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A global picture of biological invasion threat on islands

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Biological invasions are one of the main drivers of biodiversity losses. As threats from biological invasions increase, one of the most urgent tasks is to identify areas of high vulnerability. However, the lack of comprehensive information on the impacts of invasive alien species (IAS) is especially a problem on islands, where most recorded extinctions associated with IAS have occurred. Here we provide a global, network-oriented analysis of IAS on islands. Using network analysis, we structured 27,081 islands and 437 threatened vertebrates into 21 clusters, based on their profiles in term of invasiveness and shared vulnerabilities. These islands are mainly located in the southern hemisphere and many are in biodiversity hotspots. Some of them share similar characteristics regarding their connectivity that could be useful in understanding their response to invasive species. The major invaders found in these clusters of islands are feral cat, feral dog, pigs and rats. Our analyses reveal those IAS that systematically act alone or in combination, and the pattern of shared IAS among threatened species, providing new information to implement effective eradication strategies. Combined with further local, contextual information this can contribute to global strategies to deal with IAS.
Islands harbour a significant portion of the Earth’s species and have an unusually high rate of endemism\(^1\). However, many species on islands are now recorded as threatened, and most recorded extinctions of vertebrate species have occurred on islands\(^2\). Invasive alien species (IAS) are considered the second most important driver of species extinctions on islands, and are associated with nearly 25\% of birds and amphibians currently threatened worldwide\(^3\). Island ecosystems are particularly vulnerable to biological invasions\(^2\). To date, there have been over 700 attempted eradications of invasive alien mammals\(^4\), which have benefited to 600 local populations, leading to larger populations or increased distributional areas\(^4\). Specifically, 236 species have benefited from those eradication programs, including 62 species that are at risk of extinction, and four species had their extinction risk reduced as a direct result of these eradications\(^4\). Despite these encouraging results, the threat posed by invasive alien species (IAS) remains significant and widespread for native species\(^3\). Thus, prioritization of research efforts and eradication strategies needs to be more effective\(^5\) and there are many more opportunities to decrease extinction risk for island species by eradicating IAS.

Because funding allocated to conservation is limited, it is important that these interventions target islands where the conservation benefit will be highest. Efforts to prioritize research, management, and policy for IAS have traditionally relied on expert judgments, and have been limited to either single IAS\(^6\) or subsets of islands\(^7,8\). In the absence of a systematic analysis of IAS impacts, it is difficult to see how an efficient and comprehensive strategy can be developed. While several recent papers have examined the threats posed by IAS globally\(^9\) or for entire taxonomic groups (e.g., mammals\(^10\)), all of these studies implicitly assume that the distribution of IAS reflects their impacts (e.g., in terms of the decline in native species populations they cause). However, there is much evidence that the impacts of IAS are context dependent\(^3,11,12\), and spatially variable. Other large-scale studies have analyzed IAS impact on
specific archipelagoes\textsuperscript{13} or on a particularly problematic subset of IAS\textsuperscript{14}. But all these approaches are piecemeal and cannot deliver the evidence needed to support an efficient approach to focus IAS research and action at a global scale. Here we use the comprehensive data compiled by the International Union for the Conservation of Nature (IUCN) database, BirdLife International database and the Global Invasive Species Database (GISD) to extract information about vertebrates threatened by IAS, and the identity of the threatening IAS to address the three following questions: (i) How are the impacts of IAS distributed among islands and threatened species? (ii) Are there combinations of IAS for which targeted actions may have high conservation impacts? (iii) Within the targeted areas what are the characteristics of the network between IAS and IAS-threatened species that can improve strategies to deal with IAS?

Some species occur on multiple islands while others are endemic to a single island. Moreover, some IAS are shared as threats by multiple species on the same or different groups of islands, while others are very localized and specific. To gain insights into the structure of this complex interconnected system we apply network approaches. Many systems can be represented as networks of interconnected nodes. Networks are mathematical objects where a node is linked (connected) to zero, one or several other nodes. The links highlight a relationship between two nodes. For instance, each inhabitant of the world can be represented as a node in a network graph and each email sent by those inhabitants to others can be represented as a link. Of course with increasing node and link number, the complexity of network graphs grows exponentially and limits our ability to identify structure. Network theory aims at extracting significant patterns from networks.

In our study, we built two kinds of networks. In the first, the nodes are either species or islands and the links represent the presence of a species on a given island. We clustered this network to identify islands that are highly interconnected by the co-occurrence of many IAS-
threatened species, and selected the clusters with highest number and densities of IAS-threatened species. The aim of this clustering approach is to identify group of islands that share similar pattern of threatened species based on biogeographical knowledge. In the second set of networks the IAS and their threatened species were linked, and related to the island clusters identified in the first analysis (Methods and Materials for details). This allowed us to determine the IAS that are mostly responsible of threats in those clusters of islands and we used this to provide insights to deal with IAS threat.

Results

How are the impacts of different IAS distributed among islands and threatened species?

We analyzed more than 73,515 islands where the IUCN Red List recorded IAS-threatened species. First, we selected islands for which we could expect high return in investment for conservation program. Specifically, we selected islands that harbour more than 1% of the total number of IAS-threatened species, and those with a high ratio of the number of threatened species to area. We identified a total of 21 clusters (labeled in supplementary table 2) that include a total of 437 IAS-threatened species on the 27,081 islands across the world that met our criteria (figure 1, for the complete network see supplementary figure 1). These clusters represent the groups of islands that are highly inter-connected by the co-occurrence of IAS-threatened species (Figure 1) i.e., insular regions harbouring similar patterns of threatened vertebrates by IAS. Most of these islands detected, vulnerable to invasions, are located in the southern hemisphere and encompass most of the Caribbean and Pacific archipelagos (including Hawai‘i), Madagascar and islands at southern of the coasts of Africa, Indonesia, the coast of America, New Zealand and Australia (Figure 1a). The majority of the islands found in the 21 clusters are included in the insular biodiversity hotspots\textsuperscript{15}. Some clusters are fully isolated (i.e., disconnected to others in terms of IAS-threatened species: e.g., Puerto Rico islands; Okinawa islands and Seychelles) because their IAS-
threatened species are found nowhere else. Two of the Caribbean clusters (including Hispaniola and Jamaica islands), and Malaysia, Philippines, and South of east indies islands are connected only to each other (Figure 1b). Overall, the clusters that share a high number of threatened species with other clusters are Polynesia and Micronesia, North America Pacific coast islands, as well as the South American, Antarctic, sub-Antarctic and Australian islands. Our analysis revealed that most of the connections between clusters are due to bird species, but amphibians, mammals and reptiles are also responsible for connections between the southern part of New Zealand, Australia and southern-hemisphere islands, Caribbean clusters, and African islands (supplementary figure 1). Some clusters are particularly noticeable due to their high number of threatened species by IAS: New Caledonia, Hawaian islands and Madagascar and African southeastern coast for reptiles, birds, and amphibians, respectively.

The 21 identified clusters vary in terms of number of threatened species (see size of the taxa nodes of the outer circle Figure 1b), number of islands (size of the inner circle nodes, Figure 1b) and total area. Specifically, the number of threatened species ranges from 7 (the cut-off point we selected that corresponds to at least 1% of the total number of insular threatened vertebrates) to 61 species, while the number of islands ranges from 1 (i.e., Puerto Rico) to 7,460 (Table 1). Most of the threatened species found in these clusters are birds (51%), followed by reptiles (18%), amphibians (17%) and mammals (14%), which is consistent with the taxonomic groups that have been identified as threatened by IAS worldwide.

Are there combinations of IAS for which targeted actions may have high conservation impacts?

In a second step, we analyzed the patterns of interactions between IAS and the vertebrate species they threaten for the whole network and for the 21 identified clusters (Figure 2a, for the complete network see supplementary figure 1). We built interaction networks with IAS and IAS-threatened species as nodes. The links between nodes represent the vulnerability of a
given species to a known IAS (see supplementary figure 2 for each IAS-threatened species) within a cluster (Figure 2a). The global interaction network revealed that most IAS are threatening numerous species across different taxonomic groups. The top threatening IAS is the feral cat (*Felis catus*), followed by other IAS such as rat (*Rattus spp*), feral dog (*Canis familiaris*) and pig (*Sus scrofa*). Some IAS are more specialized, such as *Eucalyptus* spp. that predominantly threatens vertebrates located in clusters of Madagascar and African southeastern coast islands, the little fire ant (*Wasmannia auropunctata*) that affects reptiles in the New Caledonia cluster (see also 16) and the Chytrid Bd (*Batrachochytrium dendrobatidis*) that mainly threatens amphibians in the Caribbean clusters.

The network approach can, in theory, help to identify the best strategies for combating IAS that maximise the number of threatened species that will benefit from any eradications. For example, the feral cat and feral dog eradicated alone would directly benefit to 10 and 6 species respectively, but targeted together could benefit up to 27 species (because 11 others species are simultaneously threatened by those two IAS). Therefore, both need to be controlled to achieve the highest overall conservation benefit. Note that other threatened species will also benefit from such eradications because the IAS pressure on them will be reduced even if other IAS are still threatening them. The control or eradication of the Chytrid Bd, feral cats and feral dogs together could fully benefit at least 41 threatened island species worldwide (Figure 2B), assuming that no other threats are significant for these species.

*Within the targeted areas what are the characteristics of the network between IAS and IAS-threatened species that can improve strategies to deal with IAS?*

The characteristics of IAS and IAS-threatened species interaction networks within each cluster can also be used to focus actions to deal with the IAS threat. In each cluster, we identified the top-IAS that affect the most species (i.e., highest number of links with threatened species), and the connectivity of IAS and threatened species. We also determined
which IAS or combinations of IAS should be targeted, in theory, to maximize the number of threatened species that will fully benefit from IAS eradications per cluster. We found that the top-IAS that threatens most of the native species is not necessarily the same as the IAS that should in theory be eradicated to maximize the number of species that fully benefit (Table 1).

For most of the clusters, we found that a targeted combination of IAS will result in a better outcome for threatened species than controlling only the most important invader. For instance, the native species in the Polynesia and Micronesia cluster are highly threatened by feral cats. Yet, targeting only feral cats would, in theory, lead to only one species fully benefiting, because the other species threatened by cats are also threatened by others IAS. The combined control of black rat (*R. rattus*), pacific rat (*R. exulans*) and feral cats could, in theory, fully benefit to 13 species of IAS (Figure 3a). A specific example is Okinawa islands cluster. This insular region might also offer good opportunities as the removal of IAS from the family Herpestidae (e.g., *H. javanicus*) could directly benefit to at least 6 species and decrease pressure for 6 additional species that are also threatened by other IAS (Figure 3a). The number of links in the Okinawa cluster is quite low, so we can expect that the control of a low number of IAS would result in a high benefit for native species. In addition, most of the threatened species located in this cluster are found nowhere else (Figure 1b), so they have a particularly high value for biodiversity.

Note that neither the potential feasibility nor the cost-effectiveness of such programs has been evaluated here and so our findings should be complemented with local prioritization analyses at the island and IAS level.

We also identified some clusters where the networks share similar properties that could be helpful in understanding their response to IAS. For example, two clusters (i.e., Papua New Guinea cluster, and the South of east indies islands cluster) share both a high-density value (a high ratio of the number of links per node to the number of possible links) and a relatively low number of IAS in their clusters (Figure 3b). This means that the threatened species within...
these two clusters are threatened by few IAS but these few IAS threaten most of the species in this cluster. Hence, the control or eradication of this small number of IAS may offer great opportunity for conservation, especially as the number of IAS-threatened species is important (Figure 3a). Because these two clusters are highly disconnected from other clusters as well (Figure 1b), protecting their species might be particularly significant globally. We observed similar characteristics for Solomon, New Britain and New Ireland islands that may also offer significant opportunities for conservation (Table 1). We also observed that the Hispaniola, Jamaica and Puerto Rico clusters share similar characteristics in terms of the average number of links, and density values. Some other interaction networks are particularly distinctive and should be studied individually. For instance, Madagascar and Africa southeastern coast clusters harbour a larger number of IAS-threatened species and New Caledonia cluster more interconnections than any other clusters.

Discussion

We have identified 21 clusters of islands harbouring threatened vertebrates species that are highly significant sites of IAS threat and where focusing resources, for both research and conservation action should be most efficient. The spatial distribution of the 21 identified clusters overlaps with the majority of global biodiversity hotspots (except some coastal islands, see brown polygons represented in Figure 1a) that are priorities in terms of endemic plants threatened by habitat loss. Over $1 billion has been spent protecting the remaining natural vegetation of these biodiversity hotspots. We identified other areas important for conservation, including many small islands and island groups that may offer high return on investment. Specifically, we were able to identify clusters that harbour a unique part of vertebrate species diversity threatened by IAS. These island clusters that include Caribbean, Okinawa, Seychelles islands, and also Malaysia, Philippines, some of the Indonesian islands
and South of East Indies islands would qualify as priorities on their own while clusters that are inter-connected (i.e., where IAS-threatened species are shared) will require also trans-national efforts for conservation to be fully effective.

We also reaffirm here the role played by major invaders such as rats, cats, and the Chytrid *Bd*, which are already known to cause widespread threats to species on islands\textsuperscript{19–21}. Feral cats are well-known to drive numerous extinctions of endemic vertebrates (>1756). Yet, our analysis quantifies their roles whether they are the only invader responsible of population decline in islands or if they act in combination with other IAS on islands.

Most of the current eradication programs focus on single species, which may be ineffective when multiple IAS are involved\textsuperscript{23}. On the basis of our results, we suggest that targeting multiple IAS simultaneously would be a more efficient strategy for species conservation\textsuperscript{23} and should be achievable as eradication programmes increase in coverage and complexity\textsuperscript{24}.

In our analyses we have identified the co-occurrences of IAS threat on islands and quantified the potential number of species that, in theory, could benefit through the eradication of these IAS. However, we do not account for predator release effect that could further threaten species\textsuperscript{25,26} or other unanticipated events (e.g., changes of vegetation or trophic webs that could follow IAS eradication). In addition, we assume that all IAS have the same effect on threatened species, which may not be a safe assumption but there is currently too little information on which to improve this aspect of the analysis. Moreover, we did not assess the potential for reintroductions or the feasibility of eradication events.

The eradication of the Chytrid *Bd* could, for example, be quite challenging. Indeed, we lack of efficient methods to systematically eradicate the Chytrid *Bd*, although two recent advances have greatly improved our understanding of amphibian-chytridiomycosis dynamics\textsuperscript{27}. First, the recognition that Bd is not one species but distinct lineages that vary in distribution and virulence and, second, that species have been infected for much longer than initially thought.
with some species co-evolving without any impact (see for a review). Thus, preventing
measures to avoid further propagation of the Chytrid Bd in nearby clusters should be a
priority. In contrast, eradication attempts for vertebrates have been quite efficient for cats or
rats with failure rates of only 12% as well as for invasive ants.
In general we argue that network approaches should complement local prioritization schemes
including eradication feasibility information to target regions and IAS for which actions
should be undertaken. For example, a recent study analyzed conservation opportunities for
sea-bird populations in most of the 800 small, uninhabited, and high-middle-income countries
islands. Our analyses also revealed that in some clusters it might be quite challenging to
protect native species from extinctions, because of the high number of IAS combinations that
threaten native species as shown by their high values of connectivity. Yet, local removals of
IAS could prevent local extirpations of native populations and therefore benefit biodiversity.
This is particularly the case of the Polynesia and Micronesia cluster.

There are some limitations of our approach that are discussed in the following. First, we
considered the impacts of IAS as a reduction in population size or distribution range
determined by the IUCN Red list of threatened species, but other type of impacts on
functional or genetic diversity through hybridization or ecosystem services might also be
important. Our network-based analyses only accounted for the existence of an impact between
IAS and IAS-threatened species, but not the types of impact (predation, competition, habitat
modification) nor the population abundance of IAS-threatened species. Moreover, we focused
on IAS threat, but many IAS threatened species are also affected by habitat loss or
overexploitation, and these threats might prevent full recovery of populations even if IAS are
controlled or eradicated. Our work considered only IAS-threatened vertebrate species, for
which data are most comprehensively available, but invertebrate species are also known to be
particularly affected by IAS. In addition, IUCN and BirdLife provide comprehensive data for
some regions and taxa, but are far from being comprehensive in some regions (e.g., Africa).

Regarding these limitations, the analyses here should be considered as a first step to inform about the combination of IAS that, in theory, might offer high return for species conservation. In spite of these limitations, our results have the potential to help mitigate the impacts of invasive species in insular habitats known for their remarkably rich biodiversity.

Concluding remarks

Our network-oriented analysis of threats posed by IAS on islands allowed us (i) to structure 27,081 islands and 437 threatened vertebrates into 21 clusters that could be used to define priorities for conservation research and actions to address threats from biological invasion, and (ii) to identify the major invaders that threaten a large number of vertebrate species. We suggest that an approach based on networks that take into account islands, IAS and their impacts has been largely missing from biological invasion studies, despite its potential to guide effective responses. The clusters of islands with similar profiles in terms of IAS impacts represents an efficient and innovative way to determine priorities for both areas and species and then to better understand and mitigate the IAS threat. Continuous investment to understand, eradicate, control or prevent new invasions in islands could benefit a high number of endemic species that are predicted to be extirpated (e.g., \(^{10}\)), and the high phylogenetic and functional richness located on those islands offering an unique opportunity to mitigate the loss of biodiversity and contribute to achieve international conservation commitments such as the Aichi Targets 9.

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Author Contributions

CB and JFR conceived the study designed with the contribution of GM M. JFR and CB did the analyses, BL provided initial version of computing code. CB and JFR wrote the first draft of the manuscript and all authors significantly contributed to interpreting and writing the manuscript.

Competing Financial Interests statement

The authors declare no competing financial interests.

Material & Method

Data

Information about vertebrate species threatened by invasive species was extracted from the International Union for the Conservation of Nature (IUCN Red List\textsuperscript{33}), and the BirdLife International database\textsuperscript{34}. We used the Global Invasive Species Database (GISD\textsuperscript{35}) for information on the identity of invasive alien species responsible for the threat and the Global islands database from IUCN\textsuperscript{33} website to obtain spatial data on islands worldwide

Vertebrates threatened by IAS

The species assessments of the IUCN Red List classify the risk of species extinction into one of the following categories: extinct (EX), extinct in the wild (EW), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC) and data
deficient (DD). These categories are based on quantitative criteria that indicate the extinction risk including the rate of population decline (criterion A), the size and decline of the geographical range (criterion B), the population size, its fragmentation and decline rate (criteria C and D) or quantitative analyses (criterion E)\textsuperscript{36}. Prior to 2001, Red List assessments were based on expert opinion but now all assessments use the standard quantitative Red List Categories and Criteria, so they are objective, transparent, and repeatable. As part of the species assessment process, factors associated with decline are collated for each species\textsuperscript{37}.

Specifically, the IUCN and BirdLife International have classified these factors into 11 main threat categories (i.e. the IUCN threat classification scheme v. 3.0). These threats are: (1) residential and commercial development; (2) agriculture and aquaculture; (3) energy production and mining; (4) transportation and service corridors; (5) biological resource use; (6) human intrusion and disturbance; (7) natural system modifications; (8) invasive and other problematic species, genes and diseases; (9) pollution; (10) geological events; and (11) climate change and severe weather\textsuperscript{37}. We extracted information for terrestrial vertebrates (i.e., mammals, reptiles, amphibians and birds) that classified under (8) and identified those threatened by IAS to be included our analysis.

We selected vertebrates that were classified into one of the threatened categories (i.e., CR, EN and VU; N= 1,324) and extracted their spatial distributions (spatial polygons) from IUCN spatial data for mammals, amphibians and reptiles, and from the BirdLife database\textsuperscript{34} for birds (resulted in a total N= 1,291). Spatial data were missing for 4 mammals and 29 reptiles. Note that in our analyses any IAS-threat associated with a species is a binary response - either an invasive alien species does impact a species or it does not; we do not consider different intensities of invasive species impact (but see supplementary figure 3-4). In this way we were able to identify which vertebrates are threatened by any IAS among islands.

Information about invasive alien species
We used the Global Invasive Species Database (GISD) which interlinks the IUCN Red List with IAS information\textsuperscript{35}. The information in the GISD has been compiled from many sources including scientific papers and regional databases that have been reviewed by international expert contributors. Specifically, for vertebrate species identified as threatened by IAS, we collected information about the identity of IAS responsible.

**Island data**

We used the Global islands database from IUCN website (http://www.iucnredlist.org/technical-documents/red-list-training/iucnspatialresources), a spatial dataset of more than 180,488 islands\textsuperscript{33}. We overlaid the spatial polygon of islands and the polygon of vertebrate species distributions to derive a set of 73,515 islands where vertebrate species are threatened by IAS (see supplementary methods for more details). When an overlap between an island and the polygon of species distribution was indistinct, we visually checked the species distribution. In order to restrict the analysis to insular vertebrates (persisting only on islands), we excluded species that were both on continental coastal areas and islands. The resulting dataset includes 97 amphibians threatened by IAS on 903 islands, 120 reptiles on 2,340 islands, 336 birds on 72,433 islands and 110 mammals on 9,709 islands.

**Bipartite networks**

We first built an island and IAS-threatened species network that we clustered into groups of islands on the basis of shared IAS-threatened species. Then, for each of the clusters, we conducted analyses of IAS and IAS-threatened species interaction networks.

**Analyses of the island - IAS-threatened species network**

Recently, geographical relationships between species and localities has been abstracted as a bipartite association network, where links are the occurrences of species within geographical locations\textsuperscript{38}. Similarly, the occurrence of species on islands worldwide can be represented as a
network for which nodes are either species or islands. When a species is present on a given island, a connection between this species and the island is established in the network. As species never connect to species, and islands never connect to islands (i.e., links only connect species to island in the network), such a network is called a bipartite network. This network provides information on co-occurrences of species on islands, the number of times species co-occur, and the number of species shared by particular groups of islands. In this study, we built the network with all vertebrate species threatened by IAS on islands. We chose a biogeographical approach to represent connections between islands, IAS-threatened species and invasive without any a priori knowledge of political jurisdiction or geographical proximity. Indeed, native and invasive species do not respect political boundaries, but mostly environmental boundaries. Thus, it makes more biological sense to use biogeography of species (spatial distribution of species) to delimit the impact of invasive species across islands as it will better reflect the processes of dispersion among islands than other types of boundaries. Since such an interconnected network has a high degree of complexity (663 species, 73,515 islands), numerous techniques have been developed to synthesize information by clustering nodes (e.g., the map equation minimization approach and the modularity maximization approach). Among these techniques, the map equation algorithm has been proven particularly well suited for cluster networks in comparative studies. This technique allows us to extract meaningful ecological structure composed of islands and species that are similar. Specifically, this technique will allow us to cluster our bipartite network based on biogeographical knowledge (species distribution) and detect common patterns of threatened species among islands. The map equation algorithm is iterative: first it chooses a random node, and then randomly selects a second node that is connected to the first one. This process is repeated a random
number of times. Then another node is chosen randomly and the same process repeated. If
some nodes are strongly interconnected, this process tends to frequently select the same
nodes, which are then attached to a cluster. In groups of islands with marked structure (high
connectivity), the algorithm will focus mostly within clusters, crossing only when a cross-
cluster species is selected. Once the algorithm go through all the nodes of the system, it will
provide the list of clusters where it spent more time\textsuperscript{38}. This technique allows us to extract
meaningful ecological structure composed of islands and species that are connected.

We expected a hierarchical structure in the dataset – due to the nested nature of species
distribution - as species may be located on specific islands, which are encompass in
archipelagos, and on larger regions. Consequently, we applied the multiple-level
implementation of the map equation, which produces hierarchically nested groups of clusters.
Thus, the algorithm hierarchically partition the groups of nodes into clusters\textsuperscript{43,44}.

In this study, a three-step approach was used to identify clusters of islands and species that are
of high interest for conservation.

(1) We applied the map equation algorithm to define clusters of island based on IAS-
threatened species co-occurrences, and attributed hierarchical levels into clusters that
correspond to a subset of the original network in which species and islands are strongly inter-
connected to each other, but weakly linked to species and islands outside the group\textsuperscript{45}.

(2) We selected clusters with high conservation interest defined as those that harbour at least
1\% of all IAS-threatened species (>6 IAS-threatened species, see supplementary figure 6 for
sensitivity analyses of this parameter).

(3) We then selected, for each branch in the hierarchy, clusters that maximize the ratio of the
number of IAS threatened species to the total area. In this way we identify islands with a high
density of threatened species. Specifically, we chose to maximize the ratio between number of
threatened species and total area for a given unit area (km\textsuperscript{2} here), so the eradication events
could benefit to a high number of species. Indeed, eradication outcome are more likely to succeed on a small area than large ones. We made the assumptions here that all species have the same value and interest for conservation, without any distinctions of their originality or role for the community or ecosystem. Therefore, we attempted with this criterion to consider the opportunity for eradication to protect many species as possible. The application of those criteria results in the exclusion of 226 species (24 amphibians, 111 birds, 50 mammals, and 41 reptiles) (black nodes in Figure 1b) as they did not meet the criteria detailed below. Note that 14 of the excluded IAS-threatened species could offer particular opportunities for research and eradication programs as 4 birds, 5 reptiles and 5 amphibians are both located on single islands and are threatened by only one identified IAS (see list in the supplementary table 1). From these three steps we obtained 21 clusters that correspond to groups of strongly interconnected species and islands with a high density of IAS-threatened species (see supplementary figure 5 for illustration of the 3-step approach). For each cluster we document the number of IAS-threatened species, number of islands, total area (km²), and identities of IAS-threatened species (Table 1).

**IAS - IAS-threatened species interaction network**

Thereafter, for each of the 21 clusters, we constructed an interaction network between IAS-threatened species and their associated IAS. This relationship is based on the IUCN GISD information that identified which IAS threatens which species. The majority of IAS-threatened species are threatened by several invasive alien species. Using a network to describe the relationships between IAS-threatened species and IAS provides the means to list all species threatened by a given IAS and how they are linked to other IAS. For each of the 21 interaction networks we identified the (i) top-IAS per cluster (i.e., IAS with the highest number of links to threatened species), (ii) number of nodes (total number of IAS...
and threatened vertebrates included in the cluster), (iii) number of links (total number of
interactions between IAS and threatened vertebrates), (iv) the connectivity of IAS and their
threatened species nodes (i.e., the average number of links (interactions) per IAS and their
threatened species) and (v) graph density: a ratio of the number of links per node to the
number of possible links. Knowing a network’s property regarding connectivity is important
here for two reasons. First, it will help us to identify if control of certain IAS in the network
will have positive effects on a number of threatened species. Conversely, knowing the number
of connections of IAS-threatened species will help determine which IAS should primarily be
controlled or eradicated. Indeed, the connectivity of IAS and their threatened species nodes
will help us to identify how IAS and threatened species are connected. It can be used to
identify which IAS threaten a large number of species and if those threatened species share
the same IAS or not. This can indicate how eradication of any IAS will benefit different
threatened species. We also measured whether the network is close to saturation (density
value close to 1, indicating that all the possible interactions have been achieved). In a
saturated network where the threatened species are threatened by many IAS it will be very
difficult to release significant pressure on threatened species, as most IAS would have to be
removed to release significant pressure on threatened species. Yet, in a saturated network,
where the threatened species are threatened by a low number of IAS, it will be highly
beneficial to conduct eradication campaings, especially if the number of threatened species is
high.

Finally we calculated, for the whole network (n=21 clusters), the combination of IAS for
which control or eradication programs could theoretically benefit the largest number of
threatened species. Specifically, for each potential combination of invasive species (from 1 to
5 IAS), we calculated the number of species that would be invasive free after eradication of
that combination of IAS. We found the best strategy by testing every possible eradication
scenario (see Fig. 2b). Any IAS-threatened species could benefit from the eradication of one
or several of its associated IAS, but the highest conservation benefit would require all of its
known IAS (according to the IUCN-GISD data) to be eradicated. For this analysis, we assume
that a threatened species only benefits from the eradication, if all invasive species that affect it
are eradicated. Obviously, this assumption does not necessarily reflect of real ecological
situations because other native species might also benefit from such eradications. But, it is not
possible to predict the effect of eradication for partially benefited species (such data do not
exist at the global scale). In addition it is worth noting that many other factors, such as Allee
effects or the existence of other threats may limit recovery, even if all invasive species are
eradiated. Consequently, for the purposes of the analyses, we define conservation success as
the eradication all of the known IAS threatening a given species. Note that eradicating any
IAS may also benefit others species by releasing pressure on them, even if other IAS are still
threatening them. For example if a species_A is threatened only by a IAS_B the eradication of
this IAS_B in the cluster will theoretically allow species_A to recover. But, if species_A is
threatened by IAS_B, IAS_C, IAS_D, the removal of IAS_B will not be sufficient to permit the full
recovery of the species_A, it will only release some pressure. We report the top 5 IAS whose
eradication would most benefit IAS-threatened species across the whole network.

We conducted the same analysis for each cluster. We kept the identity of the IAS or the
combination of IAS that maximize the ratio of the number of invasive-free species to the
number of necessary eradicated IAS per cluster.

All analyses were carried out with R version 3.2.4 using ggplot2\textsuperscript{47} maptools\textsuperscript{48}, igraph\textsuperscript{49},
infomap version 0.18.2\textsuperscript{41} and dplyr\textsuperscript{50} packages, and gephi software\textsuperscript{51} under Debian-Linux
operating system.
Data availability:

The dataset of the co-occurrence of species on islands is available in Zenodo data repository (http://doi.org/10.5281/zenodo.884886). The code to create the network is available on request.

References


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<http://www.worldcat.org/isbn/9686397779>
Figure legends

**Figure 1**: Bipartite IAS-threatened species/islands network. A - The map represents the location of the 27,081 islands included in the 21 clusters coded using ID number and colour (see legend). Brown areas show the location of biodiversity hotspots originally defined by Myers and then updated to 35 hotspots\(^{17,52}\). B- Graphical summary of the 21 clusters; each cluster is defined by islands and IAS-threatened species, and distinguished using the same colour as in (a). with the ID numbers shown (see the legend for the labels). The size of the nodes in the inner circle is log-proportional to the number of islands in the cluster, and the size of the nodes in the outer circle is log-proportional to the number of species of each taxon in a cluster. Shapes representing the higher taxa are shown in the circle when possible. The width of the grey links is log-proportional to the number of species that are located in two given clusters. Nodes (islands and IAS-threatened species) represented in black on the right-hand side of the figure show the species and islands that were not included the analysis (see Materials and Methods)

**Figure 2**: A- Global interaction network between IAS in black (n=169) and individual threatened species (n=397; green = mammals, red = birds, purple = amphibians, blue = reptiles). Node size of the IAS is proportional to the number of species that it is reported to threaten, while the node size for higher taxa is log-proportional to the number of species threatened by IAS. Some IAS shapes are represented: rats (including R. exulans, R. norvegicus, R. rattus, and R. unspecified), pig (Sus scrofa), ant (Wasmannia auropunctata), feral dogs (Canis familiaris), Chytrid Bd, and feral cat (Felis catus) B- Barplot of the theoretical number of vertebrate species that would fully benefit from the removal of the top (Chytrid Bd) to top 5 IAS in the network.

**Figure 3**: A-Representation of two networks between IAS (in black) and IAS-threatened species (in color, green = mammals, red = birds, purple = amphibians, blue = reptiles) for ID 1 and ID 18. Some IAS shapes are represented: ant, pig, rats and feral cat for ID1, Herpestidae family and cat for ID 18. Note that Herpestes sp. appears twice because one node represens the whole Herpestidae family and the other represents species identified as H. javanicus B- Radarplot showing the network characteristics for Caribbean clusters (ID 13, 14, 15), and the Indonesian region clusters (ID 17, 20). All the variables (number of
threatened species, total number of nodes, total number of links, density, average number of
links per threatened species, average number of links per IAS, and number of islands) have
been normalized for comparison.

Table 1: Characteristics of the 21 clusters based on the two types of networks: the network of
IAS-threatened species and islands, and the interaction network between IAS and their
threatened species. The table reports the cluster ID, the number of IAS-threatened species, the
number of islands, the total area in km2, the top invaders, the percentage of IAS included in
the network, the average number of links per IAS-threatened species and per IAS, the density
of the network, the combination of IAS that in theory could benefit to the highest number of
vertebrate species, and the number of vertebrate species free of IAS. The latter quantity is
defined as the number of threatened species for which all known IAS in the cluster are
eradicated based on the stated combination of IAS. Note that when the ratio between the
number of targeted IAS and the number of vertebrates free of IAS is less than 1, we did not
include it in the table.
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<tr>
<th>ID</th>
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<th>Nb. of Islands</th>
<th>Area (km²)</th>
<th>Top-1st IAS</th>
<th>% of IAS</th>
<th>Mean nb. of link per IAS-threatened sp.</th>
<th>Mean nb. of link per IAS</th>
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Islands

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</table>

Islands and species outside of the 21 clusters
b  

ID 13 14 15 (Hispaniola, Jamaica, Puerto rico)  

ID 17 20 (Papua New Guinea, South of east indies islands)
Table 1:

<table>
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<tr>
<th>ID</th>
<th>Nb. of IAS-threatened</th>
<th>Nb. of Islands</th>
<th>Area (km²)</th>
<th>Top-1st IAS</th>
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<td><em>F. catus</em></td>
<td>42,3</td>
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<td>0,1</td>
<td><em>R. rattus</em> + <em>F. catus</em> + <em>R. exulans</em></td>
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