

Gray, B., & Wylie, F.R. (1974) Forest tree and timber insect pests in Papua New Guinea. II. *Pacific Insects*, 16, 67–115.

Greenslade, P., and Greenslade, P. J. M. (1971) The use of baits and preservatives in pitfall traps. *Journal of Australian Entomological Society*, 10, 253-260.

Grimaldi, D. and Engel, M. S. (2005) Evolution of the Insects. Cambridge University Press, Cambridge.

Grobler, G. C., Bastos, A. D. S., Chimimba, C. T., and Chown, S. L. (2011) Inter-island dispersal of flightless *Bothrometopus huntleyi* (Coleoptera: Curculionidae) from the sub-Antarctic Prince Edward Island archipelago. *Antarctic Science*, 23(3), 225–234.

Gronvold, J., Sommer, C., Holter, P. & Nansen, P. (1992) Reduced splash dispersal of bovine parasitic nematodes from cow pats by the dung beetle *Diastellopalpus quinquedens. Journal of Parasitology*, 78, 845–848.

Groombridge, B. 1992. Global diversity: status of the Earth's living resources. (A report compiled by the World Conservation Monitoring Centre) Chapman & Hall, London.

Grootaert, P., Pollet, M., Dekoninck, W., and Van Achterberg, C. (2010) Sampling insects: general techniques, strategies and remarks. In Eymann, J., Degreef, J., Häuser, H., Monje, J. C., Samyn, Y., and Spiegel, D. V. (eds.), Manual on Field Recording Techniques and Protocols for All Taxa Biodiversity Inventories. Belgian National Focal Point to the Global Taxonomy Initiative.

Grove, S. J. and Stork, N. E. (2000) An inordinate fondness for beetles. *Invertebrate Taxonomy*, 14, 733-739.

Haack, R. A., (2001) Intercepted Scolytidae (Coleoptera) at U.S. ports of entry:1985–2000. *Integrated Pest Management Review*, 6, 253–282.

Habeck, D. H. (2002) Family 77: Nitidulidae. In Arnett, R. H., Thomas, M. C., Skelley, P. E. and Frank, J. H. (eds.), American Beetles, Vol. 2. CRC Press, Boca Raton FL.

Haddad, N. M., and Baum, K. A. (1999) An experimental test of corridor effects on butterfly densities. *Ecological Applications*, 9:623–633.

Halffter, G. and Edmonds, W. D. (1982) The Nesting Behavior of Dung Beetles (Scarabaeinae): An Ecological and Evolutive Approach. Instituto de Ecologia, AC, Mexico, DF.

Halffter, G. and Mathews, E. G. (1966) The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomologica Mexicana,* 12–14: 1–312.

Hall, D. W. (1991) The environmental hazard of ethylene glycol of pitfall trapping for polyphagous predatory Carabidae. *Ecological Entomology*, 13, 293-299.

Hall, W. E. (2005) Ptiliidae Erichson, 1845. Pp. 251–261. In R. G. Beutel and R. A. B. Leschen (eds). Handbook of Zoology: A Natural History of the Phyla of the Animal Kingdom, Volume IV. Arthropoda: Insecta, Part 38. Coleoptera, Beetles, Volume 1. Morphology and Systematics. Walter de Gruyter, Berlin.

Hambler, C. and Speight, M. R. (1996) Biodiversity conservation in Britain: science replacing tradition. *British Wildlife*, 6, 137-147.

Hamilton, A. M., Hartman, J. H., and Austin, C. C. (2009) Island area and species diversity in the Southwest Pacific Ocean: Is the fauna of Vanuatu depauperate? *Ecography* 32:247–258.

Hammond, P. M. (1990) Insect abundance and diversity in the Dumoga-Bone national park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. In Knight, W. J. and Holloway, J. D. (eds.), Insect and Rainforest of South East Asia (Wallacea), pp. 197-254. The Royal Entomological Society of London, London.

Hammond, P. M. (1992) Species inventory. Pp. 17–39. In B. Groombridge (ed). Global Biodiversity Status of the Earth's Living Resources. A Report Compiled by the World Conservation Monitoring Centre. Chapman and Hall, London.

Hammond, P. M. (1995) Described and estimated species numbers: an objective assessment of current knowledge. In Alspp, D., Hawkesworth, D. L., Colwell, R. R. (eds.). Microbial Diversity and Ecosystem Function. CAB International, Wallingford.

Hammond, P.M. (2000) Coastal Staphylinidae (rove beetles) in the British Isles, with special reference to saltmarshes. In Sherwood, B. R., Gardiner, B. G. & Hughes, T (eds.), British Saltmarshes, pp. 247–302.

Hannah, L., D. Lohse, C. Hutchinson, and J.L. Carr. (1994) A Preliminary Inventory of Human Disturbance of World Ecosystems. *AMBIO*, 23 (4-5): 246.

Hansen, M. (1991) The hydrophiloid beetles: phylogeny, classification and a revision of the genera (Coleoptera, Hydrophiloidea). *Biologiske Skrifter, Kongelige Danske Videnskabernes Selkab*, 40: 1–367.

Hansen, M. (1997) Phylogeny and classifcation of the staphyliniform beetle families. *Biologiske Skrifter, Kongelige Danske Videnskabernes Selkab*, 48: 1–339.

Hanski, I. (1991) The dung insect community. *Dung Beetle Ecology* (ed. by I. Hanski and Y. Cambefort), pp. 5–21. Princeton University Press, Princeton, New Jersey.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, 396, 41–49.

Hanski, I. and Niemela, J. 1990. Elevetaion distribution of dung and carrion beetles in Northern Sulawesi. In Knight, W. J. and Holloway, J. D. (eds.), Insect and Rainforest of South East Asia (Wallacea), pp. 145-153. The Royal Entomological Society of London, London.

Hanski, I., Cambefort, Y. 1991. Dung Beetle Ecology. Princeton University Press, Princeton, New Jersey.

Hanski, I., Gyllenberg, M. (1997) Uniting the general patterns in the distribution of species. *Science*, 275, 397–400.

Harbaugh, D. T. and Baldwin, B. G. (2007) Phylogeny and biogeography of the sandalwoods (Santalum, Santalaceae): repeated dispersals throughout the Pacific. *American Journal of Botany,* 94, 1028–1040.

Harcourt, A. H., Parks, S. A., and Woodroffe, R (2001) Human density as an influence on species/area relationships: double jeopardy for small African reserves? *Biodiversity and Conservation,* 10, 1011–1026.

Harris, K. F. (1981) Arthropod and nematode vectors of plant viruses. Annual Rev. *Phytopathology*, 19, 391-426.

Harrison, J., Miller, K., McNeely, J. (1982) The world coverage of protected areas: development goals and environmental needs. *Ambio*, 11, 238–245.

Hassall, T. Thompson, D. J., French, G. C., and Harvey, I. F. (2007) Historical changes in the phenology of British Odonata are related to climate. *Global Change Biology*, 13, 1-9.

Hatteland, B. A., Pedersen, T. N., Mortensen, F., and Solhøy, T. (2008) Species-area relations and island distribution of carabid beetles (Coleoptera, Carabidae) on small islands off the coast of western Norway. *Norwegian Journal of Entomology,* 55, 73–80.

Hausdorf, B. and Hennig, C. (2005) The influence of recent geography, palaeogeography and climate on the composition of the fauna of the central Aegean Islands. *Biology Journal of Linnean Society,* 84: 785–795.

Hausmann, A. Haszprunar, G., Hebert, P. D. N. (2011) DNA barcoding the geometrid fauna of Bavaria (Lepidoptera): successes, surprises, and questions. *PLoS One*, 6(2).

Hawkins, B. A., Mills, N. J., Jervis, M. A., Price, P. W. (1999) Is the biological control of insects a natural phenomenon? *Oikos*, 86, 493–506.

Henderson, P.A. & Seaby, R.M.H. (2002) Species diversity and richness. Pisces Conservation Ltd. http://www.pisces-conservation.com/indexsoftdiversity.html

Henderson, S., Dawson, T. P., and Whittaker, R. J. (2006) Progress in invasive plants research. *Progress in Physical Geography*, 30, 25-46.

Hernandez, M. I. M., Vaz-de-Mello, F. Z. (2009) Seasonal and spatial species richness variation of dung beetle (Coleoptera, Scarabaeidae) in the Atlantic Forest of southeastern Brazil. *The Revista Brasileira de Entomologia*, 53, 607–613.

Hertz, M. (1927) Huomioita petokuoriaisten olinpaikoista. *Luonnon Ystava*, 31, 218-222.

Herzog, S. K., and Kessler, M. (2006) Local vs. regional control on species richness: a new approach to test for competitive exclusion at the community level. *Global Ecology and Biogeography*, 15, 163-172.

Heusi-Silveira, M., Lopes, B. C., Ide, S., Castellani, T. T., and Hernández, M. I. M. (2012) Beetle (Insecta, Coleoptera) assemblage in a Southern Brazilian restinga: effects of anthropogenic disturbance and vegetation complexity. *Studies on Neotropical Fauna and Environment*, 47(3), 203-214.

Heywood, V. H. (1979) The future of island floras. In: Bramwell, D., ed. Plants and islands. San Diego, CA: Academic Press. 459 p.

Hill, C.J. (1996) Habitat specificity and food preferences of an assemblage of tropical Australian dung beetles. *Journal of Tropical Ecology*, 12, 449–460.

Hill, M. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54: 427-432.

Hill, P. and Twist, C. (1998) Butterflies and Dragonflies: A Site Guide, 2nd edition. Arlequin, Chelmsford.

Hinkle, A. E. (2007) Population structure of Pacific *Cordyline fruticosa* (Laxmanniaceae) with implications for human settlement of Polynesia. *American Journal of Botany*, 94(5), 828-839.

Hinton, H. E. 1945. A Monograph of the Beetles Associated with Stored Products. British Museum, London.

Hobbs, R. J. and Huenneke, L. F. (1992) Disturbance, Diversity, and Invasion: Implications for Conservation. *Conservation Biology*, 6, 324-337.

Hodge, S., Marshall, S.A., Oliver, H., Berry, J., Marris, J. & Andrew, I. (2010) A preliminary survey of the insects collected using mushroom baits in native and exotic New Zealand woodlands. *New Zealand Entomologist*, 33, 43–54.

Hodkinson, I. D. and D. Casson. (1991) A lesser predilection for bugs: Hemiptera (Insecta) diversity in tropical rain forests. *Biological Journal of the Linnean Society*, 43: 101–109.

Holdgate, M. (1996) The ecological significance of biological diversity. *Ambio*, 25(6).

Holland, K. D., McDonnell, M. J., and Williams, N. S. G. (2007) Abundance, species richness and feeding preferences of introduced molluscs in native grasslands of Victoria, Australia. *Australian Ecology,* 32, 626-634.

Holsinger, K. E., and Gottlieb, L. D. (1991) Conservation of rare and endangered plants: principles and prospects. Pages 195–208 in D. A. Falk and K. E. Holsinger, editors. Genetics and conservation of rare plants. Oxford University Press, New York, New York, USA.

Holt, R. D. (1996) Food webs in space: an island biogeo- graphic perspective. Pages 313-323 *in* G. A. Polls and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Honek, A., Martinkova, Z., Jarosik, V. (2003) Ground beetles (Carabidae) as seed predators. *European Journal of Entomology*, 100: 531–544

Horgan, F.G. (2005) Effects of deforestation on diversity, biomass and function of dung beetles on the eastern slope of the Peruvian Andes. *Forest Ecology and Management*, 216, 117–133.

Hornschemeyer, T. (2005) ArchostemataKolbe, 1908. Pp.29–42. In R. G. Beutel and R. A. B. Leschen (eds). Handbook of Zoology: A Natural History of the Phyla of the Animal Kingdom, Volume IV. Arthropoda: Insecta, Part 38. Coleoptera, Beetles, Volume 1. Morphology and Systematics. Walter de Gruyter, Berlin.

Hortal, J., Triantis, K. A., Meiri, S., Thebault, E., and Sfenthourakis, S. (2009) Island Species Richness Increases with Habitat Diversity. *The American Naturalist*, 174(6).

Howden, H. F. (1982) Larval and adult characters of *Frickius* Germain, its relationship to the Geotrupini, and a phylogeny of some major taxa in the Scarabaeoidea (Insecta: Coleoptera).*Canadian Journal of Zoology*, 60: 2713–2724.

Howden, H. F., and Howden, A. (2001) Change through time: a third survey of the Scarabaeinae (Coleoptera: Scarabaeidae) at Welder Wildlife Refuge. *Coleopterists Bulletin*, 55: 356–362.

Howden, H. F. and Nealis, V. G. (1978) Observations on height of perching in some tropical dung beetles (Scarabaeidae). *Biotropica,* 10: 43–46

Howden, H. F. and Young, O. P. (1981) Panamanian Scarabaeidae. *Contributions of the American Entomological Institute,* 18: 1–204.

Hughes, L. (2000) Biological consequences of global warming: s the signal already apparent? *Trends in Ecology and Evolution*, 15, 56-61.

Hughes, J., Longhorn, S. J., Papadopoulou, A., Theodorodes, K., de Riva, A., Mejia-Chang, M., Foster, P. G., and Vogler, A. P. (2006) Dense taxonomic EST sampling and its applications for molecular systematics of the Coleoptera (beetles). *Molecular Biology and Evolution*, 23: 268–278.

Hughes, R. D., Ferrar, P., Macqueen, A., Durie, P., McKinney, G. T., and Morley, F. H. W. 1975. Introduced dung beetles and Australian pasture ecosystems: papers presented at a symposium during the meeting of the Australian and New Zealand Association for the Advancement of Science at Canberra in January 1975. *Journal of Applied Ecology*,12: 819–837.

Huijbregts, J., and Krikken, J. (2011) Taxonomy of Onthophagus javanensis and its closest relatives in Sundaland (Coleoptera: Scarabaeidae: Scarabaeinae). *Tijdschrift voor Entomologie*, 154, 33–59.

Hulcr, J. & Cognato, A.I. (2010) New genera of Palaeotropical Xyleborini (Coleoptera: Curculionidae: Scolytinae) based on congruence between morphological and molecular characters. *Zootaxa* (in review).

Hunt, R.H., Coetzee, M. and Fettene, M. (1998) The *Anopheles gambiae* complex: a new species from Ethiopia. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 92 (2), 231-235.

Hyatt, L. A., Rosenberg, M. S., Howard, T. G., Bole, G., Fang, W., Anastasia, J., Brown, K., Grella, R., Hinman, K., Kurdziel, J. P. and Gurevitch, J. (2003) The distance dependence prediction of the Janzen-Connell hypothesis: a meta-analysis. *Oikos*, 103, 590–602.

Hyman, P. S. and Parsons, M. S. (1994) A Review of the Scare and Threatened Coleoptera of Great Britain, Part 2. United Kingdom Nature Conservation Committee, Peterborough.

Ikeda, H., Homma, K., Kubota, K. (2008) Ground-dwelling beetle community in beech forests of Sado Island, Japan: comparison with the mainland. *Journal of Forest Research,* 13, 357–364.

Imhoff, M. L., Lahouari, B., Taylor, R., Colby, L., Harriss, R., Lawrence, W. T. (2004) Global patterns in human consumption of net primary production. *Nature*, 429, 870-873.

Ishitani, M. (1996) Ecological studies on ground beetles (Coleoptera: Carabidae, Brachinidae) as environmental indicators. In: Miscellaneous report of the Hiwa Museum for Natural History, no 34. Hiroshima, pp 1–110

IUCN. (2009) The state of amphibians in Indonesia. Available at: <http://www.iucn.org/about/union/secretariat/offices/asia/regional_activities/asian_amphibian_crisis/indonesia/>

IUCN. (2011) The IUCN Red List of Threatened Species.

IUCN. (2012) Biological invasions: a growing threat to biodiversity, human health and food security. IUCN Policy Brief, IUCN.

Ivie, M. A. (2002a) Nosodendridae Erichson 1846. Pp.224–227. In R. H. Arnett, M. C. Thomas, P. E. Skelley, and J. H. Frank (eds). American Beetles, Volume 2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.

Ivie, M. A. (2002b) Bostrichidae Latreille 1802. Pp.223–244. In R. H. Arnett, M. C. Thomas, P. E. Skelley, and J. H. Frank (eds). American Beetles, Volume 2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.

Jach, M. A. (1998) Annotated check list of aquatic and riparian/littoral beetle families of the world (Coleoptera). Pp. 25–42. In M. A. Jach and L. Ji (eds). Water Beetles of China, Volume 2. Zoologisch-Botanische Gesellschaftin Osterreich and Wiener Coleopterologenverein, Wien.

Jach, M. A., Beutel, R. G., Delgado, J. A., and Diaz, J. A. (2005) Hydraenidae Mulsant,1844. Pp.224–251. In R. G. Beutel and R. A. B. Leschen (eds). Handbook of Zoology: A Natural History of the Phyla of the Animal Kingdom, Volume IV. Arthropoda: Insecta, Part 38. Coleoptera, Beetles, Volume 1. Morphology and Systematics. Walter de Gruyter, Berlin.

Jaenike, J., and Perlman, S. J. (2002) Ecology and evolution of host-parasite associations: mycopha gous Drosophila and their parasitic nematodes. *American Naturalist*, 160, S23-S39.

Jagadeesan, R., Collins, P. J., Daglish, G. J., Ebert, P. R., Schlipalius, D. I., Feldlaufer, M. F. (2012) Phosphine Resistance in the Rust Red Flour Beetle, *Tribolium castaneum* (Coleoptera: Tenebrionidae): inheritance, gene interactions and fitness costs (Phosphine Resistance in *T. castaneum*). *PLoS ONE*, 7(2).

Jakarta Animal Aid Network (JAAN). (2012) (jakartaanimalaid.com).

James, H. F. (1995) Prehostoric extinctions and ecological changes on oceanic islands. In Vitousek, P. M., Loope, L. L., and Adsersen, H. (eds.), Islands: Biological Diversity and Ecosystem Function, pp. 7-21. Berlin: Springer-Verlag.

Jameson, M. L. and Ratcliffe, B. C. (2002) Series Scarabaeiformia Crowson 1960. (=Lamellicornia): Superfamily Scarabaeoidea Latreille 1802: Introduction. Pp.1–5. In R. H. Arnett, M. C. Thomas, P. E. Skelley, and J. H. Frank (eds). American Beetles, Volume 2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.

Jameson, M. L., and Ratcliffe, B. C. (2009) Revision of the genus Chalcasthenes Arrow (Coleoptera: Scarabaeidae: Dynastinae: Oryctoderini) from the Solomon Islands. *Australian Journal of Entomology*, 48, 149–163.

Janzen, D. H. (1966) Coevolution of mutualism between ants and acacias in Central America. *,* 20: 249–275.

Janzen, D. H. (1979) How to be a fig. *Annual Review of Ecology and Systematics,* 10: 13–51.

Janzen, D. H. (1987) Insect diversity in a Costa Rican dry forest: why keep it and how? *Biological Journal of the Linnean Society,* 30: 343–356.

Jarvinen, 0. & Haila, Y. (1984) Assembly of land bird communities on northern islands: A quantitative analysis of insular impoverishment. Ecological communities. conceptual issues and the evidence (ed. by D. R. Strong, Jr, D. Simberloff, L. G. Abele and A. B. Thistle), pp. 138-147. Princeton University Press.

Jenny, H. 1980. The soil resource: Origin and behaviour. *Ecological Studies*, 37, Springer, Berlin Heidelberg New York.

Jepma, C. J. 1995. Tropical Deforestation: A Socio-Economic Approach. Earthscan.

Jepson, P. & Whittaker, R. J. (2002) Histories of protected areas: internationalisation of conservationist values in their adoption in theNetherlands Indies. *Environment & History,* 8(2), 129-172.

Johns, C. V., Hughes, L. (2004) Feeding preferences of the Christmas beetle Anoplognathus chlorophyrus (Coleoptera: Scarabaeidae) and four Paropsine species (Coleoptera: Chrysomelidae) on selected Eucalyptus grand is clonal foliage*. Australian Forestry Journal*, 67, 184-190.

Johnson, M. P., Simberloff, D. S. (1974) Environmental determinants of island species numbers in the British Isles. *Journal of Biogeography*, 1, 149-154.

Johnson, T. H. and Stattersfield, A. J. 1990. A global review of island endemic birds*. Ibis*, 132, 167-180.

Jones, A. G., Forgie, S. A., Scott, D. J., and Beggs, J. R. (2012) Generalist dung attraction response in a New Zealand dung beetle that evolved with an absence of mammalian herbivores. *Ecological Entomology,* 37, 124–133.

Jordal, B. H., Emerson, B. C., Hewitt, G. M. (2006) Apparent 'sympatric' speciation in ecologically similar herbivorous beetles facilitated by multiple colonizations of an island. *Molecular Ecology*, 15, 2935–2947.

Jordal, B. H., Beaver, R. A., Kirkendall, L. R. (2001) Breaking taboos in the tropics: inbreeding promotes colonization by wood-boring beetles. *Global Ecology and Biogeography*, 10: 345–358.

Jordal, B. H., Normark, B. B., Farrell, B. D., Kirkendall, L. R. (2002) Extraordinary haplotype diversity in haplodiploid inbreeders: phylogenetics and evolution of the bark beetle genus Coccotrypes. *Molecular Phylogenetics and Evolution*, 23, 171–188.

Jost, L. (2006) Entropy and diversity. *OIKOS*, 113(2), 363-375.

Kahono, S., Setiadi, L. K. (2007) Keragaman dan Distribusi Vertikal Kumbang Tinja Scarabaeids (Coleoptera: Scarabaeidae) di Hutan Tropis Basah Pegunungan Taman Nasional Gede Pangrango, Jawa Barat, Indonesia. *Biodiversitas*, 7(4), 118-122.

Kalmar, A. & Currie, D. J. (2006) A global model of island biogeography. *Global Ecological Biogeography*, 15, 72–81.

Kamoun, S. (1996) Occurrence of the threatened Cicindela senilis frosti Varas-Arangua in inland salt marsh in Riverside County, California (Coleoptera: Cicindelidae). *Coleopterist Bulletin*, 50, 369-371.

Kaneshiro, K. Y. (1995) Evolution, speciation, and the genetic structure of island population. In: Vitousek, P. M., Loope, L. L., Adsersen, H. 1995. Islands, Biological Diversity and Ecosystem Function. Springer-Verlag, New York.

Kaplan, J. K. (2003) We don't cotton to boll weevil 'round here anymore. *Agricultural Research February*, 51: 4–8.

Kappes, H., Topp, W. (2004) Emergence of Coleoptera from deadwood in a managed broadleaved forest in central Europe. *Biodiversity and Conservation*, 13, 1905–1924.

Kareiva, P. (1987) Habitat fragmentation and the stability of predator-prey interactions. *Nature*, 326:388±390

Kato, M. and T. Inoue. (1994) Origin of insect pollination. *Nature*, 368:195.

Kaufman, L. V., and Wright, M. G. Parasitism of a Hawaiian endemic moth by invasive and purposely introduced Hymenoptera species. *Environmental Entomology,* 39, 430-439.

Keeley, J. E. (2003) Relating species abundance distributions to species–area curves in two Mediterranean-type shrublands. *Diversity and Distribution*, 9, 253–259.

Kellert, S. R. (1993) Values and perceptions of invertebrates. *Conservation Biology,* 7(4).

Kennedy, A. D. (1995) Antarctic terrestrial ecosystem response to global environmental change. *Annual Review of Ecology and Systematics*, 26, 683-704.

Keppel, G., Lowe, A. J., Possingham, H. P. (2009) Changing perspectives on the biogeography of the tropical South Pacific: influences of dispersal, vicariance and extinction. *Journal of Biogeography*, 36, 1035–1054.

Kevan, P. and Baker, H. G. (1983) Insects as flower visitors and pollinators. *Annual Review of Entomology*, 28, 407-453.

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J., Barthlott, W. (2009) A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences*, 106(23), 9322-9327.

Kingsland, S.(2002) Designing nature reserves: adapting ecology to real-world problems. *Endeavour*, 26(1), 9-14.

Kirejtshuk, A. G. 1998. Nitidulidae (Coleoptera) of the Himalayas and Northern Indochina. Part 1: 81(1), 201–208.

Kirkendall, L. R. (1993) Ecology and evolution of biased sex ratios in bark and ambrosia beetles (Scolytidae). In: Wrensch DL, Ebbert MA, eds. Evolution and diversity of sex ratio: insects and mites. New York: Chapman & Hall, 235–345.

Kirkendall, L. R., and Jordal, B. H. (2006) The bark and ambrosia beetles (Curculionidae, Scolytinae) of Cocos Island, Costa Rica and the role of mating

systems in island zoogeography. *Biological Journal of the Linnean Society*, 89, 729–743.

Kisel, Y., and Barraclough, T. G. (2010) Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, 175(3), 316-334.

Kishita, M., Arakaki, N., Kawamura, F., Sadoyama, Y., Yamamura, K. (2003) Estimation of population density and dispersal parameters of the adult sugarcane wireworm, Melanotus okinawensis Ohira (Coleoptera: Elateridae), on Ikei Island, Okinawa, by mark-recapture experiments. *Applied Entomological Zoology*, 38(2), 233-240.

Klecka, J., Boukal, D. S. (2012) Who eats whom in a pool? A comparative study of prey selectivity by predatory aquatic insects. *PLoS ONE*, 7(6): e37741.

Klein, B.C. (1989) Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology*, 70, 1715–1725.

Kinsley, C. B. & Haines, R. D. (2007) Description and conservation status of a new subspecies of Cicindela tranquebarica (Coleoptera: Cicindelidae) from the San Joaquin Valley of California, U.S.A. *Entomological News,* 118, 109–126.

Knapp, S., Peralta, I. E. (2003) Taxonomy of tomatoes in the Galapagos Islands: native and introduced species of Solanum section Lycopersicon (Solanaceae). *Systematics and Biodiversity*, 1(1), 29-53.

Kocarek, P. (2003) Decomposition and Coleoptera succession on exposed carrion of small mammal in Opava, the Czech Republic. *European Journal of Soil Biology*, 39, 31–45.

Kohn, D. Walsh, D. M. (1994) Plant species richness -the effect of island size and habitat diversity. *Journal of Ecology*, 82 (2), 367-377.

Kolibac, J. (1992) Revision of Thanerocleridae n. stat. (Coleoptera: Cleridae). *Mitteilungender Schweizerischen Entomologischen Gesellschaft*, 65:303–340.

Kolibac, J. (2004) Metaxinidae fam. nov., a new family of Cleroidea (Coleoptera). *Entomologica Basiliensia*, 26: 239–268.

Kolibac, J. (2005) A review of the Trogossitidae. Part 1: Morphologyofthegenera (Coleoptera: Cleroidea). *Entomologica Basiliensia et Collectionis Frey*, 27: 39–159.

Korte, A., Ribiera, I., Beutel, R. G., and Bernhard, D. (2004) Interrelationships of Staphyliniform groups inferred from 18S and 28S rDNA sequences, with special emphasis on Hydrophiloidea (Coleoptera, Staphyliniformia). *Journal of Zoological Systematics and Evolutionary Research*, 42: 281–288.

Kotze, D. J. (2008) The occurrence and distribution of carabid beetles (Carabidae) on islands in the Baltic Sea: a review. *Journal of Insect Conservation*, 12, 265–276.

Kotze, D. J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M. J., Lövei, G. L., Mossakowski, D., Noordijk, J., Paarmann, W., Pizzolotto, R., Saska, P., Schwerk, A., Serrano, J., Szyszko, J., Aboada, A., Turin, H., Venn, S., Vermeulen, R., and Zetto, T. (2011) Forty years of carabid beetle research in Europe – from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. *ZooKeys*, 100: 55–148.

Kotze, D. J. and O'Hara, R. B. (2003) Species decline: but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia*, 135(1), 138-148.

Kotze, D. J., Niemelä, J., and Nieminen, M. (2000) Colonization success of carabid beetles on Baltic islands. *Journal of Biogeography*, 27, 807–819

Koul, O. and G. S. Dhaliwal (eds) (2003) Predators and Parasitoids. Taylor and Francis, London. 191pp.

Kreft, H., Jetz, W., Mutke, J., Kier, G., Barthlott, W. (2008) Global diversity of island floras from a macroecological perspective. *Ecology Letters*, 11, 116–127.

Kremen, C., Colwell, R. K., Erwin, T. L., Murphy, D. D., Noss, R. F., and Sanjayan, M. A. (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology,* 11, 849-856.

Kruess, A., Tscharntke, T. (1994) Habitat fragmentation, species loss and biological control. *Science*, 264:1581-1584.

Kruskal, J. B. & Wish, M. (1978) Multidimensional Scaling. Sage Publications, Beverly Hills, California.

Kubisz, D., Kajtoch, Ł., Mazur, M., Rizun, V., (2012) Molecular barcoding for central-eastern European Crioceris leaf-beetles (Coleoptera: Chrysomelidae). *Central European Journal of Biology*, 7(1), 69-76.

Kubota, K., Lee, C. Y., Kim, J. K. (2000) Invertebrates on the forest floor in Kangwon Province, Republic of Korea, with special reference to Japanese red pine forest infested with the pine needle gall-midge (Thecodiplosis japonensis). In: Review of forestry culture, vol 21. Japan Forestry Culture Association, Tokyo, pp 137–146

Lacey, E. S., Ginzel, M. D., Mallar, J. G., Hanks, L. M. (2004 Male-produces aggregation pheromone of the cerambycid beetle *Neoclytus acuminatus* acuminatus. *Journal of Chemical Ecology*, 30, 1493-1507.

Lack, D. (1976) Island biology illustrated by the land birds of Jamaica. University of California Press, Berkeley, CA, USA. de Lattin, G. de (1967) Grundriss der Zoogeographie. Fischer, Jena.

Lamarre, G. P. A., Molto, Q., Fine, P. V. A., Baraloto, C. (2012) A comparison of two common flight interception traps to survey tropical arthropods. *ZooKeys*, 2(6), 43-55.

Langellotto, G. A., Denno, R. F. (2001) Benefits of dispersal in patchy environments: mate location by males of a wing-dimorphic insect. *Ecology*, 82, 1870–1878.

Langellotto, G. A., Denno, R. F., Ott, J. R. (2000) A trade-off between flight capability and reproduction in males of a wing-dimorphic insect. *Ecology*, 81, 865–875.

Larsen, T.H., Lopera, A. & Forsyth, A. (2008) Understanding trait-dependent community disassembly: dung beetles, density functions, and forest fragmentation. *Conservation Biology*, 22, 1288–1298.

Larson, B. M. H., Barrett, S. C. H. (1998) Reproductive biology of island and mainland populations of Primula mistassinica (Primulaceae) on Lake Huron shorelines. *Canadian Journal of Botany*, 76, 1819-1827.

Laurance, W. F (1991) Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology*, 5, 79-89.

Laurance, W. F., Carolina U. D., Shoo, L. P., Herzog, S. K., Kessler, M., Escobar, F., Brehm, G., Axmacher, J. C., Chen, I-Ching., Gámez, L. A., Hietz, P., Fiedler, K., Pyrcz, T., Wolf, J., Merkord, C. L., Cardelus, C., Marshall, A. R., Ah-Peng, C., Aplet, G. H., del Coro Arizmendi, M. ; Baker, W. J., Barone, J., Brühl, C. A., Bussmann, R. W., Cicuzza, D., Eilu, G., Favila, M. E., Hemp, A., Hemp, C., Homeier, J., Hurtado, J., Jankowski, J., Kattán, G., Kluge, J., Krömer, T., Lees, D. C., Lehnert, M., Longino, J. T., Lovett, J., Martin, P. H., Patterson, B. D., Pearson, R. G., Peh, K. S. H., Richardson, B., Richardson, M., Samways, M. J., Senbeta, F., Smith, T. B., Utteridge, T. M. A., Watkins, J. E., Wilson, R., Williams, S. E., Thomas, C. D. (2011) Global warming, elevational ranges and the vulnerability of tropical biota. *Biological Conservation*, 144(1), 548-557.

Le Pelley, R.H. (1968) Pests of coffee. Longmans, London and Harlow. 590 pp.

Plavilstshikov, N. N. (1958) Coleoptera. Cerambycidae, Part 3. Lamiinae, Part 1. Fauna of USSR. 23:592pp.

Lawesson, J. E. 1990. Alien plants in the Galápagos Islands, a summary. In Lawesson, J.E., Hamann, O., Rogers, G., Reck, G. & Ochoa, H. (eds), Botanical research and management in Galápagos. Monographs in Systematic Botany from the Missouri Botanical Garden, 32, 15-20.

Lawler, S. P. (1993) Species richness, species composition and population dynamics of protists in experimental microcosms. *Journal of Animal Ecology,* 62, 711-719.

Lawrence, J. F. (1982) Coleoptera. Pp. 482–553. In S. P. Parker (eds). Synopsis and Classification of Living Organisms, Volume 2. McGraw-Hill, NewYork.

Lawrence, J. F. (1987) Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of Elateriformia. *Invertebrate Taxonomy*, 2:1–53.

Lawrence, J. F. (1988) Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of the Elateriformia. *Invertebrate Taxonomy*, 2:1–53.

Lawrence, J. F. (1991) Order Coloeptera. In F. W. Stehr (eds). Immature Insects, Volume 2. Kendall/Hunt Publishing, Dubuque, IA. 975pp.

Lawrence, J. F. and Britton, E. B. 1994. Australian Beetles. Melbourne University Press.

Lawrence, J. F., Hastings, A. M., Dalwitz, M. J., Paine, T. A., and Zurcher, E. J. (1999) Beetles of the World, Version 1.0. CSIRO Division of Entomology, Canberra.

Lawrence, J. F. and Hlavac, T. (1979) Review of the Derodontidae (Coleoptera: Polyphaga) with new species from North America and Chile. *Coleopterists Bulletin*, 33:369–414.

Lawrence, J. F. and Newton, A. F. (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). Pp. 779–1006. In J. Pakaluk and S. A. Slipinski (eds). Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson. Muzeum i Instytut Zoologii PAN, Warszawa.

Lawrence,J. F.,Nikitsky, N. B., and Kirejtshuk, A. G. (1995) Phylogenetic position of Decliniidae (Coleoptera:Scirtoidea) and comments on the classification of Elateriformia (sensu lato). Pp. 375–410. In J. Pakaluk and S. A. Slipinski (eds). Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson. Muzeum i Instytut Zoologii PAN, Warszawa.

Lawton, J. H. (1994) Population dynamic principles. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences,* 344, 61-68.

Lawton, J. H. 1995. Population dynamics principles. Pages 147-163 in J. H. Lawton and R. M. May, editors. Extinction rates. Oxford University Press, Oxford, UK

Lazaro, A., Traveset, A. (2005) Spatio-temporal variation in the pollination mode of Buxus balearica (Buxaceae), an ambophilous and selfing species: mainland-island comparison. *Ecograph*y, 28, 640-652.

Leader-Williams, N. and Dublin, H. T. (2000) Charismatic megafauna as 'flagship species'. In Entwistle, A. and Dunstone, N. (eds.), Priorities for the Conservation of Mammalian Diversity: Has the Panda had its Day?, pp. 53-81. Cambridge University Press, Cambridge.

Leather, S. R., and Watt, A. D. (2005) Sampling theory and practice. In Leather, S. R. (eds), Insect Sampling in Forest Ecosystem, pp. 1-15. Blackwell Publishing, Oxford.

Leclaire, M., and Brandl, R. (1994) Phenotypic plasticity and nutrition in a phytophagous insect: conse quences of colonizing a new host. *Oecologia*, 100, 379-385.

Lecocq, T., Vereecken, N. J., Michez, D., Dellicour, S., Lhomme, P., Valterova, I., Rasplus, J. Y. Rasmont, P. (2013) Patterns of Genetic and Reproductive Traits Differentiation in Mainland vs. Corsican Populations of Bumblebees. *PLOS ONE*, 8(6), 1-14.

Lee, J. C., Haack, R. A., Negrón, J. F., Witcosky, J. J., Seybold, S. J. (2005) Invasive Bark Beetles Forest Insect & Disease. U.S. Department of Agriculture.

Legendre, P. & Gallagher, E. D. Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129, 271-280.

Legendre, P. & Legendre, L. (1998) Numerical ecology. 2nd English edition. Elsevier Science BV, Amsterdam.

Lemieux, J. P. and Lindgren, B. S. (1999) A pitfall trap for large-scale trapping of Carabidae: comparison against conventional design using two different preservatives. *Pedobiologia*, 43, 245-253.

Leschen, R. A. B., Lawrence, J. F., and Slipinski,S. A. (2005) Classification of basal Cucujoidea (Coleoptera: Polyphaga): cladistic analysis, keys and review of new families. *Invertebrate Systematics,* 19:17–73.

Leschen, R. A. B. (2002) Derodontidae LeConte 1861. Pp.221–223. In R. H. Arnett, M. C. Thomas, P. E. Skelley, and J. H. Frank (eds). American Beetles, Volume 2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.

Leuschner, C. (1996) Timber line and alpine vegetation on the tropical and warm-temperate oceanic islands of the world: elevation, structure, and floristics. *Vegetatio*, 123:193–206.

Lewinsohn, T. M., Novotny, V., Basset, Y. (2005) Insects on plants: diversity of herbivore assemblages revisited. *Annual Review of Ecological Evolution and Systematic*, 36, 597–620.

Li, Guo - Qing. (2010) Insecticide resistance status of Colorado Potato Beetle (Coleoptera: Chrysomelidae) adults in Northern Xinjiang Uygur Autonomous Region. *Journal of Economic Entomology*, 103(4), 1365-1371.

Lim, H. C., and Sodhi, N. S. (2004) Responses of avian guilds to urbanisation in a tropical city. *Landscape and Urban Planning*, 66:199-215

Lindgren, C. J., Corrigan, J., and De Clerck-Floate, R. A. (2002) Lythrum salicariaL., purple loosestrife (Lynthaceae). Pp. 383-390. In Mason, P. G. and Huber, J. T. (eds.). Biological Control Programmes in Canada, 1981-2000. CABI Publishing, Wallingford.

Lindroth, C. H. (1985) The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*, (part 1). Scandinavian Science Press Ltd, Copenhagen.

Lindroth, C. H. (1986) The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*, (part 2). Scandinavian Science Press Ltd, Copenhagen.

Liu, Y., Axmacher, J. C., Li, L., Wang, C. Yu, Z. (2007) Ground beetle (Coleoptera: Carabidae) inventories: a comparison of light and pitfall trapping. Bulletin of Entomological Research, 97, 577–583.

Lomba, A., Vaz, A. S., Moreira, F., Honrado, J. P. (2013) Hierarchic species–area relationships and the management of forest habitat islands in intensive farmland. *Forest Ecology and Management,* 291, 190-198.

Lomolino, M. V. (1982) Species-area and species-distance relationships of terrestrial mammals in Thousand Island Region, *Oecologia*, 54, 72-75.

Lomolino, M. V. (1984) Immigrant selection, predatory exclusion and the distributions of *Microtus pennsylvanicus* and *Blarina brevicauda* on islands. *American Naturalist*, 123, 468–483.

Lomolino, M. V. (1985) Body size of mammals on islands: the island rule re-examined. *American Naturalist*, 125, 310–316.

Lomolino, M. V. (1986) Mammalian community structure on islands: immigration, extinction and interactive effects. *Biological Journal of Linnean Society*, 28, 1–21.

Lomolino, M. V. (1993) Winter filtering, immigrant selection and species composition of insular mammals of Lake Huron. *Ecography*, 16, 24–30.

Lomolino, M. V. (2000a) A call for a new paradigm of island biogeography. *Global Ecology & Biogeography*, 9, 1–6.

Lomolino, M.V. (2000b) A species-based theory of insular zoogeography. *Global Ecology & Biogeography*, 9, 39–58.

Lomolino, M. V. (2010) Four Darwinian themes on the origin, evolution and preservation of island life. *Journal of Biogeography*, 37, 985-994.

Lomolino, M. V., and Brown, J. H. (2009) The reticulating phylogeny of island biogeography theory. *The Quarterly Review of Biology,* 84(4), 357-390.

Lomolino, M. V., and Weiser, M. D. (2001) Towards a More General Species-Area Relationship: Diversity on All Islands, Great and Small. *Journal of Biogeography*, 28(4), 431-445.

Lomolino, M.V., Weiser, M.D. (2001) Towards a more general species-area relationship: diversity on all islands, great and small. *Journal of Biogeography*, 28, 431-445.

Lonsdale, W. M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, 80, 1522-1536.

Loope, L. L., Hamann, O. and Stone, C. P. (1988) Comparative conservation biology of oceanic archipelagoes — Hawaii and Galápagos. *Bioscience* 38, 272-282.

Lopez, P. D., Lugo, E., Valle, S., Espinosa, P., Lopez, M. M. M., Delgado, M., Riveraetal, P. (1997) Aquatic insects as biological control agents of mosquito larvae in Nicaragua. *Revista Nicaraguense de Entomologia,* 39: 27–30.

Losey, J. E. and Vaughan, M. (2006) The economic value of ecological services provided by insects. *BioScience*, 56, 311-323.

Losos, J. B., and Schluter, D. (2000) Analysis of an evolutionary species–area relationship. *Nature,* 408, 847-850.

Lövei, G. L. & Sunderland, K. D. (1996) Ecology and behaviour of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, 41, 231–256.

Lovejoy, T E., Bierregaard, R. O., Rylands, A. B., Malcolm, J. R., Quintela, C. E., Harper, L. H., Brown, K. S., Powell, A. H., Powell, G. V. N., Schubart, H. O. R., and Hays, M. B. (1986) Edge and other effects of isolation on Amazon forest fragments. In M. E. Soule, editor. Conservation biology: The science of scarcity and diversity. Sinauer, Sunderland, Massachusetts, USA.

Lovejoy, T. E., Rankin, J. M., Bierregaard, R. O., Brown, K. S., Emmons, L. H., and van der Voort, M. E.. (1984) Ecosystem decay of Amazon forest remnants. In M. H. Nitecki, editor. Extinctions. University of Chicago Press, Chicago, Illinois, USA.

Luff, M. L. (1975) Some features influencing the efficiency of pitfall traps. *Oecologia*, 19, 345-357.

Lumaret, J. P. (1978) Biogeographie et ecologie des Scarabaeides coprophages du sud de la France. *Vie Milieu Series C*, 28: 1–34.

Lundkvist, E., J. Landin, M. Jackson, and C. Svensson. (2003) Diving beetles (Dytiscidae) as predators of mosquito larvae (Culicidae) in field experiments and in laboratory tests of prey preference. *Bulletin of Entomological Research*, 93: 219–226.

MacArthur, R. (1965) Patterns of species diversity. *Biology Revision*, 40: 510-533.

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Monographs in Population Biology, Princeton University Press, New York, Princeton, NJ, 203 pp.

MacArthur, R. H. and Wilson, E. O. (1967) The Theory of Island Biogeography. Princeton University Press, Princeton.

MacArthur, R. H., and Wilson, E. O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, 17, 373– 83.

MacDonald, I. A. W., Cooper, J. (1995) Insular lessons for global diversity conservation with particular reference to alien invasions. In Vitousek, P. M., Loope, L. L., and Adsersen, H. (eds.), Islands: Biological Diversity and Ecosystem Function, pp. 7-21. Berlin: Springer-Verlag.

MacKenzie, B. (1988) Guidelines for the sustained use of indigenous forests and forest products. Occasional Report No. 35, Ecosystem Programmes, CSIR, Pretoria.

MacKinnon, K. (1992) Nature's Treasurehouse: The Wildlife of Indonesia. Gramedia Pustaka Utama, Indonesia.

Macneale, K. H., Peckarsky, B. L., Likens, G. E. (2004) Contradictory results from different methods for measuring direction of insect flight. *Freshwater Biology,* 49, 1260–1268.

Macneale, K. H., Peckarsky, P. L., & Likens, G. E. (2004) Contradictory results from different methods for measuring direction of insect flight. *Freshwater Biology,* 49, 1260–1268.

Magagula, C. N. (2003) Changes in carabid beetle diversity within a fragmented agricultural landscape. *African Journal of Ecology*, 41: 23–30.

Magura, T., Bogyo, D., Mizser, S., Nagy, D. D., Tothmeresz, B. (2015) Recovery of ground-dwelling assemblages during reforestation with native oak depends on the mobility and feeding habits of the species. *Forest Ecology and Management*, 339, 117-126.

Magura, T., Tothmeresz, B., and Elek, Z. (2003) Diversity and composition of carabids during a forestry cycle. *Biodiversity and Conservation*,12: 73–85.

Majka, C. G., Sikes, D. S. (2009) Thomas L. Casey and Rhode Island's precinctive beetles: Taxonomic lessons and the utility of distributional checklists. *ZooKeys,* 22, 267-283.

Major, J. (1951) A functional, factorial approach to plant ecology. *Ecology,* 32, 392-412.

Majer, J. D. (1987) The conservation and study of invertebrates in remnants of native vegetation. Pp. 333– 335. In D. A. Saunders, G. W. Arnold, A. A. Burbridge, and A. J. M. Hopkins (eds). Nature Conservation: The Role of Remnants of Native Vegetation. Surrey Beatty and Sons, Sydney.

Makihara, H., Ohira, H. (2005) Notes on the elaterid-beetles from the Ogasawara Islands in the collection of Forestry and Forest Products Research Institute (FFPRI). *Bulletin of the Forestry and Forest Products Research Institutetute*, 4:53–64.

Malcolm, J. R., Markham, A., Neilson, R. P., and Garaci, M. (2002) Estimated migration rates under scenarios of global climate change. *Journal of Biogeography,* 29, 835-849.

Marinoni, R. C., Ganho, N. G. (2006) A diversidade diferencial beta de Coleoptera (Insecta) em uma paisagem antropizada do Bioma Araucária. *Revista Brasileira De Entomologia*, 50(1):64–71.

Marris, W. M. (2000) The beetle (Coleoptera) fauna of the Antipodes Islands, with comments on the impact of mice; and an annotated checklist of the insect and arachnid fauna. *Journal of the Royal Society of New Zealand*, 30(2), 169-195.

Marshall, C. J. and Leibherr, J. K. (2000) Cladisticbiogeography of the Mexican transition zone. *Journal of Biogeography*, 27: 203–216.

Marske, K. A. and Ivie, M. A. (2003) Beetle fauna of the United States and Canada. *Coleopterists Bulletin,* 57: 495–503.

Martikainen, P. Kouki, J. (2003) Sampling the rarest: threatened beetles in boreal forest biodiversity inventories. *Biodiversity and Conservation*, 12, 1815-1831.

Masner, L., and Goulet, H. (1981) A new model of flight interception trap for some hymenopteraous insects. *Entomological News*, 92, 199-202.

Mason, W. K., Lodge, G. M., Allan, C. J., Andrew, M. H., Johnson, T., Russell, B. & Simpson, I. H. (2003) An appraisal of sustainable grazing systems: the program, the triple bottom line impacts and the sustainability of grazing systems. *Australian Journal of Experimental Agriculture* 43, 1061-1082.

May, R. M. (1988) How many species are there on earth? *Science*, 241:1441–1449.

May, R. M. (1990) How many species? *Philosophical Transactions of the Royal Society of Biological Sciences,* 330: 293–304.

Mayr, E. (1941) The origin and the history of the bird fauna of Polynesia. *Proceedings of the Sixth Pacific Science Congress*, 4, 197–216.

Mayr, E. (1965) The nature of colonization in birds. The genetics of colonizing species (ed. by H.G. Baker and G.D. Stebbins), pp. 30–47. Academic Press, New York.

Mayr, E. (1976) Evolution and the diversity of life: selected essays. Belknap, Harvard University Press, Cambridge, MA, USA.

Mayr, E. & Diamond, J. (2001) The birds of northern Melanesia: speciation, ecology, and biogeography. Oxford University Press, Oxford.

McCutcheon, G. S. (2002) Consumption of tobacco budworm (Lepidoptera: Noctuidae) by hooded beetle (Coleoptera: Anthicidae) and big eyed bug (Hemiptera: Lygaeidae). *Journal of Agricultural and Urban Entomology*,19:55–61.

McElroy, W. D., DeLuca, M. A. (1983) Firefly and bacterial luminescence: basic science and applications. *Journal of Applied Biochemistry*, 5, 197-209.

McGavin, G. C. (1997) Expedition field techniques: insect and other terrestrial arthropods. The Royal Geographical Society, London.

McGeoch, M. A. (1998) The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews*, 73, 181-201.

McGeoch, M. A. (2002) Bioindicators. In: El-Shaarawi, A. H. and Piergorsch, W. W. (eds.) Encyclopedia of Environmetrics, p. 186-189. Wiley, Chichester.

McGeoch, M. A., Schroeder, M., Ekbom, B., and Larsson, S. (2007) Saproxylic beetle diversity in a managed boreal forest: importance of stand characteristics and forestry conservation measures. *Diversity and Distributions*, 13, 418-429.

McKinney, M. L. (2002) Influence of settlement time, human population, park shape and age, visitation and roads on the number of alien plant species in protected areas in the USA. *Diversity and Distributions*, 8(6), 311-318.

McMaster, R. T. (2005) Factors influencing vascular plant diversity on 22 islands off the coast of eastern North America. *Journal of Biogeography*, 32, 475-492.

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H. & Nowakowski, M. (2002 The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation*, 106, 259–271.

Melbourne, B. A. (1999) Bias in the effects of habitat structure on pitfall traps: an experimental evaluation. *Australian Journal of Ecology*, 24, 228-239.

Melville, R. (1979) Endangered island floras. In: Bramwell, D., ed. Plants and islands. San Diego, CA: Academic Press. 459 p.

Meiri, S. (2005) Area, isolation and body size evolution in insular carnivores. *Ecology Letter,* 8: 1211–1217.

Messina, F. J. (2004) How labile are the egg-laying preferences of seed beetles? *Ecological Entomology*, 29, 318-326

Michel, P., White, H., Dickinson, K. J. M., Barratt, B. I. P., Fitzgerald, B. M., Johns, P. M., Nunn, J., Eyles, A. C., Andrew, I. G. (2008) Invertebrate survey of coastal habitats and podocarp forest on Ulva Island, Rakiura National Park, New Zealand. *New Zealand Journal of Zoology*, 35(4), 335-349.

Millennium Ecosystems Assessment (2005) Ecosystems and Human Well-Being: Biodiversity Synthesis (World Resources Institute, Washington, DC).

Miller, L. H. and B. Greenwood. (2002) Malaria – a shadow over Africa. *Science*, 298: 121–122.

Mittal, I. C. (1993) Natural manuring and soil conditioning by dung beetles.*Tropical Ecology*, 34:150–159.

Munks, S., Richards, K., Meggs, J., Wapstra, M., and Corkrey, R. (2004) Distribution, habitat and conservation of two threatened stag beetles, *Hoplogonus bornemisszai* and *H. vanderschoori* (Coleoptera: Lucanidae) in north-east Tasmania. *Australian Zoologist*, 32: 586–596.

Hanski, I. and Y. Cambefort (eds). (1991) Dung Beetle Ecology. Princeton University Press, Princeton, NewJersey. 520pp.

Hanski, I., M. Saastamoinen, and O. Ovaskainen. (2006) Dispersal-related life-history trade-offs in a butterfly metapopulation. *Journal of Animal Ecology*, 75: 91–100.

Hanski, I. and M. C. Singer. (2001) Extinction-colorization dynamics and host-plant choice in butterfly metapopulations. *American Naturalist*, 158: 341–353.

Leps, J., and Smilauer, P. (2003) Multivariate Analysis of Ecological Data using CANOCO. Cambridge University Press, Cambrodge.

Malaise, R. (1937) A new insect-trap. *Entomologisk Tidskrift*, Stockholm. 58: 148— 60.

Meier, H. E. M. (2007) Modeling the pathways and ages of inflowing salt- and freshwater in the Baltic Sea. *Estuary Coast Shelf Science*, 74:610–627

Mills, H. R., Bradshaw, F. J., Lambert, C., Bradshaw, S. D., Bencini, R. (2012) Reproduction in the marsupial dibbler, Parantechinus apicalis; differences between island and mainland populations. *General and Comparative Endocrinology*, 178, 347-354.

Minelli, A. (1990) Faunal turnover and equilibrium models in island biogeography: some problems in the study of species diversity in island biota. *Atti dei Convegni Lincei*, 85, 85–95.

Minister of Forestry and Estate Crop, Republic of Indonesia. 2002. In: Nagy, L., Mardiastuti, A., Proctor, J., Bruenig, E. F., Miller, H. G. (eds.) Curriculum, Sustainable Forest Management and Conservation of Biodiversity in Indonesia. University of Stirling, Stirling, Scotland.

Mitchell, A., Maddox, C. (2010) Bark beetles (Coleoptera: Curculionidae: Scolytinae) of importance to the Australian macadamia industry: an integrative taxonomic approach to species diagnostics. *Australian Journal of Entomology*, 49(2), 104 -113.

Moller, H. (1996) Lessons for invasion theory from social insects. *Biological Conservation*, 78, 125-142.

Moore, I. T., Greene, M. J., Lerner, D. T., Asher, C. E., Krohmer, R. W., Hess, D., Whittier, J., Mason, R. T. (2005) Physiological evidence for reproductive suppression in the introduced population of brown tree snakes (Boiga irregularis) on Guam. *Biological Conservation*, 121, 91-98.

Moore, I., and Legner, E. F. (1976) Intertidal rove beetles (Coleoptera: Staphylinidae. In Cheng, L. (eds) Marine Insects. North-Holland Publishing, Amsterdam.

Morais, H. C., Sujii, E. R., Almeida-Neto, M., De-Carvalho, P. S., Hay, J. D., Diniz, I. R. (2011) Host plant specialization and species turnover of caterpillars among hosts in the Brazilian Cerrado. *Biotropica*, 43: 467–472.

Morrill, W. L., Lester, D. G., Wrona, A. E. (1990) Factors affecting efficacy of pitfall traps for beetles (Coleoptera: Carabidae and Tenebrionidae). *Journal of Entomological Science,* 25, 284-293.

Morrison, L. W. (2002) Determinants of plant species richness on small Bahamian islands. *Journal of Biogeography*, 29, 931–941

Morrone, J. J. (2011) Island evolutionary biogeography: analysis of the weevils (Coleoptera: Curculionidae) of the Falkland Islands (Islas Malvinas). *Journal of Biogeography*, 38, 2078-2090.

Morse, R. A., Calderone, N. W. (2000) The value of honey bees as pollinators of U.S. crops in 2000. *Bee Culture*, 128, 1–15.

Morwood, M. J., Jungers, W. L. (2009) Conclusions: implications of the Liang Bua excavations for hominin evolution and biogeography. *Journal of Human Evolution,* 57, 640-648.

Mueller-Dombois, D. (1981) Island ecosystems: What is unique about their ecology. In: Mueller-Dombois, D., Bridges, K. W., Carson, H. L. (eds.) Island Ecosystems. Biological Organisation in Selected Hawaiian Communities. Hutchinson Ross, Stroudsburg.

Munks, S., Richards, K., Meggs, J., Wapsttra, M., Corkrey, R. (2004) Distribution, habitat, and conservation of two threatened stag beetles, Haplogonus bonemisszai and H. vanderschoori (Coleoptera: Lucanidae) in north-east Tasmania. *Australian Zoologist*, 32, 586-596.

Munoz, J., Felicisimo, A. M., Cabezas, F., Burgaz, A. R., Martinez, I. (2004) Wind as a long-distance dispersal vehicle in the southern hemisphere. *Science*, 304, 1144-1147.

Mylonas, M. A. (1982) The zoogeography and ecology of the terrestrial molluscs of Cylades. PhD Thesis, University of Athens, Greece.

Nagy, L. and Proctor, J. (1999) Early secondary forest growth after shifting cultivation. Management of Secondary and Logged-over Forests in Indonesia, Selected Proceedings of an International Workshop held in Bogor, Indonesia 17-19 Nove,ber 1997. Sist, P., Sabogal, C., Byron, Y. (eds.). Centre for International Forestry Research, Bogor.

Nahrung, H. F. (2004) Biology of Chrysophtharta agricola (Coleoptera: Chrysomelidae), a pest of Eucalyptus plantations in south-eastern Australia. *Australian Forestry*, 67, 60-67.

NASS, National Agricultural Statistics Service. (2004) Cattle Inventory Report. Washington (DC): US Department of Agriculture, NASS. (http//usda.mannlib.cornell.edu/ reports/nassr/livestock/pct-bb/catl0104.pdf)

National Development Agency (Badan Perencana Pembangunan Nasional). (1993) Biodiversity Action Plan for Indonesia, Jakarta.

Naughton-Treves, L., Holland, M., & Brandon, K. (2005) The role of protected areas in conserving biodiversity and sustaining local livelihoods. *Annual Review of Environment and Resources,* 30, 219–252.

Naylor, L. H. (1999) Reporter gene technology: the future looks bright. *Biochemical Pharmacology*, 58, 749-757.

Nealis, V. G. (1977) Habitat association and community analysis of south Texas dung beetles (Coleoptera: Scarabaeidae). *Canadian Journal of Zoology*,55: 138–147.

Neto, M. A., Prado, P. I., Lewinsohn, T. M. (2011) Phytophagous insect fauna tracks host plant responses to exotic grass invasion. *Oecologia*, 165, 1051–1062.

New, T. R. (1988) Associations between Insects and Plants. New South Wales University Press, Kensington, NSW. 113pp.

New, T. R. (1995) An Introduction to Invertebrate Conservation Biology. Oxford University Press, Oxford. 194pp.

New, T. R. (2010) Beetles in Conservation. Wiley-Blackwell, Chichester.

Newton, J. A. F. (1977) Review of Agyrtidae (Coleoptera), with a new genus and species from New Zealand. *Annales Zoologici*,47: 111–156.

Newton, J. A. F. (1998) Phylogenetic problems, current classification and generic catalog of world Leiodidae (including Cholevidae). Pp. 41–178. In P. M. Giachino and S. B. Peck (eds). Phylogeny and Evolution of Subterranean and Endogean Cholevidae (Leiodidae). Proceedings of the 20th International Congress of Entomology, Florence, 1996. Museo Regionale di Scienze Naturali, Torino. 295pp.

Newton,J. A. F. (2005) Leiodidae Fleming, 1821. Pp.269–280. In R. G. Beutel and R. A. B. Leschen (eds). Handbook of Zoology: A Natural History of the Phyla of the Animal Kingdom, VolumeIV. Arthropoda: Insecta, Part 38. Coleoptera, Beetles, Volume 1. Morphology and Systematics. Walter de Gruyter, Berlin.

Newton, J. A. F. and Thayer, M. K. (1995) Protopselaphinae new subfamily for Protopselaphus new genus from Malaysia, with a phylogenetic analysis and review of the Omaliine Group of Staphylinidae including Pselaphidae (Coleoptera). Pp.219–320. In J. Pakaluk and S.A. Slipinski (eds). Biology, Phylogeny and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson. Muzeum I Instytut Zoologii PAN, Warszawa.

Nichols, E., Larsen, T., Spector, S., Davis, A. L., Escobar, F., Favila, M., Vulinec, K. (2007) Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. *Biological Conservation*, 137(1), 1-19.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M. & Network, T.S.R. (2008) Ecological functions and ecosystem services of Scarabaeinae dung beetles: a review. *Biological Conservation*, 141, 1461–1474.

Nielsen, E. S., Mound, L. A. (1999) Global diversity of insects: the problems of estimating numbers. In: Raven, P. H. and Williams, T. (eds.) Nature and Human Society: The Quest for Sustainable World. National Academy Press, Washington DC.

Niemeli, J. and Halroe, E., (1992) Habitat associations of carabid beetles in fields and forests on the Aland Islands, SW Finland. Ecography, 15, 3-11. *ZooKeys*, 147, 497 - 526.

Niemela, J. (1988a) Carabid beetles in shore-habitats on the Aland Islands, SW Finland: the effect of habitat availability and species characteristics. *Acta Oecological*, 9, 379–395.

Niemela, J. (1988b) Distribution of carabid beetles in Fennoscandian archipelagoes: an island-mainland comparison. PhD Thesis, University of Helsinki, Finland.

Niemelä, J. (1988c) Habitat occupancy of carabid beetles on small islands and the adjacent Åland mainland, SW Finland. *Annales Zoologici Fennici*, 25, 121–131.

Niemela, J. (1990) Effect of changes in the habitat on carabid assemblages in a wooded meadow on the Aland Islands. *Not Entomol*, 69, 169–174.

Niemelä, J., and Halme, E. (1992) Habitat associations of carabid beetles in fields and forests on the Åland Islands, SW Finland. *Ecography*, 15(1), 3-11.

Niemela, J., Haila, Y., Halme, E. (1988) Carabid beetles on isolated Baltic Islands and on the adjacent Aland mainland: variation in colonization success. *Annales Zoologici Fennici,* 25, 133–143.

Niemela, J., Haila, Y., Ranta, E. (1986) Spatial heterogeneity of carabid beetle dispersion in uniform forests on the Aland Islands, SW Finland. *Annales Zoologici Fennici,* 23, 289–296.

Niemelä, J., Haila, Y., Ranta, E., Tiainen, J., Vepsäläinen, K. & Ås, S. (1987) Distribution of carabid beetles in four boreal archipelagoes. *Annales Zoologici Fennici*, 24, 89–100.

Niemela, J., Halme, E. (1992) Habitat associations of carabid beetles in fields and forests on the Aland Islands, SW Finland. *Ecography*, 15, 3–11.

Niemela, J., Ranta, E., Haila, Y. (1985) Carabid beetles in lush forest patches on the Aland Islands, SW Finland: an island-mainland comparison. *Journal of Biogeography,* 12, 109–120.

Niemela, J., Spence, J. R. (1991) Distribution and abundance of an exotic ground-beetle (Carabidae): a test of community impact. *Oikos,* 62, 351–359.

Niemela,J., Spence, R., Langor, D., Haila, Y., and Tukia, H. (1993) Logging and boreal ground-beetle assemblages on two continents: implications for conservation. Pp.29–50. In K. J. Gaston, T. R. New, and M. J. Samways (eds). Perspectives on Insect Conservation. Intercept Ltd, Andover.

Nieminen, M. & Hanski, I. (1998) Metapopulations of moths on islands: a test of two contrasting models. *Journal of Animal Ecology*, 67, 149–160.

Nilsson, S. G., Bengtsson, J. and As, S. (1988) Habitat diversity or area per se? species Richness of woody plants, carabid beetles and land snails on islands. *Journal of Animal Ecology*, 57(2), 685-704.

Noerdjito, W. A. (2003) Keragaman kumbang (Coleoptera). In: Amir, M. dan S. Kahono. (ed.). Serangga Taman Nasional Gunung Halimun Jawa Bagian Barat. Bogor: JICA Biodiversity Conservation Project.

Noerdjito, W. A., Nakamura, K. (1999) Population dynamics of two species of tortoise beelte Aspidomorpha miliaris and A. sanctaecrucis (Coleoptera: Chrysomelidae: Cassidinae) in East Java, Indonesia: seasonal changes in population size and longevity of adult beetles. *Tropics*, 8, 409-425

Novotny, V., Basset, Y. (2005) Host specificity of insect herbivores in tropical forests. *Proceedings of Royal Society B*, 272(1568), 1083–1090.

Nunn, P. D. (1994) Oceanic islands. Oxford, U.K.: Blackwell Scientific Publications. 413 p.

Nur, Y., Fazi, S., Wirjoatmodjo, N, and Han, Q. (2001) Towards wise coastal management practice in a tropical megacity—Jakarta. *Ocean and Coastal Management*, 44, 335-353.

Öberg, S., Ekbom, B. & Bommarco, R. (2007) Influence of habitat type and surrounding landscape on spider diversity in Swedish agroecosystems. *Agriculture, Ecosystems & Environment,* 122, 211–219.

Ødegaard, R., Diserud, O. H., Østbye, K. (2005) The importance of plant relatedness for host utilization among phytophagous insects. *Ecology Letter,* 8:612–617.

Ogden, R., and Thorpe, R. S. (2002) Molecular evidence for ecological speciation in tropical habitats. *Proceedings of the National Academy of Science USA*, 99: 13612–13615

Ohno, S. (1990) The Scolytidae and Platypodidae (Coleoptera) from Borneo found in logs at Nagoya port. 1. *Research Bulletin of the Plant Protection Service, Japan,* 26, 83–94.

O'Keefe, S. T. (2005) Scydmaenidae Leach, 1815. Pp.280–288. In R. G. Beutel and R. A. B. Leschen (eds). Handbook of Zoology: A Natural History of the Phyla of the Animal Kingdom, VolumeIV. Arthropoda: Insecta, Part 38. Coleoptera, Beetles, Volume 1. Morphology and Systematics. Walter de Gruyter, Berlin.

Oksanen, J. (2015) Multivariate Analysis of Ecological Communities in R: vegan tutorial.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Simpson, G., Solymos, P., Stevens, M., & Wagner, H. (2012) vegan: Community Ecology Package. R package version 2.0-3.

Olson, S.L. (1990) The prehistoric impact of man on biogeographical patterns of insular birds. *Atti dei Covegni Lincei*, 85, 45–51.

Ongkosongo, O. S. R. and Sukarno. (1986) Background to the study sites in the Bay of Jakarta and Kepulauan Seribu. In Brown, B. E. (eds), Human Induced Damage to Coral Reefs. UNESCO, Paris.

Orians, G. H. (1966) Food of nestling yellow-headed blackbirds, Cariboo Parklands, British Columbia. *Condor*, 68 : 321–337.

Oringanje, C., Alaribe, A. A. A., Oduola, A. O., Oduwole, O. A., Adeogun, A. O. Meremikwu, M. M., Awolola, T. S. (2011) Vector abundance and species composition of Anopheles mosquito in Calabar, Nigeria. *Journal of Vector Borne Diseases*, 48 (3): 171-173.

Osbourne, P. L. (2012) Tropical Ecosystems and Ecological Concepts. Cambridge University Press, Cambridge.

Ovaskainen, O. (2002) Long-term persistence of species and the SLOSS problem. *Journal of Theoretical Biology*, 218, 419–433.

Paine, T. D., Raffa, K. F., and Harrington, T. C. (1997) Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annual Review of Entomology*, 42: 179–206.

Pakaluk, J., Slipinski, S. A., and Lawrence, J. F. (1994) Current classification and family-group names in Cucujoidea (Coleoptera).*Genus,* 5: 223–268.

Palmer, M. (2002) Testing the 'island rule' for a tenebrionid beetle (Coleoptera, Tenebrionidae). *Acta Oecologica*, 23, 103–107.

Palumbi, S. R. (2001) Humans as the World's Greatest Evolutionary Force. *Science*, 293.

Panitsa, M., Tzanoudakis, D., Triantis, K. & Sfenthourakis, S. (2006) Patterns of species richness on very small islands: the plants of the Aegean archipelago. *Journal of Biogeography* 33(7), 1223-1234.

Parmain, G., Bouget, C., Müller, J., Horak, J., Gossner, M. M., Lachat, T., Isacsson, G. (2015) Can rove beetles (Staphylinidae) be excluded in studies focusing on saproxylic beetles in central European beech forests? *Bulletin of Entomological Research*, 105: 101-109

Parmenter, R. R., Parmenter, C. A. & Cheney, C. D. (1989). Factors influencing microhabitat partitioning in arid-land darkling beetles (Tenebrionidae): temperature and water conservation. *Journal of Arid Environments,*17: 57–67

Pattemore, D. E., and Wilcove, D. S. (2012) Invasive rats and recent colonist birds partially compensate for the loss of endemic New Zealand pollinators. *Proceedings of the Royal Society B*, 279(1733): 1597-1605.

Pau, S., MacDonald, G. M., and Gillespie, T. W. (2012) A dynamic history of climate change and human impact on the environment from Keālia Pond, Maui, Hawaiian Islands. *Annals of the Association of American Geographers*, 102(4), 748-762.

Payne, J. A. 1965. A summer carrion study of the baby pig *Sus scrofa* Linnaeus. *Ecology*, 46, 592-602.

Pearce, J. L., Venier, L. A. (2006) The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. *Ecology Indicator,* 6(4):780–793.

Pearse, I. S, Altermatt, F. (2013) Extinction cascades partially estimate herbivore losses in a complete Lepidoptera–plant food web. *Ecology*, 94:1785–1794

Peck, S. B. (1994) Sea-surface (plueston) transport of insects between islands in the Galapagos Archipelago, Ecuador. *Annals of the Entomological Society of America,* 87, 576-582.

Peck, S. B., and Davis, A. E. (1980) Collecting small beetles with large-area "window traps". *Coleopterist Bulletin*, 34, 237-239.

Peck, S. B. and Howden, H. F. (1984) Response of a dung beetle guild to different sizes of dung bait in a Panamanian rain forest. *Biotropica*, 16: 235–238.

Pemerintah Kecamatan Kepulauan Seribu. (2010) Laporan penyelenggaraan pemerintah wilayah Kecamatan Kepulauan Seribu tahun 2010. (Report of the government activities of Kecamatan Kepulauan Seribu in 2010).

Pennington, D. N., Hansel, J., and Blair, R. B. (2008) The conservation value of urban riparian areas for landbirds during spring migration-land cover, scale, and vegetation effects. *Biological Conservation*, 141:1235-12

Perkins, L. E., Cribb, B. W., Brewer, P. B., Hanan, J., Grant, M., Torres, M., and Zalucki, M. P. Generalist insects behave in a jasmonate-dependent manner on their host plants, leaving induced areas quickly and staying longer on distant parts. *Proceedings of Royal Society,* 280.

Perner, J., Schueler, S. (2004) Estimating the density of ground-dwelling arthropods with pitfall traps using a nested-cross array. *Journal of Animal Ecology,* 73, 469–477.

Perre, P., Loyola, R. D., Lewinsohn, T. M., Almeida-Neto, M. (2011) Insects on urban plants: contrasting the flower head feeding assemblages on native and exotic hosts. *Urban Ecosystem,* 14:711–722.

Petersen, R. G., Lucas, H. L., Woodhouse, W. W. (1956) The distribution of excreta by freely grazing cattle and its influence on pasture fertility: I. Excretal density. *Agronomy Journal*, 48: 440–444.

Peterson, M. A. (1996) Long-distance gene flow in the sedentary butterfly, Euphilotes enoptes (Lepidoptera: Lycaenidae). *Evolution*, 50(5), 1990-1999.

Phillips, A. (2004) The history of the international system of protected area management categories. *Parks*, 14, 4-14.

Philips, K., Pretorius, E., Scholtz, C. (2004) A phylogenetic analysis of dung beetles (Scarabaeinae: Scarabaeidae): unrolling an evolutionary history. *Invertebrate Systematics*, 18, 53–88.

Philips, T. K. (2001) A record of *Micromalthus debilis* (Coleoptera: Micromalthidae) from Central America and a discussion of its distribution. *Florida Entomologist*, 84: 159–160.

Philips, T. K. (2002) Anobiidae Fleming 1821. Pp. 245–260. In R. H. Arnett, M. C. Thomas, P. E. Skelley, and J. H. Frank (eds). American Beetles, Volume 2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.

Philips,T. K., Ivie, M.A., and Giersch, J. J. (2002) Jacobsoniidae Heller 1926. Pp. 219–220. In R. H. Arnett, M. C. Thomas, P. E. Skelley, and J. H. Frank (eds). American Beetles, Volume 2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.

Philosophical Transactions of The Royal Society B Biological Sciences, 364 (2009), 3429–3438.

Pielou, E. C. (1979) Biogeography. Wiley, New York

Pimm, S. L. (1991) The Balance of Nature? University of Chicago Press, Chicago, Illinois, USA.

Pimm, S. L. and Raven, P. (2000) Biodiversity: Extinction by numbers. *Nature*, 403, 843-845.

Pimm, S. L., and Lawton, J. H. (1977) Number of trophic levels in ecological communities. *Nature,* 268, 329-331.

Pimm, S. L., Jones, H. L., and Diamond, J. (1988) On the risk of extinction. *American Naturalist,* 132, 757-785.

Pitelka, L. F., Plant Migration Workshop Group (1997) Plant migration and climate change. *American Scientist,* 85, 464-473.

Powell, J. A. 1992. Interrelationships of yuccas and yucca moths. *Trends in Ecology and Evolution*, 7: 10–15.

Prasifka, J. R., Lopez, M. D., Hellmich, R. L., Lewis, L. C., Dively, G. P. (2007) Comparison of pitfall traps and litter bags for sampling ground-dwelling arthropods. *Journal of Applied Entomology* 131(2), 115-120.

Price, P. W. (1981) Semiochemicalsin evolutionary time. Pp. 251–279. In D. A. Nordlund, R. L. Jones, and W.J.Lewis (eds). Semiochemicals: Their Role in Pest Control. Wiley, NewYork.

Price, P. W. (1984) Insect Ecology. Second Edition. John Wiley and Sons, New York. 607pp.

Price, J. P. (2004) Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. *Journal of Biogeography*, 31, 287-500.

Price, M. B., Young, D. K. (2006) An annotated checklist of Wisconsin sap and shortwinged flower beetles (Coleoptera: Nitidulidae, Kateretidae). Insecta Mundi Center for Systematic Entomology, Gainesville, University of Nebraska - Lincoln.

Purchart, L. (2013) A New Species of the Genus Deretus Gahan, 1900 (Coleoptera: Tenebrionidae) from the Island of Socotra. *Annales Zoologici*, 63(1), 79-83.

Purtauf, T., Dauber, J., and Wolters, V. (2005) Source: The response of carabids to landscape simplification differs between trophic groups. *Oecologia*, 142(3), 458-464.

Puskonser (Pusat Penelitian dan Pengembangan Konservasi dan Rehabilitas). (2012) <http://www.p3kr.com/hutan-penelitian-dramaga/>

Qie, L., Lee, T. M., Sodhi, N. S. and Lim, S. L. H. (2011) Dung beetle assemblages on tropical land-bridge islands: small island effect and vulnerable species. *Journal of Biogeography*, 38, 792–804.

Qiu, W., Wang, B., Jones, P. J. S., Axmacher, J. C. (2009) Challenges in developing China's marine protected area system. *Marine Policy*, 33(4), 599-605.

Raby, P. (2001) Alfred Russel Wallace: a life. Princeton University Press, Princeton.

Raffa, K. F., Berryman, A. A. (1983) The role of host plant resistant in the colonisation behaviour and ecology of bark beetles (Coleoptera; Scolytidae). *Ecological Monographs*, 53, 27-49.

Rainey, W. E, Pierson, D. E., Elmqvist, T., and Cox, P. A. (1995) The role of flying foxes (Pteropodidae) in oceanic island ecosystems of the Pacific. Symposium of the Zoological Society of London, 67, 47-62.

Rainio, J., Niemela, J. (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity Conservation*, 12: 487–506

Ratcliffe, B. C. (1970) Scarab beetles. Dung feeders, jewelled pollinators, and horned giants. University of Nebraska News, 59: 1–4.

Ravenel, R.M. and Redford, K. H. (2005) Understanding IUCN protected area categories. *Natural Areas Journal*, 25, 381-389.

Razak, H. (1994) Kadar Poliklorobifenil (PCB) di Perairan Sunter–Teluk Jakarta. In: Hutagalung H. P. et al., (eds). Support Paper at Workshop on Sea Pollution Monitoring, Jakarta.

Razak, H., and Khozanah. (1994) Kadar pestisida organoklorin di perairan Teluk Jakarta, Makalah Penunjang Seminar Pemantauan Pencemaran Laut. Jakarta.

R Development Core Team (2013) The R Project for Statistical Computing. Available at www. r-project.org/.

Richardson, J. S. (1993) Limits to productivity in streams: evidence from studies of macroinvertebrates. Pp. 9–15. In R. J. Gibson and R. E. Cutting (eds). Production of Juvenile Atlantic Salmon, *Salmo salar*, in Natural Waters. Canada Special Publication of Fisheries and Aquatic Sciences 118. National Research Council of Canada and Department of Fisheries and Oceans,Ottawa.

Rigby, C. & Lawton, J. H. (1981). Species-area relationships of arthropods on host plants: herbivores on bracken. *Journal of Biogeography*, 8, 125-133

Rigg, J. (1996) The Indonesian world. In: Rigg, J. (ed.). The Human Environment: Indonesian Heritage. Editions Didier Millet, Singapore.

Rizali, A., Lohman, D. J., Buchori, D., Prasetyo, L. B., Triwidodo, H., Bos, M. M., Yamane, S., Schulze, C. H. (2010) Ant communities on small tropical islands: effects of island size and isolation are obscured by habitat disturbance and 'tramp' ant species. *Journal of Biogeography*, 37(2), 229-236.

Roberts, E. M., Rogers, R. R., Foreman, B. Z. (2007) Continental insect borings in dinosaur bone: examples from the late Cretaceous of Madagascar and Utah. *Journal of Paleontology*, 81(1), 201–208.

Rodriguez, J. P. (2001) Exotic species introductions into South America: an underestimated threat? *Biodiversity and Conservation,* 10, 1983–1996.

Roff, D. A., Fairbairn, D. J. (1991) Wing dimorphisms and the evolution of migratory polymorphisms among the Insecta. *American Zoologists*, 31, 243–251.

Rolston, H. III. (1994) Conserving Natural Value. Columbia University Press, New York.

Romero-Alcaraz, E., Ávila, J. M. (2000) Landscape heterogeneity in relation to variations in epigaeic beetle diversity of a Mediterranean ecosystem. Implications for conservation. *Biodiversity & Conservation*, 9(7), 985-1005.

Rosenzweig, M. L. (1995) Species Diversity in Space and Time. Cambridge University Press, Cambridge.

Sabu, T. K., Shiju, R. T., Vinod, K. V., & Nithya, S. (2011) A comparison of the pitfall trap, Winkler extractor and Berlese funnel for sampling ground-dwelling arthropods in tropical montane cloud forests. *Journal of Insect Science*, 11(28).

Salm, R. V., M. Halim, and A. Abdullah. (1982) Proposed Pulau Seribu Marine National Park: Conservation and tourism. *Parks,* 7(2), 15-20.

Samways, M. J. (1993) Insects in biodiversity conservation: some perspectives and directives. Biodiversity and Conservation, 2: 258–282.

Samways, M. J. (1994) Insect Conservation Biology. Chapman and Hall, London. 358pp.

Samways, M. J. (1997) Classical biological control and biodiversity conservation: what risks are we prepared to accept? *Biodiversity and Conservation*, 6: 1309–1316.

Samways, M. J. (2002) Red-listed Odonata of Africa. *Odonatologica,* 31, 151–170.

Samways, M. J. (2003) Conservation of an endemic dragonfly fauna in the ancient tropical Seychelles archipelago. *Odonatologica*, 32, 177-182.

Samways, M. J. (2005) Insect Diversity Conservation. Cambridge University Press, New York. 342pp.

Samways, M. J. (2007a). Insect conservation: a synthetic management approach. *Annual Review of Entomology*, 52: 465–487.

Samways, M. J. (2007b). Implementing ecological networks for conserving insects and other biodiversity. Pp.127–143. In A. Stewart, O. Lewis, and T. R. New (eds). Insect Conservation Biology. CABI, Wallingford, United Kingdom.

Samways, M. J., (2009) Extreme weather and climate change impacts on South African dragonflies. In: Ott, J. (ed.) Monitoring Climate Change Using Dragonflies. Pensoft, Sofia. In Press

Samways, M. J., McGeoch, M. A., New, T. R. (2010) Insect Conservation. Oxford University Press, Oxford.

Samways, M. J. and Osborn, R. (1998) Divergence in a transoceanic circumtropical dragonfly on a remote island. *Journal of Biogeography*, 25, 935-946.

Sanderson, E. W. et al. (2002) The human footprint and the last of the wild. *BioScience,* 52, 10, 891–904.

Santos, A. A., De Nicola´s, J. P., Ferrer, F. (2002) Habitat selection and assemblage structure of darkling beetles (Col. Tenebrionidae) along environmental gradients on the island of Tenerife (Canary Islands). *Journal of Arid Environments*, 52, 63–85.

Santos, A. M. C., Whittaker, R. J., Triantis, K. A., Borges, P. A. V., Jones, O. R., Quicke, D. L. J., Hortal, J. (2010) Are species–area relationships from entire archipelagos congruent with those of their constituent islands? *Global Ecology and Biogeography*, 19, 527–540.

Santos, A. M. C., Whittaker, R. J., Triantis, K. A., Borges, P. A. V., Jones, O. R., Quicke, D. L. J., Hortal, J. (2010) Are species–area relationships from entire archipelagos congruent with those of their constituent islands? *Global Ecology and Biogeography,* 19, 527–540.

Sasakawa, K. (2007) Laboratory studies on larval feeding habits of *Amara macronota* (Coleoptera: Carabidae: Zabrini). *Applied Entomology and Zoology*, 42: 669–674.

Sasakawa, K. (2009) Effects of maternal diet on fecundity and larval development in the 'primitive' granivorous carabid *Amara* (Curtonotus) *macronota*. *Entomologia Experimentalis et Applicata*, 130: 106–112.

Savalli, U. M., and C W. Fox (2002) Proximate mechanisms influencing egg size plasticity in the seed beetle, *Stator limbatus*. *Annals of the Entomological Society of America,* 95, 724-734.

Sax, D. F., Gaines, S. D., and Brown, J. H. (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *The American Naturalist*, 160(6).

Schedl, K.E. (1935) Scolytidae and Platypodidae. New species from the Philippine islands and Formosa. *Philippine Journal of Science*, 57, 479–489

Schedl, K.E. (1963) Scolytidae und Platypodidae Afrikas. Band II. Familie Scolytidae (Fortsetzung), Unterfamilie Ipinae (Fortsetzung). *Revista de Entomologia de Moçambique*, 5, 1–593.

Scheiner, S. M. (2003) Six types of species–area curves. *Global Ecology and Biogeography*, 12, 441–447.

Scheiner, S. M. (2004) A me ́lange of curves – further dialogue about species–area relationships. *Global Ecology and Biogeography*, 13, 479–484.

Scherer, K. Z., Romanowski, H. P. (2005) Predação de Megacerus baeri (Pic, 1934) (Coleoptera: Bruchidae) sobre sementes de Ipomoea imperati (Convolvulaceae), na praia da Joaquina, Florianópolis, sul do Brasil. *Biotemas*, 18(1), 39–55.

Schmidt, M. H., Clough, Y., Schulz, W., Westphalen, A. & Tscharntke, T. (2006) Capture efficiency and preservation attributes of different fluids in pitfall traps. *Journal of Arachnology*, 34: 159–162.

Schoener, T. W. (1976) The species–area relation within archipelagos: models and evidence from island land birds. *Proceedings of the International Ornithological Congress*, 16, 628–642.

Schoenly, K., Reid, W. (1987) Dynamics of heterotrophic succession in carrion arthropod assemblages: discrete seres or a continuum of change?. *Oecologia*, 73, 192-202.

Scholtz, C. H. and Grebennikov, V. V. (2005) Scarabaeiformia Crowson, 1960. Pp. 345–366. In R. G. Beutel and R. A. B. Leschen (eds). Coleoptera, Beetles, Volume1. Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphagapartim). Walter de Gruyter, Berlin.

Schulze, C. H. and Fiedler, K. (2003) Hawkmoth diversity in Northern Borneo is not reflect the influence of anthropogenic habitat disturbance. *Society for Tropical Ecology,* 9, 9-102.

Scudder, G. G. E. (1976) Are insects perfect? *Bulletin of the Entomological Society of Canada*, 8:2–6.

Scudder, G. G. E. (2009) The Importance of Insects. In: Footit, R. G., Adler, P. H. (eds.) Insect Biodiversity, Science and Society. Wiley-Blackwell, Oxford.

Schwartz, M. W., C. A. Brigham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J. Van Mantgem (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia*, 122: 297–305.

Selmi, S., and Boulinier, T. Ecological biogeography of Southern Ocean Islands: the importance of considering spatial issues. *The American Naturalist*, 158(4), 426-437.

Serez, A., Ramirez, N. (1995) Biologia floral y polinizacion de algunas monocotiledoneas de un bosque nublado venezolano. *Annals of the Missouri Botanical Garden*, 82, 61-81.

Sfenthourakis, S. (1996) A biogeographical analysis of terrestrial isopods (Isopoda: Oniscidea) from the central Aegean Islands (Greece). *Journal of Biogeography*, 23, 687-698.

Sfenthourakis, S. and Panitsa, M. (2012) From plots to islands: species diversity at different scales. *Journal of Biogeography*, 39, 750–759.

Shahabuddin, Hidayat, P. Noedjito, W. A., Manuwoto, S. (2005) Research on insect biodiversity in Indonesia: Dung beetles (Coleoptera: Scarabaeidae) and its role in ecosystem. *Biodiversitas,* 6, 141-146.

Shahabuddin, Hidayat, P., Manuwoto, S., Noerdjito, W. A., Tscharntke, T., & Schulze, C. H. (2010) Diversity and body size of dung beetles attracted to different dung types along a tropical land-use gradient in Sulawesi, Indonesia. *Journal of Tropical Ecology*, 26(01), 53-65.

Shannon, C. E. (1948) A Mathematical Theory of Communication. *Bell System Technical Journal*, 27: 623-656.

Sharanowski, B. J., Walker, E. R., and Anderson, G, S. (2008) Insect succession and decomposition patterns on shaded and sunlit carrion in Saskatchewan in three different seasons. *Forensic Science International,* 179, 219-240.

Shepherd, V. E. and C. A. Chapman. (1998) Dung beetles as secondary seed dispersers: impact on seed predation and germination. *Journal of Tropical Ecology*, 14: 199–215.

Shochat, E., Warren, P. S., Faeth, S. H., Mcintyre, N. E., Hope, D. (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology and Evolution*, 21:186-1

Shurin, J.B. and Seabloom, E.W. (2005) The strength of trophic cascades across ecosystems: predictions from allometry and energetics. *Journal of Animal Ecology*, 74, 1029–1038.

Sikes, D. S. (2004) The beetle fauna of Rhode Island. An annotated checklist. The Biota of Rhode Island. Volume 3. Rhode Island Natural History Survey, Kingston. 6 - 295pp.

Sikes, D. S. (2005) Silphidae Latreille, 1807. Pp. 288–296. In R. G. Beutel and R. G. B. Leschen (eds). Handbook of Zoology: A Natural History of the Phyla of the Animal Kingdom, Volume IV. Arthropoda: Insecta, Part 38. Coleoptera, Beetles, Volume 1. Morphology and Systematics. Walter de Gruyter, Berlin.

Siliceo, I. and Diaz, J. A. (2010) A comparative study of clutch size, range size, and the conservation status of island vs. mainland lacertid lizards. *Biological Conservation*, 143: 2601-2608.

Silveira, M. H., Benedito C. Lopes , Sérgio Ide , Tânia T. Castellani & Malva I. M. Hernández (2012) Beetle (Insecta, Coleoptera) assemblage in a Southern Brazilian restinga: effects of anthropogenic disturbance and vegetation complexity. *Studies on Neotropical Fauna and Environment*, 47(3), 203-214.

Simaiakis, S. (2006) Systematics, biogeography and elements of ecology of Centipedes of the south Aegean islands [PhD dissertation]. [Heraklion]: University of Crete.

Simberloff, D. & Abele, L.G. (1982) Refuge design and island biogeographic theory: effects of frag- mentation. *American Naturalists*, 120, 41-50.

Simberloff, D. (1995) Why Do Introduced Species Appear to Devastate Islands More Than Mainland Areas*? Pacific Science*, 49(1), 87-97.

Simberloff, D. S. (1974) Equilibrium theory of island biogeography and ecology. *Annual Review of Ecological System,* 5, 161-182.

Simberloff, D.S. (1978) Use of rarefaction and related methods in ecology. Biological data in water pollution assessment: quantitative and statistical analyses (ed. by K. L. Dickson, J. Garins, Jr and R. J. Livingston), pp. 150-165. Am. Soc. for Testing and Materials STP 652.

Simmons, L. W., Ridsdill-Smith, T. J. (2011) Reproductive competition and its impact on the evolution and ecology of dung beetles. In: Simmons, L. W., Ridsdill-Smith, T. J., editors. Ecology and evolution of dung beetles. Oxford: Blackwell Publishing. 1–20.

Simpson, E. H. (1949) Measurement of Diversity. *Nature,* 163: 688-688.

Slade, E. M., Mann, D. J., Lewis, O. T. (2011) Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. *Biological Conservation*, 144, 166-174.

Slade, E. M., Mann, D. J., Villanueva, J. F., Lewis, O. T. (2007) Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology*, 76, 1094–1104.

Slatkin, M. 1993. Isolation by distance in equilibrium and nonequilibrium populations. *Evolution*, 47: 264–279.

Smith, A. B. T. (2006) A review of the family-group names for the superfamily Scarabaeoidea (Coleoptera) with corrections to nomenclature and a current classification. *Coleopterists Society Monographs*, 5: 144–204.

Smith, K. G. V. (1986) A Manual of Forensic Entomology. Cornell University Press, Ithaca, NY.

Smith, A. B. T. and Paucar, A. (2000) Taxonomic review of *Platycoelia lutescens* (Scarabaeidae: Rutelinae: Anoplognathini) and a description of its use as food by the people of the Ecuadorian Highlands. *Annals of the Entomological Society of America*, 93: 408–414.

Smith, A. B. T., Hawks, D. C., and Heraty, J. M. (2006) An overview of the classification and evolution of the major scarab beetle clades (Coleoptera: Scarabaeoidea) based on preliminary molecular analyses. *Coleopterists Society Monographs*, 5:35–46.

Smithers, C. 1982. Handbook of Insect Collecting: Collection, Preparation, Preservation and Storage. David & Charles.

Sodhi, N. S., Wilcove, D. S., Subaraj, R., Yong, D. L., Lee, T. M. Bernard, H., Lim, S. H. L. (2010) Insect extinctions on a small denuded Bornean island. *Biodiversity Conservation*,19, 485–490.

Sole, C. L., Scholtz, C. H., Bastos, A. D. S. (2005) Phylogeography of the Namib Desert dung beetles Scarabaeus (Pachysoma) Macleay (Coleoptera: Scarabaeidae). *Journal of Biogeography,* 32, 75-84.

Solem, A. (1982) Endodontoid land snails from Pacific islands (Mollusca: Pulmonata: Sigmurethra). Part II. Families Punctidae and Charopidae, zoogeography. Field Museum of Natural History, Chicago.

Solem, A. (1990) Limitations of equilibrium theory in relation to land snails. *Atti dei Covegni Lincei,* 85, 97–116.

Sorace, A., and Gustin, M. (2008) Homogenisation processes and local effects on avifaunal composition in Italian towns. *Acta Oecologica*, 33:15-26

Sorensson, M. (1997) Morphological and taxonomical novelties in the world's smallest beetles, and the first Old World record of Nanosellini (Coleoptera: Ptiilidae). *Systematic Entomology*, 22, 257-283.

SOS (State of Observed Species). (2010) International Institute for Species Exploration, Arizona State University.

Soule, M. E., Orians, G. H. (2001) Conservation Biology: Research Priorities for the Next Decade. Society for Conservation Biology. Island Press, Washington, D. C., USA.

Southwood, T.R.E. (1978) Ecological methods, 2nd eds, p. 524. Chapman & Hall, London.

Spears Jr., E. E. (1987) Island and Mainland Pollination Ecology of *Centrosema Virginianum and Opuntia Stricta. Journal of Ecology*, 75(2), 351-362.

Spector, S. and Forsyth, A. B. (1998) Indicator taxa in the vanishing tropics. In Mace, G. M., Balmford, A., Ginsberg, J. R. (Eds.), Conservation in a Changing World. Cambridge University Press, London, pp. 181–210.

Spence, J. R. & Niemelä, J. K. (1994) Sampling carabid assemblages with pitfall traps: the madness and the method. *Canadian Entomologist*, 126, 881–894.

Spence, J. R., and Niemela, J. K. (1994) Sampling carabid assemblages with pitfall traps: the madness and the methods. *The Canadian Entomologist*, 126, 881-1894.

Spence, J. R., Spence, D. H. (1988) Of ground-beetle and men: introduced species and the synanthropic fauna of western Canada. *Memoirs of the Entomological Society of Canada*, 144, 151-168.

Spengler, A., Hartmann, P., Buchori, D., Schulze, C. H. (2011) How island size and isolation affect bee and wasp ensembles on small tropical islands: a case study from Kepulauan Seribu, Indonesia. *Journal of Biogeography*, 38(2), 247-258.

Stabach, J. A., Dabek, L., Jensen, R., Wang, Y. Q. (2009) Discrimination of dominant forest types for Matschie's tree kangaroo conservation in Papua New Guinea using high-resolution remote sensing. *International Journal of Remote Sensing*, 30, 405-422.

Stack, R. W., McBride, D. K., and Lamey, H. E. (1996) Dutch elm disease. North Dakota State University Extension Service, Fargo, ND

Staines, C. L. (2008) The Cerambycidae or Longhorned Wood-Boring Beetles (Insecta: Coleoptera) of Plummers Island, Maryland. *Bulletin of the Biological Society of Washington*, 15(1), 145-148.

Stavert, J. R., Gaskett, A. C., Scott, D. J., Beggs, J. R. (2014) Dung beetles in an avian-dominated island ecosystem: feeding and trophic ecology. *Oecologia*, 176, 259–271.

Steadman, D. W. (1997) The historic biogeography and community ecology of Polynesian pigeons and doves. *Journal of Biogeography*, 24, 737-753.

Steinbauer, M. J., Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C., and Fernández-Palacios, J. M. (2012) Increase of island endemism with altitude – speciation processes on oceanic islands. *Ecography*, 35, 23–32.

Stevens, M. I., Greenslade, P., Hogg, I. D. & Sunnucks, P. (2006) Southern Hemisphere springtails: could any have survived glaciation of Antarctica? *Molecular Biology and Evolution*, 23, 874–882.

Stohlgren, T. J., Barnett, D. T., Kartesz, J. T. (2003) The rich get richer: Patterns of plant invasions in the United States. *Frontier of Ecological Environment,* 1(1):11–14.

Stone, D., (1994) Tanah Air - Indonesia's Biodiversity. Editions Didier Millet, Singapore.

Stork, N. E. (1988) Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society*, 35: 321–337.

Stork, N. E. (1993) How many species are there? *Biodiversity and Conservation*, 2: 215–232.

Stork, N. E. (1999) The magnitude of biodiversity and its decline. In Cracraft, J. and Novacek, M. (eds.). The Living Planet in Crisis: Biodiversity, Science, and Policy. American Museum of Natural History, New York.

Stork, N. E. and K. G. Gaston. (1990) Counting species one by one. *New Scientist*, 1729: 43–47.

Stork, N. E., and Paarmann, W. (1992) Reproductive seasonality of ground and tiger beetle (Coleoptera: Carabidae, Cicindelidae) fauna in North Sulawesi (Indonesia). *Studies on Neotropical Fauna and Environment,* 27, 101-115

Strom, B. L., Clarke, S. R., and Shea, P. J. (2004) Efficacy of 4-allylanisole-based products for protecting individual loblolly pines from Dendrotonus frontalis Zimmermann (Coleoptera: Scolytidae). *Canadian Journal of Forest Research*, 34, 659-665.

Strong, D. R., Jr., J. H. Lawton, and T. R. E. Southwood. 1984. Insects on Plants: Community Patterns and Mechanisms. Blackwell Scientific,Oxford. 313pp.

Stuart, Y. E., Losos, J. B., Algar, A. C. (2012) The island−mainland species turnover relationship. *Proceedings of the Royal Society*, 279, 4071-4077.

Sugiura, S., Tsuru, T., Yamaura, Y., Hasegawa, M., Makihara, H., & Makino, S. (2008) Differences in endemic insect assemblages among vegetation types on a small island of the oceanic Ogasawara Islands. *Entomological Science*, 11, 131-141.

Sugiura, S., Yamaura, Y., Tsuru, T., Goto, H., Hasegawa, M., Makihara, H., & Makino, S. (2009) Beetle responses to artificial gaps in an oceanic island forest: implications for invasive tree management to conserve endemic species diversity. *Biodiversity Conservation*, 18, 2101–2118.

Sugiura, S., Yamaura, Y., Tsuru, T., Goto, H., Hasegawa, M., Makihara, H., Makino, S. (2009) Beetle responses to artificial gaps in an oceanic island forest: implications for invasive tree management to conserve endemic species diversity. *Biodiversity Conservation*, 18, 2101-2118.

Sukardjo, S., (2002) Integrated Coastal Zone Management (ICZM) in Indonesia: A view from a mangrove ecologist. *Southeast Asian Studies*, 40(2), 200-218.

Sverdrup-Thygeson, A., Birkemoe, T. (2009) What window traps can tell us: effect of placement, forest openness and beetle reproduction in retention trees. *Journal of Insect Conservation*, 13, 183-191.

Symondson, W. O. C., Glen, D. M., Ives, A. R., Langdon, C. J., and Wiltshire, C. W. (2002) Dynamics of the relationship between a generalist predator and slugs over five years. *Ecology,* 83,137-147.

Szyszko, J., (1983) State of Carabidae (Cal.) Fauna in Fresh Pine Forest and Tentative Valorisation of this Environment. Treatises and Monographs. Agricultural University Press, Warsaw.

Tabashnik, B. E. (1983) Host range evolution: the shift from native legume hosts to alfalfa by the butterfly, *Colias eriphyle. Evolution*, 37, 150-162.

Tabor, K. L., Brewster, C. C., and Fell, R. D. (2004) Analysis of the successional patterns of insects on carrion in southwest Virginia. *Journal of Medical Entomology*, 41, 785-795.

Talley, T. S., Holyoak, M. (2006) The effect of dust on the federally threatened valley elderberry longhorn beetle. *Environmental Management*, 37, 647-658.

Terborgh, J., L. Lopez, P. Nũ nez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, and T. D. Lambert. (2001) Ecological meltdown in predator-free forest fragments. *Science*, 294: 1923–1926.

Ter Braak, C. J. (1988) CANOCO - an extension of DECORANA to analyze species-environment relationships. *Plant Ecology*, 75, 159-160.

Terell-Nield, C. (1990) Is it possible to age woodlands on the basis of their carabid beetle diversity? *The Entomologist*, 109, 136-145.

Thiele, H. U. 1977. Carabids Beetles in Their Environment: A Study o Habitat Selection by Adaptation in Physiology and Behaviour. Springer, New York.

Thomas, C. D., Singer, D. Ng, M. C., Mallet, L. B., Parmesan, C., and Billington, H. L. (1987) In corporation of a European weed into the diet of North American herbivore. *Evolution*, 41, 892 901.

Thomas, C. D., and Palmer, G. (2015) Non-native plants add to the British flora without negative consequences for native. *PNAS*, 112(14): 4387–4392.

Thomas, C. F. G. & Marshall, E. J. P. (1999) Arthropod abundance and diversity in differently vegetated margins of arablefields. *Agriculture, Ecosystems & Environment,* 72, 131–144.

Thomas, J. D. and Sleeper, E. L. (1977) The use of pitfall traps for estimating the abundance of arthropods, with special reference to the Tenebrionidae (Coleoptera). *Annals of the Entomological Society of America*, 70, 242-248.

Thompson, J. N. (1998) Rapid evolution as an ecological process. *Trends in Ecology and Evolution,* 13, 329-332.

Thornhill, N. W. (1993) The natural history of inbreeding and outbreeding: theoretical and empirical perspectives. Chicago: University of Chicago Press.

Thornton, I.W.B. (1992) Krakatau: a century of change. GeoJournal,Thornton, I.W.B. (Scientific Ed.) (1992). Krakatau: a Century of Change. *GeoJournal*, 28(2), 83–304.

Thorpe, R. S., Reardon, J. T., Malhotra, A. (2005) Common garden and natural selection experiments support ecotypic differentiation in the Dominican anole (*Anolis oculatus*). *American Naturalist*, 165: 495–504.

Tilman, D., Fargione, J., Wollf, B. et al. (2001) Forecasting agriculturally driven global environmental change. *Science*, 292, 281-284.

Tjørve, E. (2010) How to resolve the SLOSS debate: Lessons from species-diversity models. *Journal of Theoretical Biology,* 264, 604-612.

Topping, C. J. and Sunderland, K. D. (1992) Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in the field of winter wheat. *Journal of Applied Ecology*, 29, 485-491.

Tratalos, J., Fuller, R. A., Evans, K. L., Davies, R. G., Newson, S. E., Greenwood, J. J. D., and Gaston, K. J. (2007) Bird densities are associated with household densities. *Global Change Biology* 13:1685-16

Trewick, S. A. (2000) Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Catham Islands, New Zealand. *Journal of Biogeography*, 27, 1180-1200.

Triantis, K. A. (2006) Biogeography and ecology of land snails and isopods on 3 island groups of the Aegean Sea in relationship to environmental heterogeneity and area. PhD thesis. University of Crete.

Triantis, K. A., Mylonas, M. Weiser, M. D., Lika, K., and Vardinoy-annis, K. (2005) Species richness, environment heterogeneity and area: a case study based on land snail in Skyros archipelago (Aegean Sea, Greece). *Journal of Biogeography*, 32, 1727-1735.

Triantis, K. A., Mylonas, M., Lika, K., Vardinoyannis, K. (2003) A model for the species-area-habitat relationship. *Journal of Biogeography*, 30(1), 19-27.

Triantis, K. A., Nogué́s-Bravo, D., Hortal, J., Borges, P. A. V., Adsersen, H., Fernandez-Palacios, J. M., Araujo, M. B., and Whittaker, R. J. (2008) Measurements of area and the (island) species-area relationship: new directions for an old pattern. *Oikos*, 117, 1555-1559.

Triantis, K. A., Vardinoyannis, K., Weiser, M. D., Lika, K., Mylonas, M. (2005) Species richness, environmental heterogeneity and area: a case study based on the land snails of Skyros Archipelago (Aegean Sea, Greece). *Journal of Biogeography*, 32, 1727–1735.

Trichas, A., Lagkis, A., Triantis, K. A., Poulakakis, N., & Chatzaki, M. (2008) Biogeographic patterns of tenebrionid beetles (Coleoptera, Tenebrionidae) on four island groups in the south Aegean Sea. *Journal of Natural History*, 42(5-8), 491-511.

Trueblood, D.D., Gallagher, E.D. & Gould, D.M. (1994) The three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbour. *Limnological Oceanography*, 39, 1440–1454.

Tscharntke, T., Brandl, R. (2004) Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology,* 49:405–430.

Tscharntke, T., Klein, A. M., Kruess, A., Stefan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters*, 8, 857–874.

Tuomela, M., Vikman, M., Hatakka, A. & Itävaara, M. (2000) Biodegradation of lignin in a compost environment: a review. *Bioresource Technology*, 72: 169–183.

Turchin, P., Taylor, A. D., Reeve, J. D. (1999) Dynamical role of predators in population cycles of a forest insect: An experimental test. *Science*, 285, 1068–1071.

Tyndale-Biscoe, M. (1994) Dung burial by native and introduced dung beetles (Scarabaeidae). *Australian Journal of Agricultural Research*, 45:1799–1808.

Uehara-Prado, M., Fernandes, J. O., Bello, A. M., Machado, G., Santos, A. J., Vaz-de-Mello, F. Z., Freitas, A. V. L. (2009) Selecting terrestrial arthropods as indicators of small-scale disturbance: a first approach in the Brazilian Atlantic. *Forest Biology Conservation*, 142(6):1220–1228.

Ueno, Y., Hori, M., Noda, T., and Muka, H. (2006) Effects of material inputs by the Grey Heron *Ardea cinerea* on forest-floor necrophagous insects and understory plants in the breeding colony. *Ornithological Science*, 5, 199–209.

Uetz, G. W. and Unzicker, J. D. (1976) Pitfall trapping in ecological studies of wandering spiders. *Journal of Arachnology*, 3, 101-111.

Umbgrove, J. H. F., (1949) Structural history of the East Indies. Cambridge University Press, Cambridge.

Uneputty, P. A. and Evans, S. M. (1997) Accumulation of beach litter on Islands of the Kepulauan Seribu Archipelago, Indonesia. *Marine Pollution Bulletin*, 34, 652–655.

Uys, V. M. & Urban, R. P. (2006) How to Collect and Preserve Insects and Arachnids. Pretoria.

Van Bremmelen, R. W. (1970) The Geology of Indonesia. Government Printing Office, The Hague.

Van der Meij, S. E. T, Suharsono, Hoeksemaa, B. W. (2010) Long-term changes in coral assemblages under natural and anthropogenic stress in Jakarta Bay (1920–2005). *Marine Pollution Bulletin*, 60, 1442-1454.

Van Srtraalen, N. M., Krovolutsky, D. A. (1996) Bioindicator System for Soil Pollution. Kluwer, Dordrecht.

Vasconcelos, S. D., Araujo, M. C. S. (2012) Necrophagous species of Diptera and Coleoptera in northeastern Brazil: state of the art and challenges for the Forensic Entomologist. *Revista Brasileira de Entomologia*, 56(1), 7–14.

Verstappen, H., (1988) Old and new observations on coastal changes of Jakarta Bay: an example of trends in urban stress on coastal environments. *Journal of Coastal Research* 4 (4), 573-587.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., and Westbrooks, R. (1996) Biological invasions as global environmental change. *American Scientist*, 84, 468 478.

Vitousek, P. M., Ehrlich, P. R., Ehrlich, A. H., Matson, P. A. (1986) Human appropriation of the products of photosynthesis. *BioScience*, 36(6), 368-373.

Vitousek, P. M., Loope, L. L., Adsersen, H. (1995) Islands, Biological Diversity and Ecosystem Function. Springer-Verlag, New York.

Viviani, V. R. (2002) The origin, diversity, and structure function relationships of insect luciferases. *Cellular and Molecular Life Sciences*, 59, 1833-1850.

Vogel, S. and C. Westerkamp. (1991) Pollination: an integrating factor in biocenoses. Pp. 159–170. In A. Seitz and V.Loeschcke (eds). Species Conservation: A Population Biological Approach. Birkha¨user Verlag, Basel.

Walker, L. R. and Bellingham, P. (2011) Island Environment in a Changing World. Cambridge University Press, Cambridge.

Wallace, A. R. (1869) The Malay Archipelago. Periplus Editions.

Wallace. A. R. (1881) Island Life. Harper and Brothers, New York.

Wallace, M. G. (2005) Observations of urban dung beetles utilising dog faces (Coleoptera: Scarabaeidae). *Coleopterist Bulletin*, 59, 400-401

Walsh, J. C., Venter, O., Watson, J. E. M., Fuller, R. A., Blackburn, T. M., Possingham, H. P. (2012) Exotic species richness and native species endemism increase the impact of exotic species on islands. *Global Ecology and Biogeography*, 21, 841–850.

Walter, H. S. (2004) The mismeasure of islands: implications for biogeographical theory and the conservation of nature. *Journal of Biogeography*, 31, 177–197.

Walther, G. R., Post, E., Convey, P. et al. (2002) Ecological responses to recent climate change. *Nature*, 416, 389-395.

Wardhaugh, C. W., Stork, N. E., and Edwards, W. (2012) Feeding guild structure of beetles on Australian tropical rainforest trees reflects microhabitat resource availability. *Journal of Animal Ecology*, 81, 1086-1094.

Warner, R. E. (1968) The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor*, 70, 101-120.

Warren, M.S., Bourn, N., Brereton, T., Fox, R., Middlebrook, I. & Parsons, M. (2007) What have Red Lists done for us? The value and limitation of protected species listing for invertebrates. In: Stewart, A. J. A, New, T. R., Lewis, O. T. (eds.), Insect Conservation Biology. CABI publishing, Wallingford, UK.

Warren-Thomas, E., Zou, Y., Dong, L., Yaoc, X., Yangc, M., Zhangc, X., Qinc, Y., Liud, Y., Sang, W., and Axmacher, J. C. (2014) Ground beetle assemblages in Beijing's new mountain forests. *Forest Ecology and Management,* 334, 15, 369–376.

Watson, D. W., Kaufman, P. E., Rutz, D. A., Glenister, C. S. (2001) Impact of the darkling beetle Aphitobius diaperinus (Panzer) on establishment of the

predaceous beetle Carcinops pumilio (Erichson) for Musca domestica control in caged-layer poultry houses. *Biological Control*, 20, 8-15.

Watts, C. H., Gibbs, G. W. (2002) Revegetation and its Effect on the Ground-Dwelling Beetle Fauna of Matiu-Somes Island, New Zealand. *Restoration Ecology*, 10(1), 96–106.

Webster, R. P. Anderson, R. S., Sweeney, J. D., DeMerchant, I. (2012) New Coleoptera records from New Brunswick, Canada: Anthribidae, Brentidae, Dryophthoridae, Brachyceridae, and Curculionidae, with additions to the fauna of Quebec, Nova Scotia and Prince Edward Island. *ZooKeys,* 179, 349–406.

Weigelt, P. Kreft, H (2012) Quantifying island isolation – insights from global patterns of insular plant species richness. *Ecography,* 36, 417-429.

Werner, S. H. and Raffa, K. F. (2000) Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the Great Lakes Region. *Forest Ecology and Management*,139: 135-155.

Weslien, J., Djupstro, L. B., Schroeder, M., Widenfalk, O. (2011) Long-term priority effects among insects and fungi colonizing decaying wood. *Journal of Animal Ecology,* 80, 1155–1162.

Wheeler, Q. D. (1986) Revision of the genera of Lymexylidae (Coleoptera: Cucujiformia). *Bulletin of the American Museum of Natural History*, 183: 113–210.

Wheeler, Q. D. (1990) Insect diversity and cladistic constraints. *Annals of the Entomological Society of America*, 83: 1031–1047.

Wheeler, W. C., P. Cartwright, and C. Y. Hayashi. (1993) Arthropod phylogeny: a combined approach. *Cladistics*, 9: 1–39.

Wheeler, W. C., M. Whiting, Q. D. Wheeler, and J.M.Carpenter. (2001) The phylogeny of the extanthexapod orders. *Cladistics*, 17: 113–169.

White, M. J. D. (1973) Animal Cytology and Evolution. Third Edition. Cambridge University Press Cambridge. 961pp.

Whitehead, D. R., and Jones, C. E. (1969) Small islands and the equilibrium theory of insular biogeography. *Evolution*, 23, 171-179.

Whittaker, R. J. (1998) Island biogeography: ecology, evolution, and conservation. Oxford University Press, Oxford.

Whittaker, R. J. & Fernandez-Palacios, J. M. (2007) Island biogeography: ecology, evolution, and conservation, 2nd edn. Oxford University Press, Oxford.

Whittaker, R. J., Triantis, K. A. & Ladle, R. J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, 35, 977–994.

Whittaker, R. J., Willis, K. J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, 28, 453–470.

Wiebes, J. T. (1979) Co-evolution of figs and their pollinators. *Annual Review of Ecology and Systematics*, 10: 1–12.

Wiensr, J. A, and Milne, B. T. (1989) Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology*, 3(2): 87-96.

Wiles, G. J., Payne, N. H. (1986) The Trade in Fruit Bats Pteropus spp. on Guam and other Pacific Islands. *Biological Conservation* 38, 143-161.

Williamson, M. (1981) Island populations. Oxford, U.K.: Oxford University Press. 286 p.

Willougby, N. G., Sangkoyo, H., Lakaseru, B. O. (1998) Long-term changes in stadline litter around the Thousand Islands, Jakarta Bay, Indonesia. Proceedings of the Coral Reef Evaluation Workshop, Kepulauan Seribu, Jakarta, 11–20 September 1995.

Wilsey, B., Stirling, G. (2007) Species richness and evenness respond in a different manner to propagule density in developing prairie microcosm communities. *Plant Ecology,* 190, 259–273.

Wilson, E. O. (1992) The Diversity of Life. Penguin, USA.

Wilson, E. O. and Peter, F. M. (1988) Biodiversity. National Academy Press, Washington.

Wilson, R. J., Davies, Z. G., and Thomas, C. D. (2007) Insects and climate change: processes, patterns and implications for climate change. In: Srewart, A. J., New, T. R., and Lewis, O. T. (eds.) *Insect Conservation Biology,* pp. 245-279. CABI, Wallingford.

Wirta, H., Orsini, I., Hanski, I. (2008) An old adaptive radiation of forest dung beetles in madagascar.*Molecular Phylogenetic Evolution,* 47:1076–1089.

Wirta, H., Viljanen, H., Orsini, I., Montreuil, O., Hanski, I. (2010) Three parallel radiations of canthonini dung beetles in Madagascar. *Molecular Phylogenetic Evolution,* 57:710–727.

Witt, C. C., and Maliakal-Witt, S. (2007) Why are diversity and endemism linked on islands? *Ecography* 30, 331 - 333.

Wonhoon, L., Koh, S., Choi, W. I., Jung, C. S., Kim, I., Byun, B., Lee, B., Kim, Y., Lim, J., Kim, S., Akimoto, S., Lee, S. (2012) Barcoding forest insect pests in South Korea: Constructing a basic endemic species dataset. *Journal of Asia-Pacific Entomology,* 15(3), 363-368.

Wood, B. C., and Pullin, A. S. (2002) Persistence of species in fragmented urban landscape: the importance of dispersal ability and habitat availability for grassland butterflies. *Biodiversity and Conservation,* 11, 1451-1468.

Woods, C. A. & Sergile, F. E. (2001) Biogeography of the West Indies: patterns and perspectives, 2nd edn. CRC Press, Boca Raton.

Wood,S. L. and Bright, D. E. (1992) A catalog of Scolytidae and Platypodidae (Coleoptera): part 2: taxonomic index (volumes A and B). *Great Basin Naturalist Memoirs* 13: 1–1553.

Woodcock, B. A. (2005) Pitfall trapping in ecological studies. In (eds.) Leather, S. Insect Sampling in Forest Ecosystems. Blackwell Publishing, Oxford.

Work, T.T., McCullough, D. G., Cavey, J. F., Komsa, R., (2005) Arrival rate of non-indigenous insect species into the United States through foreign trade. *Biological Invasions,* 7, 323–332.

Wrensch, D. L, Ebbert, M. A, eds. (1993) Evolution and diversity of sex ratio in insects and mites. New York: Chapman & Hall.

Wright, D. H., Patterson, B. D., Mikkelson, G. M. (1998) A comparative analysis of nested subset patterns of species composition. *Oecologia*, 131.

Yamada, D., Imura, O., Shi, K. & Shibuya, T. (2007) Effect of tunneler dung beetles on cattle dung decomposition, soil nutrients and herbage growth. *Grassland Science*, 53, 121–129.

Yan, G. (2003) Rapid female multiple mating in red flour beetles (Tribolium castaneum). *Canadian Journal of Zoology,* 81(5), 888-896.

Yates, B. F. (1994) Implementing coastal zone management policy: Kepulauan Seribu Marina Park, Indonesia. I, 22, 235-249.

Yeates, D.K., Harvey, M. S., and Austin, A. D. (2003) New estimates for terrestrial arthropod species – richness in Australia. Records of the South Australian Museum, *Monograph Series*, 7: 231–241.

Young, A. M. (1981) The ineffectiveness of the stingless bee *Trigona jaty* (Hymenoptera: Apidae: Meliponinae) as a pollinator of cocoa (*Theobroma cacao* L.). *Journal of Applied Ecology*, 18,149-155.

Young, O. P. (1981) The attraction of neotropical Scarabaeinae (Coleoptera, Scarabaeidae) to reptile and amphibian fecal material. *The Coleopterists Bulletin,* 35: 345–348.

Yu, A. D., Lei, S. A. (2001) Equilibrium Theory of Island Biogeography: A Review. *USDA Forest Service Proceedings*, 21.

Yu, X. D., Luo, T. H., Yang, J., and Zhou, H. Z. (2006) Distribution of ground-dwelling beetles (Coleoptera) across a forest-clearcut ecotone in Wolong Natural Reserve, southwestern China. *Insect Science,* 13, 127-135.

Zalewski, M., Ulrich, W. (2006) Dispersal as a key element of community structure: the case of ground beetles on lake islands. *Diversity and Distributions,* 12, 767–775.

Zera, A. J. (2004) The endocrine regulation of wing polymorphism in insects: state of the art, recent surprises and future directions. *Integrative and Compaative Biology*, 43, 607–616.

Zera, A. J., Denno, R. F. (1997) Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology*, 42, 207–230.

Zou, Y., Sang, W., Wang, S., Warren-Thomas, E., Liu, Y., Yu, Z., Wang, C., & Axmacher, J. C. (2015) Diversity patterns of ground beetles and understory vegetation in mature, secondary, and plantation forest regions of temperate northern China. *Ecology and Evolution*, 5(3): 531–542.

Appendix 1 Expression of used biodiversity measurement

Equation number	Equation names	Equation expression	Explanation
1	Hill Number	$${}^{q}D = \left(\sum_{i=1}^{S} p_i^q \right)^{1/(1-q)}$$	S is the number of species in the assemblage, and the ith species has relative abundance p_i, $i = 1, 2, ..., S$. The parameter q determines the sensitivity of the measure to the relative frequencies. When $q = 0$, the abundances of individual species do not contribute to the sum in this equation. Rather, only presences are counted, so that ${}^{0}D$ is simply species richness.
2	Exponential Shannon index	$${}^{1}D = \lim_{q \to 1} {}^{q}D = \exp\left(-\sum_{i=1}^{S} p_i \log p_i \right)$$	For $q = 1$, equation no 1 is undefined, but its limit as q tends to 1 is the exponential of the familiar Shannon index, reffered here as Exponential Shannon index
3	Inverse Simpson's index	$${}^{2}D = 1 \bigg/ \sum_{i=1}^{S} p_i^2$$	The variable ${}^{1}D$ weighs species in proportion to their frequency. When $q = 2$, equation 1 yields Simpson diversity, the inverse of the Simpson concentration is shown by equation 3.

Appendix 2. Number of beetle individuals for each species sampled in Java and on small islands

Species	Java		Total Java	Bokor	Damar Besar		Kotok Besar	Lancang Besar	Opak Besar		Pemagaran		Pramuka		Putri Barat		Rambut		Untung Jawa		Total Small islands
	PT	FIT		PT	PT	FIT	PT	PT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	
Anthicidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
Anthribidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2
Anthribidae sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Anthribidae sp.3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Anthribidae sp.4	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Anthribidae sp.5	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	2	0	5
Anthribidae sp.6	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthribidae sp.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Anthribidae sp.8	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	3
Anthribidae sp.9	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2
Anthribidae sp.10	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	5	6
Anthribidae sp.11	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3
Anthribidae sp.12	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anthribidae sp.13	1	0	1	1	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	9
Anthribidae sp.14	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthribidae sp.15	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthribidae sp.16	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Anthribidae sp.17	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthribidae sp.18	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3
Anthribidae sp.19	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthribidae sp.20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	8
Anthribidae sp.21	0	0	0	0	0	0	0	0	1	0	0	0	2	2	0	0	0	0	0	0	5
Anthribidae sp.22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1

Species	Java PT	Java FIT	Total Java	Bokor PT	Damar Besar PT	Damar Besar FIT	Kotok Besar PT	Lancang Besar PT	Opak Besar PT	Opak Besar FIT	Pemagaran PT	Pemagaran FIT	Pramuka PT	Pramuka FIT	Putri Barat PT	Putri Barat FIT	Rambut PT	Rambut FIT	Untung Jawa PT	Untung Jawa FIT	Total Small islands
Anthribidae sp.23	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	4
Anthribidae sp.24	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Anthribidae sp.25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	4
Anthribidae sp.26	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Anthribidae sp.27	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2
Anthribidae sp.28	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Anthribidae sp.29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Anthribidae sp.30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Anthribidae sp.31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Anthribidae sp.32	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	1	0	10
Anthribidae sp.33	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anthribidae sp.34	0	0	0	0	0	0	4	3	1	0	2	0	0	0	0	0	7	0	0	0	17
Anthribidae sp.35	0	0	0	4	0	0	0	0	3	0	1	0	0	0	2	0	0	0	0	0	10
Brentidae sp.1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachinini sp.1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carabidae sp.1	0	0	0	0	0	0	1	6	0	0	0	0	0	0	0	0	0	0	4	0	11
Carabidae sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4
Carabidae sp.3	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2
Carabidae sp.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	2	0	6
Carabidae sp.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4
Carabidae sp.6	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	20	0	0	0	34
Cicindela aurulenta	0	0	0	0	0	0	0	6	0	0	0	0	12	0	0	0	0	0	0	0	18
Cicindelini sp.1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyindidina sp.1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Diplocheila sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
Dromiina sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	10

| Species | Java | | Total Java | Small islands | | | | | | | | | | | | | | | | | Total Small islands |
| | | | | Bokor | Damar Besar | | Kotok Besar | Lancang Besar | Opak Besar | | Pemagaran | | Pramuka | | Putri Barat | | Rambut | | Untung Jawa | | |
	PT	FIT		PT	PT	FIT	PT	PT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	
Harpalini sp.1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2
Harpalini sp.2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Perigona sp.1	0	11	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Platymetopus sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4
Pseudozaena sp.1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	15	0	17
Pterostichinae sp.1	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	10
Tachyina sp.1	0	0	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	1	0	0	5
Tachyina sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Tachyina sp.3	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	2	4
Tachyina sp.4	0	6	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tachyina sp.5	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tachyina sp.6	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tachyina sp.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Tachyina sp.8	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tachyina sp.9	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cerambycidae sp.1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2
Cerylonidae sp.1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2
Chrysomelidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chrysomelidae sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chrysomelidae sp.3	1	0	1	1	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	9
Chrysomelidae sp.4	0	2	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Chrysomelidae sp.5	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chrysomelidae sp.6	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Chrysomelidae sp.7	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chrysomelidae sp.8	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3
Chrysomelidae sp.9	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	Java		Total Java	Small islands																	Total Small islands
				Bokor	Damar Besar		Kotok Besar	Lancang Besar	Opak Besar		Pemagaran		Pramuka		Putri Barat		Rambut		Untung Jawa		
	PT	FIT		PT	PT	FIT	PT	PT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	
Ciidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	5	6
Clambidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	8
Clambidae sp.2	0	0	0	0	0	0	0	0	1	0	0	0	2	2	0	0	0	0	0	0	5
Clambidae sp.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Clambidae sp.4	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	3
Clambidae sp.5	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Clambidae sp.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	4
Clambidae sp.7	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Coccinelidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coccinelidae sp.2	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Coccinelidae sp.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Coccinelidae sp.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Coccinelidae sp.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Cucujidae sp.1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cryptophagidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	1	0	10
Curculionidae sp.1	0	0	0	0	0	0	4	1	0	0	2	0	0	0	0	0	3	0	0	0	10
Curculionidae sp.2	0	0	0	0	0	0	1	0	2	0	1	0	0	0	2	0	0	0	0	0	6
Curculionidae sp.3	0	0	0	0	10	0	2	1	0	0	0	0	0	0	0	0	2	0	0	0	15
Curculionidae sp.4	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Curculionidae sp.5	0	0	0	0	0	0	0	4	0	0	0	0	1	0	0	0	0	0	0	0	5
Curculionidae sp.6	0	0	0	3	9	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	14
Curculionidae sp.7	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Curculionidae sp.8	0	3	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
Curculionidae sp.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Curculionidae sp.10	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	5	0	0	0	0	11
Curculionidae sp.11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1

Species	Java		Total Java	Small islands																	Total Small islands
				Bokor	Damar Besar		Kotok Besar	Lancang Besar	Opak Besar		Pemagaran		Pramuka		Putri Barat		Rambut		Untung Jawa		
	PT	FIT		PT	PT	FIT	PT	PT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	
Curculionidae sp.12	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Curculionidae sp.13	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Curculionidae sp.14	0	0	0	0	0	0	0	0	0	1	0	5	0	0	0	2	0	0	0	0	8
Curculionidae sp.15	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Curculionidae sp.16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Curculionidae sp.17	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Curculionidae sp.18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Elateridae sp.1	0	0	0	0	0	0	0	196	0	0	0	0	0	1	0	0	0	0	38	0	235
Elateridae sp.2	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Elateridae sp.3	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	4	0	26
Elateridae sp.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Elateridae sp.5	0	0	0	0	0	0	0	211	0	0	0	0	174	2	0	0	0	0	18	0	405
Elateridae sp.6	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	4
Elateridae sp.7	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elateridae sp.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Endomycidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Histeridae sp.1	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Histeridae sp.2	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Histeridae sp.3	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Histeridae sp.4	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Histeridae sp.5	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	2	5
Histeridae sp.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Histeridae sp.7	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	21	22
Hyborosidae sp.1	0	0	0	0	8	0	17	0	0	0	0	0	0	0	0	0	0	0	8	0	33
Hydrophilidae sp.1	2	12	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophilidae sp.2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	Java		Total Java	Small islands																	Total Small islands
				Bokor	Damar Besar		Kotok Besar	Lancang Besar	Opak Besar		Pemagaran		Pramuka		Putri Barat		Rambut		Untung Jawa		
	PT	FIT		PT	PT	FIT	PT	PT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	
Hydrophilidae sp.3	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophilidae sp.4	0	14	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophilidae sp.5	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophilidae sp.6	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophilidae sp.7	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophilidae sp.8	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophilidae sp.9	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laemophloidae sp.1	0	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2
Laemophloidae sp.2	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laemophloidae sp.3	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laemophloidae sp.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Laemophloidae sp.5	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laemophloidae sp.6	0	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laemophloidae sp.7	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lampyridae sp.1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Latridiidae sp.1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Latridiidae sp.2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Latridiidae sp.3	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Latridiidae sp.4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2
Monotoma sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Mordelidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2
Nitidulidae sp.1	0	1	1	0	0	0	0	14	0	0	0	1	0	2	0	0	0	0	28	13	58
Nitidulidae sp.2	1	0	1	0	1	0	0	14	0	0	10	0	4	9	0	0	0	0	12	7	57
Nitidulidae sp.3	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	3
Nitidulidae sp.4	0	1	1	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	6
Nitidulidae sp.5	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

| Species | Java | | Total Java | Small islands | | | | | | | | | | | | | | | | | Total Small islands |
| | | | | Bokor | Damar Besar | | Kotok Besar | Lancang Besar | Opak Besar | | Pemagaran | | Pramuka | | Putri Barat | | Rambut | | Untung Jawa | | |
	PT	FIT		PT	PT	FIT	PT	PT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	
Nitidulidae sp.6	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	3	5
Nitidulidae sp.7	1	27	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nitidulidae sp.8	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nitidulidae sp.9	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	2
Nitidulidae sp.10	0	4	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	3
Nitidulidae sp.11	0	4	4	0	0	0	0	0	0	0	0	2	1	5	0	0	0	0	1	0	9
Nitidulidae sp.12	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nitidulidae sp.13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Nitidulidae sp.14	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
Nitidulidae sp.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Nitidulidae sp.16	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	2	5
Nitidulidae sp.17	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nitidulidae sp.18	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	3
Nitidulidae sp.19	0	1	1	0	0	0	0	0	0	0	0	0	1	4	0	0	0	0	0	1	6
Nitidulidae sp.20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4
Nitidulidae sp.21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4
Nitidulidae sp.22	12	0	12	27	22	1	0	0	0	0	0	0	0	0	0	0	2	2	1	0	55
Nitidulidae sp.23	0	9	9	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Nitidulidae sp.24	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Caccobius aff.unicornis	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	1	0	8	0	18
Dynastinae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	2	1	9
Oniticellus tessellatus	0	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus accendens	17	2	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus javacupreus	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

| Species | Java | | Total Java | Small islands | | | | | | | | | | | | | | | | | Total Small islands |
| | PT | FIT | | Bokor | Damar Besar | | Kotok Besar | Lancang Besar | Opak Besar | | Pemagaran | | Pramuka | | Putri Barat | | Rambut | | Untung Jawa | | |
	PT	FIT		PT	PT	FIT	PT	PT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	
Onthophagus javanensis	32	1	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus limbatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	1	0	6
Onthophagus rudis	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp.1	0	1	1	6	0	0	6	0	1	0	0	0	2	0	0	0	75	1	6	37	134
Onthophagus sp.2	2	4	6	0	0	0	0	29	0	0	0	0	12	16	0	0	1	0	23	7	88
Onthophagus sp.3	8	13	21	0	0	0	0	8	0	0	0	0	31	34	0	0	0	0	29	29	131
Onthophagus sp.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	6	0	7
Onthophagus sp.5	2	1	3	391	0	0	17	0	2	0	8	1	4	0	4	5	63	0	13	2	510
Onthophagus sp.6	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp.7	67	8	75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp.8	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp.9	2	14	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp.10	0	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp.11	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp.12	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp.13	1	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp.14	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus tricornis	9	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
Onthophagus trituber	10	20	30	0	0	0	6	100	0	0	0	0	19	8	0	0	1	0	19	4	157
Rhysemus sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	6
Rhysemus sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	6
Platypodidae sp.1	0	4	4	0	2	14	1	0	0	0	0	0	0	3	0	0	0	3	0	0	23
Ptiliidae sp.1	0	15	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptiliidae sp.2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

| Species | Java | | Total Java | Small islands | | | | | | | | | | | | | | | | | Total Small islands |
| | | | | Bokor | Damar Besar | | Kotok Besar | Lancang Besar | Opak Besar | | Pemagaran | | Pramuka | | Putri Barat | | Rambut | | Untung Jawa | | |
	PT	FIT		PT	PT	FIT	PT	PT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	
Ptilodactylidae sp.1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	6	0	0	0	0	7
Ptilodactylidae sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	4
Rhizophagidae sp.1	0	16	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scydmaenidae sp.1	0	13	13	0	0	0	0	0	0	0	0	1	16	22	0	1	0	0	0	2	42
Scydmaenidae sp.2	0	17	17	0	1	0	0	2	0	0	1	2	1	0	0	1	0	2	0	5	15
Silvanidae sp.1	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allerulinae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Leichenum sp.1	0	0	0	0	0	0	0	639	0	0	0	0	20	0	0	0	0	0	8	0	667
Leichenum sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
Tenebrionidae sp.1	0	0	0	0	4	0	0	123	0	0	0	0	21	0	0	0	0	0	4	0	152
Tenebrionidae sp.2	0	0	0	0	0	0	0	7	0	0	0	0	22	0	0	0	48	0	0	0	77
Tenebrionidae sp.3	0	0	0	0	6	0	18	10	0	0	42	0	13	0	0	0	0	0	0	0	89
Tenebrionidae sp.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
Tenebrionidae sp.5	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3
Tenebrionidae sp.6	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	4	0	6
Tenebrionidae sp.7	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2
Tenebrionidae sp.9	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Tenebrionidae sp.10	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	3
Tenebrionidae sp.12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Tenebrionidae sp.13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Trogidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	6
Xylosandrus compactus (Einchhoff, 1875)	14	6	20	6	0	0	107	0	14	0	62	8	77	18	12	0	0	0	0	0	304
Xylosandrus morigerus (Blandford, 1894)	2	1	3	0	0	0	17	0	0	0	2	0	1	0	0	0	0	0	0	0	20

Species	Java		Total Java	Small islands																		Total Small islands
				Bokor	Damar Besar		Kotok Besar	Lancang Besar	Opak Besar		Pemagaran		Pramuka		Putri Barat		Rambut		Untung Jawa			
	PT	FIT		PT	PT	FIT	PT	PT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	PT	FIT	
Xylonsandrus crassiusculus (Motcshulsky, 1866)	29	22	51	0	0	0	165	0	0	0	3	0	1	0	0	0	7	0	0	0	176
Xyleborus perforans (Wollaston, 1857)	21	62	83	20	18	10	192	23	157	148	93	8	55	130	21	68	11	19	46	4	1023
Xyleborus affinis (Eichhoff, 1868)	23	13	36	1	18	0	29	36	16	9	40	1	99	9	10	4	4	0	21	2	299
Xyleborus similis (Ferrari, 1867)	0	9	9	29	1	1	0	0	0	0	0	1	2	0	0	5	23	14	2	0	78
Dryocoetiops coffeae (Eggers, 1923)	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xyleborinus perminutissimus (Schedl, 1934)	1	4	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xyleborinus andrewesi (Blandford, 1896)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Xyleborinus exiguus (Walker, 1859)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Hypothenemus spp.	0	28	28	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	28	32
Cryphalus spp.	0	0	0	1	0	0	7	1	0	1	0	0	2	10	0	1	0	0	2	7	32
Coccotrypes spp.	23	5	28	1	1	0	32	11	2	0	5	0	0	1	9	3	0	0	6	2	73
Scolytidae sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3
Scolytidae sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	3

Appendix 3. Abbreviation of beetle species

Code	Species Name	Code	Species Name	Code	Species Name
Atc1	Anthicidae sp.1	Cla5	Clambidae sp.5	Nit13	Nitidulidae sp.13
Atb1	Anthribidae sp.1	Cla6	Clambidae sp.6	Nit14	Nitidulidae sp.14
Atb2	Anthribidae sp.2	Cla7	Clambidae sp.7	Nit15	Nitidulidae sp.15
Atb3	Anthribidae sp.3	Coc1	Coccinelidae sp.1	Nit16	Nitidulidae sp.16
Atb4	Anthribidae sp.4	Coc2	Coccinelidae sp.2	Nit17	Nitidulidae sp.17
Atb5	Anthribidae sp.5	Coc3	Coccinelidae sp.3	Nit18	Nitidulidae sp.18
Atb6	Anthribidae sp.6	Coc4	Coccinelidae sp.4	Nit19	Nitidulidae sp.19
Atb7	Anthribidae sp.7	Coc5	Coccinelidae sp.5	Nit20	Nitidulidae sp.20
Atb8	Anthribidae sp.8	Cuc1	Cucujidae sp.1	Nit21	Nitidulidae sp.21
Atb9	Anthribidae sp.9	Cry1	Cryptophagidae sp.1	Nit22	Nitidulidae sp.22
Atb10	Anthribidae sp.10	Cur1	Curculionidae sp.1	Nit23	Nitidulidae sp.23
Atb11	Anthribidae sp.11	Cur2	Curculionidae sp.2	Nit24	Nitidulidae sp.24
Atb12	Anthribidae sp.12	Cur3	Curculionidae sp.3	Sca1	*Caccobius aff.unicornis*
Atb13	Anthribidae sp.13	Cur4	Curculionidae sp.4	Sca2	Dynastinae sp.1
Atb14	Anthribidae sp.14	Cur5	Curculionidae sp.5	Sca3	*Oniticellus tessellatus*
Atb15	Anthribidae sp.15	Cur6	Curculionidae sp.6	Sca4	*Onthophagus accendens*
Atb16	Anthribidae sp.16	Cur7	Curculionidae sp.7	Sca5	*Onthophagus javacupreus*
Atb17	Anthribidae sp.17	Cur8	Curculionidae sp.8	Sca6	*Onthophagus javanensis*
Atb18	Anthribidae sp.18	Cur9	Curculionidae sp.9	Sca7	*Onthophagus limbatus*
Atb19	Anthribidae sp.19	Cur10	Curculionidae sp.10	Sca8	*Onthophagus rudis*

Atb20	Anthribidae sp.20	Cur11	Curculionidae sp.11	Sca9	*Onthophagus* sp.1
Atb21	Anthribidae sp.21	Cur12	Curculionidae sp.12	Sca10	*Onthophagus* sp.2
Atb22	Anthribidae sp.22	Cur13	Curculionidae sp.13	Sca11	*Onthophagus* sp.3
Atb23	Anthribidae sp.23	Cur14	Curculionidae sp.14	Sca12	*Onthophagus* sp.4
Atb24	Anthribidae sp.24	Cur15	Curculionidae sp.15	Sca13	*Onthophagus* sp.5
Atb25	Anthribidae sp.25	Cur16	Curculionidae sp.16	Sca14	*Onthophagus* sp.6
Atb26	Anthribidae sp.26	Cur17	Curculionidae sp.17	Sca15	*Onthophagus* sp.7
Atb27	Anthribidae sp.27	Cur18	Curculionidae sp.18	Sca16	*Onthophagus* sp.8
Atb28	Anthribidae sp.28	Ela1	Elateridae sp.1	Sca17	*Onthophagus* sp.9
Atb29	Anthribidae sp.29	Ela2	Elateridae sp.2	Sca18	*Onthophagus* sp.10
Atb30	Anthribidae sp.30	Ela3	Elateridae sp.3	Sca19	*Onthophagus* sp.11
Atb31	Anthribidae sp.31	Ela4	Elateridae sp.4	Sca20	*Onthophagus* sp.12
Atb32	Anthribidae sp.32	Ela5	Elateridae sp.5	Sca21	*Onthophagus* sp.13
Atb33	Anthribidae sp.33	Ela6	Elateridae sp.6	Sca22	*Onthophagus* sp.14
Atb34	Anthribidae sp.34	Ela7	Elateridae sp.7	Sca23	*Onthophagus tricornis*
Atb35	Anthribidae sp.35	Ela8	Elateridae sp.8	Sca24	*Onthophagus trituber*
Bre1	Brentidae sp.1	End1	Endomycidae sp.1	Sca25	*Rhysemus* sp.1
Car7	*Brachinini* sp.1	His1	Histeridae sp.1	Sca26	*Rhysemus* sp.2
Car1	Carabidae sp.1	His2	Histeridae sp.2	Pla1	Platypodidae sp.1
Car2	Carabidae sp.2	His3	Histeridae sp.3	Pti1	Ptiliidae sp.1
Car3	Carabidae sp.3	His4	Histeridae sp.4	Pti2	Ptiliidae sp.2
Car4	Carabidae sp.4	His5	Histeridae sp.5	Pti1	Ptilodactylidae sp.1

Car5	Carabidae sp.5	His6	Histeridae sp.6	Pti2	Ptilodactylidae sp.2
Car6	Carabidae sp.6	His7	Histeridae sp.7	Rhi1	Rhizophagidae sp.1
Car8	*Cicindela aurulenta*	Hyb1	Hyborosidae sp.1	Scy1	Scydmaenidae sp.1
Car9	*Cicindelini* sp.1	Hyd1	Hydrophilidae sp.1	Scy2	Scydmaenidae sp.2
Car10	*Cyindidina* sp.1	Hyd2	Hydrophilidae sp.2	Sil1	Silvanidae sp.1
Car11	*Diplocheila* sp.1	Hyd3	Hydrophilidae sp.3	Ten14	*Allerulinae* sp.1
Car12	*Dromiina* sp.1	Hyd4	Hydrophilidae sp.4	Ten15	*Leichenum* sp.1
Car13	*Harpalini* sp.1	Hyd5	Hydrophilidae sp.5	Ten16	*Leichenum* sp.2
Car14	*Harpalini* sp.2	Hyd6	Hydrophilidae sp.6	Ten1	Tenebrionidae sp.1
Car15	*Perigona* sp.1	Hyd7	Hydrophilidae sp.7	Ten2	Tenebrionidae sp.2
Car16	*Platymetopus* sp.1	Hyd8	Hydrophilidae sp.8	Ten3	Tenebrionidae sp.3
Car17	*Pseudozaena* sp.1	Hyd9	Hydrophilidae sp.9	Ten4	Tenebrionidae sp.4
Car18	*Pterostichinae* sp.1	Lae1	Laemophloidae sp.1	Ten5	Tenebrionidae sp.5
Car19	*Tachyina* sp.1	Lae2	Laemophloidae sp.2	Ten6	Tenebrionidae sp.6
Car20	*Tachyina* sp.2	Lae3	Laemophloidae sp.3	Ten7	Tenebrionidae sp.7
Car21	*Tachyina* sp.3	Lae4	Laemophloidae sp.4	Ten8	Tenebrionidae sp.9
Car22	*Tachyina* sp.4	Lae5	Laemophloidae sp.5	Ten9	Tenebrionidae sp.10
Car23	*Tachyina* sp.5	Lae6	Laemophloidae sp.6	Ten10	Tenebrionidae sp.12
Car24	*Tachyina* sp.6	Lae7	Laemophloidae sp.7	Ten11	Tenebrionidae sp.13
Car25	*Tachyina* sp.7	Lam1	Lampyridae sp.1	Tro1	Trogidae sp.1
Car26	*Tachyina* sp.8	Lat1	Latridiidae sp.1	Sco3	*Xylosandrus compactus* (Einchhoff, 1875)

Car27	*Tachyina* sp.9	Lat2	Latridiidae sp.2	Sco4	*Xylosandrus morigerus* (Blandford, 1894)
Crb1	Cerambycidae sp.1	Lat3	Latridiidae sp.3	Sco5	*Xylonsandrus crassiusculus* (Motcshulsky, 1866)
Cry1	Cerylonidae sp.1	Lat4	Latridiidae sp.4	Sco6	*Xyleborus perforans* (Wollaston, 1857)
Chr1	Chrysomelidae sp.1	Mo1	*Monotoma* sp.1	Sco7	*Xyleborus affinis (*Eichhoff, 1868)
Chr2	Chrysomelidae sp.2	Mor1	Mordelidae sp.1	Sco8	*Xyleborus similis* (Ferrari, 1867)
Chr3	Chrysomelidae sp.3	Nit1	Nitidulidae sp.1	Sco9	*Dryocoetiops coffeae* (Eggers, 1923)
Chr4	Chrysomelidae sp.4	Nit2	Nitidulidae sp.2	Sco10	*Xyleborinus perminutissimus* (Schedl, 1934)
Chr5	Chrysomelidae sp.5	Nit3	Nitidulidae sp.3	Sco11	*Xyleborinus andrewesi* (Blandford, 1896)
Chr6	Chrysomelidae sp.6	Nit4	Nitidulidae sp.4	Sco12	*Xyleborinus exiguus* (Walker, 1859)
Chr7	Chrysomelidae sp.7	Nit5	Nitidulidae sp.5	Sco13	*Hypothenemus* spp.
Chr8	Chrysomelidae sp.8	Nit6	Nitidulidae sp.6	Sco14	*Cryphalus* spp.
Chr9	Chrysomelidae sp.9	Nit7	Nitidulidae sp.7	Sco15	*Coccotrypes* spp.
Cii1	Ciidae sp.1	Nit8	Nitidulidae sp.8	Sco1	Scolytidae sp. 1
Cla1	Clambidae sp.1	Nit9	Nitidulidae sp.9	Sco2	Scolytidae sp. 2
Cla2	Clambidae sp.2	Nit10	Nitidulidae sp.10		
Cla3	Clambidae sp.3	Nit11	Nitidulidae sp.11		
Cla4	Clambidae sp.4	Nit12	Nitidulidae sp.12		