Species-specific responses to land-use change in island insectivorous bats

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Abstract

Due to their ability to disperse over water, over half of the extant bat species occur on islands and ca. 25% of these are island endemics. They are often the sole native island mammals and play key roles in the maintenance of insular ecosystems. Yet, due to increasing anthropogenic pressures, ca. 60% of island-restricted bats are now threatened. The sub-tropical island of Madeira is home to the Macaronesian endemic *Pipistrellus maderensis*, to *Nyctalus leisleri verrucosus* - an endemic subspecies to Madeira - and *Plecotus austriacus.* These species each represent the three main foraging guilds of insectivorous bats namely, edge space foragers, open space foragers and narrow space foragers. Despite the great conservation value and potential to provide pest suppression services, little is known about the habitat associations of Macaronesian bats. We used low-cost autonomous sensors to conduct an island-wide bioacoustic survey to investigate how Madeiran bats are affected by human-induced land-use change and orography. Overall we obtained >63,000 bat passes across 216 sites and at each site, we quantified land-use cover and altitude within a radius of 250, 500 and 1000 m. *Pipistrellus maderensis* was the most widespread and commonly recorded species, whereas *Plecotus austriacus* had the most restricted distribution and lowest number of detected bat passes. We found species-specific and scale-dependent responses to land-use cover, with the activity of *Pipistrellus maderensis* being positively associated with landscape-scale shrubland, cropland and Laurisilva (primary forest) cover, whereas the activity of *Nyctalus leisleri verrucosus* and *Plecotus austriacus* were negatively influenced by Laurisilva and cropland cover, respectively. Furthermore, we found that altitude had a negative effect on the activity of *Nyctalus leisleri verrucosus* and *Plecotus austriacus*. This study provides the first insights into the effects of land-use type on Madeiran bats and showcases the great potential of low-cost bioacoustic detectors for island-wide bat surveys.

Keywords: bioacoustic detectors, Chiroptera, island bats, landscape composition, Macaronesia, Madeira Island.

Introduction

Islands account for less than 8% of the global terrestrial surface but due to exceptionally high levels of species endemicity contribute disproportionately to Earth’s biodiversity (Russell & Kueffer 2019). However, with >40% of the global highly threatened terrestrial vertebrates living on islands, insular ecosystems are particularly sensitive to the ongoing Anthropocene defaunation (Spatz et al 2017). Anthropogenic land-use change is a key historical and present day driver of the ongoing insular biodiversity crisis (Norder et al 2020). Indeed, the erosion of populations and extinction of species has occurred much more rapidly in insular ecosystems than in their mainland counterparts (Tershy et al 2015). Human-induced turnover of native vegetation – alongside the impact of invasive species and overexploitation – has contributed significantly to this (Nogué et al 2021). The biological uniqueness of many insular taxa greatly exacerbates the impacts of land-use change in insular settings, as evolutionary divergence due to limited genetic exchange with mainland populations and selective pressure associated with the peculiar habitat conditions of islands has often moulded communities tightly associated with native vegetation.

Bats have managed to colonize a large portion of the planet’s islands. Of the over 1,400 extant bat species, ca. 60% occur on islands and around one quarter of all species are insular endemics, a proportion that is higher in bats than in mammals as a whole (Jones et al 2010; Conenna et al 2017). Indeed, due to the poor ability of most terrestrial mammals to disperse over water, bats are frequently the sole mammalian representatives in island ecosystems (Fleming & Racey 2009), where they often play key ecological roles. For example, the island-restricted Mauritian flying fox *Pteropus niger* is a key seed disperser of plants that constitute over half of the basal area of the remnant native forest of Mauritius (Florens et al 2017). Nonetheless, subjected to increasing human pressures, insular endemic bats are significantly more threatened than non-insular endemics (Jones et al 2010; Conenna et al 2017).

Over 60% of the insular endemic Chiroptera are laryngeal echolocating bats (Jones & Teeling 2006), most of which can be classified as aerial insectivores. Of these, over one quarter are assessed as Critically Endangered, Endangered, or Vulnerable by the IUCN and ca. 40% of the remaining are classified as Data Deficient (IUCN, 2021). Some "microbats" classified as Data Deficient have not been detected for >100 years (e.g., the Malagasy slit-faced bat *Nycteris madagascariensis*) and the Christmas Island pipistrelle *Pipistrellus murrayi*, the only "microbat" in Christmas Island, has recently been classified as Extinct (IUCN 2021). "Microbats" are often inconspicuous and thus population declines, and extinctions often go unnoticed. Fortunately, the increasing availability of affordable autonomous ultrasound detectors greatly facilitates large-scale surveys of echolocating bats for extended periods of time (Hill et al 2018; Gibb et al 2019), offering an opportunity to expand the knowledge regarding the distribution, habitat associations and population trends of poorly known island endemic echolocating bats.

The Macaronesian biogeographic region (composed by the archipelagos of Azores, Madeira, the Canaries and Cape Verde) is an outstanding biodiversity hotspot (Whittaker & Fernandez-Palacios 2007; Florencio et al 2021), particularly within the European context. It is home to three species of IUCN Vulnerable insular endemic bats, namely: the Madeiran pipistrelle *Pipistrellus maderensis* (present in the archipelagos of Madeira, Canaries and probably Azores), the Canary big-eared bat *Plecotus teneriffae* (restricted to the Canaries) and the Azores noctule *Nyctalus azoreum* (restricted to Azores). Furthermore, multiple bats, such as the Madeiran Leisler's Noctule *Nyctalus leisleri verrucosus*, are currently classified as endemic subspecies. Yet, despite the uniqueness of the Macaronesian bat fauna, no study has yet investigated how Macaronesian bats respond to human-induced land-use change.

Landscape characteristics have long been recognized as important determinants of bat species persistence in modified landscapes (Heim et al. 2015; Treitler et al. 2016; Rocha et al. 2017a; Put et al. 2019; López-Bosch et al 2021). In insular ecosystems, landscape-scale responses are constrained by the intrinsic boundaries that define the island. Nonetheless, similarly to their mainland counterparts (e.g., Perry et al 2008; Pinto & Keitt, 2008; Mendes et al 2017), island bats are likely to react to landscape-scale habitat composition in a scale-sensitive manner. Scale-dependent responses are likely to be associated with species-level differences in ecological traits (e.g., diet, wing morphology and home range), which are linked to the scale at which individual species perceive and interact with their environment (Pinto & Keitt 2008). Furthermore, scale-dependent responses to habitat composition might also be indicative that ecological processes that operate at larger spatial scales are influenced by smaller scale drivers (McGill 2015).

Here, we use low-cost acoustic detectors to conduct an island-wide survey of aerial insectivorous bats in Madeira and investigate their response to landscape-scale land-use composition and altitude. Our capacity to investigate the influence of historical antecedents was limited by the lack of previous island-wide bat surveys and thus we have assessed the effects of land-use using a synchronic approach. Based on their capacity to forage in more or less cluttered habitat - which is closely associated with echolocation and morphological characteristics - the three bat species found in Madeira can be classified as either edge space foragers (*Pipistrellus maderensis*), open space foragers (*Nyctalus leisleri verrucosus*), or narrow space foragers (*Plecotus austriacus*) (Teixeira & Jesus 2009; Denzinger & Schnitzler 2013), thus representing the three main foraging guilds of insectivorous bats. Specifically, we address the following questions:

i) How does landscape-scale habitat composition affects species-level relative bat activity (proxy of abundance)? We anticipated species-specific responses, with all species being benefited by native primary forest cover (Laurisilva). Furthermore, and as per the findings for other *Pipistrellus* species in mainland ecosystems (e.g., Fuentes-Montemayor et al 2011, 2017; Puig-Montserrat et al 2015), we expected that the activity of *Pipistrellus maderensis* would increase with increasing agriculture cover.

ii) How does the relationship between relative bat activity and environmental metrics vary across multiple spatial scales? We predicted that responses would be scale-dependent for all three species, but particularly so for *Plecotus austriacus* since its relatively low wing loading values and aspect ratio values (7.9 N m^{-2} and 6.1, respectively; Norberg & Rayner 1987) suggests *P. austriacus* to be the less mobile of all three Madeiran bats.

iii) Are Madeiran bats equally affected by the island's orography? We hypothesized that due to the occurrence of *Plecotus austriacus* and *Nyctalus leisleri* in colder environments at more northern latitudes throughout their mainland ranges, the activity levels of these two species would be less negatively affected by altitude than that of *Pipistrellus maderensis*, which is restricted to more southern latitudes. Additionally, we antecipated that for some land-use types, the relationship between bat activity and land-use might be mediated by altitude.

Material and methods

Study Area

Our study was carried out in the Portuguese Island of Madeira, a volcanic island with a maximum elevation of 1,889 m a.s.l., located in the north-eastern Atlantic Ocean (32º30'N and 16º30'W; Carvalho & Brandão, 1991). The island is climatically and ecologically diverse having a subtropical climate up to 1,300 m a.s.l. and a temperate climate above that altitude (Carvalho & Brandão, 1991). Also, due to prevalent north-eastern trade winds, the northern parts of the island are more humid and colder, while the southern and eastern parts are arider and hotter (Jesus et al., 2009). Madeira is characterized by a mosaic of built-up areas (16% of the island), native and non-native vegetation. The dominant native vegetation encompasses the subtropical laurel forest (Laurisilva; 16%), shrublands (17%) and woodlands (10%), while the non-native vegetation is mostly composed by cropland (13%; mostly vineyards, banana and sugarcane plantations), production forests (10%;

mostly composed by *Eucalyptus* and *Pinus*), and (invasive) *Acacia* woodland (5%) (Figure 1). The Laurisilva of Madeira is home to numerous endemic plants and animals and is currently classified as a Natural World Heritage Site by UNESCO (Claudino-Sales 2019).

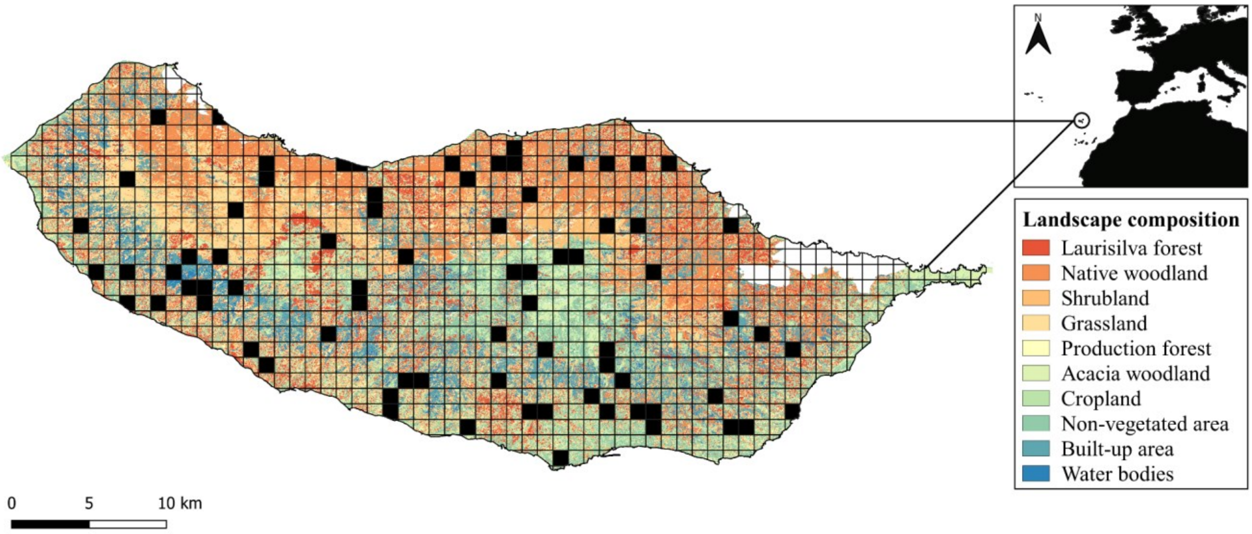


Figure 1 – Map of Madeira Island classified according to landscape composition and divided by grids of 1 km^2 . Sampled grids are denoted in black. Areas in white correspond to unclassified habitats (see Table A.1 and Massetti et al (2016) for details regarding land-use categories and classification methodology).

Bioacoustic survey

To ensure that all land-use types were adequately sampled across the different altitudinal levels, we divided Madeira into 1 km^2 grid cells and conducted stratified random sampling by the main land-use type and altitude. Seventy-five grid cells were selected for sampling, representing ~ 9% of the area of Madeira Island (Figure 1). Following Newson et al. (2015) each grid cell was sampled for 3 consecutive nights and detectors were moved to different sites within the same grid each night. The deployment of the recorders was constrained by accessibility and the rugged terrain, but our aim was to select sites that covered as much as possible the habitat heterogeneity of the cell. Hence, distances between sites within each grid ranged from 100 to 800 m, while altitudinal differences within each cell varied from 0 to 328 m. The highest altitude of a sampling site was 1,581 m, while the lowest was 67 m a.s.l. In total, we conducted 225 sampling nights (75 grids x 3 sampling nights). However, only 216 sampling nights were included in our analyses, due to technical problems and vandalism.

Bats were recorded between mid-August to late-September of 2016 (mid- to late-summer; survey period was selected so to minimize potential sampling issues associated with rainfall) using an early prototype of the AudioMoth acoustic logger, that used the same audio front-end and microphone as the later released AudioMoth 1.0.0 and 1.1.0 models (Hill et al. 2018), but used a Silicon Labs Giant Gecko micro-controller, rather than the Silicon Labs Wonder Gecko micro-controller, and 3 x AAA rather than 3 x AA batteries for power. Detectors were attached to poles at ca. 1 m above the ground with the microphone pointed perpendicularly to the substrate (Figure A.1) and programmed to record at mid gain with a 192 kHz sample rate from sunset until sunrise for 1 min. in every 5 min. Since the detectors were left unattended in public areas, a personal message explaining the purpose of study and with the respective contacts, was attached to each pole to reduce the chances of vandalism and theft (Clarin et al 2014). During the sampling period only two persons contacted the researchers and only one case of vandalism occurred.

Bioacoustic analysis

Our unit of measure for bat activity was a ‘bat-pass’, defined as two or more pulses of a single species detected in a 5-second recording (see e.g., Torrent et al. 2018). AudioMoth wav recordings were split into 5-second long files using Kaleidoscope v.1.1.1. software (Wildlife Acoustics, USA). Using the Kaleidoscope pulse detection algorithm, files containing bat calls were separated from those without any call. We selected recordings containing pulses with a frequency of maximum energy between 10 and 96 kHz, with a minimum pulse length of 2 ms and a maximum of 500 ms. When two or more sonotypes were identified in one 5-second file, a single bat pass for each sonotype was counted. File tagging was conducted manually using Avisoft SasLab Pro 5.2.12 software (Avisoft Bioacoustics, Germany) and, to optimise the process and manage the files, all 5-second files were clustered according to their similarity using a custom R script (following Tuneu-Corral et al., 2020). Species identification followed Teixeira & Jesus (2009; see Table 1 for echolocation call characteristics).

Environmental variables

Landscape-scale land-use metrics were obtained from a 6.5 m spatial resolution land-use map based on RapidEye multispectral vegetation mapping of Madeira for August 2011 (Massetti et al., 2016). For this study, the map was classified into the 10 major land cover types in our study area: "Cropland", "Laurisilva forest", "Production forest", "Native woodland", "Acacia woodland", "Shrubland", "Grassland", "Water bodies", "Non-vegetated area" and "Built-up area" (see Table A.1 and Massetti et al. (2016) for additional information about land-use categories). To assess scale-dependency in bat responses to landscape-scale land-use composition, we used buffers of three different sizes (250, 500 and 1000 m) centred on each of the 216 sampling sites. Buffer scales were selected to try to encompass the home range of the target species, while considering the complex orography of the island and at the same time minimizing the spatial overlap between neighboring buffers. For each of the three focal scales, we calculated the area in hectares occupied by each land cover type using the R package “landscapemetrics” (Hesselbarth et al., 2019). We also measured altitude based on DIVA-GIS (Hijmans et al. 2004) and distance to the sea (DTTS) for each sampling site using the QGIS v3.16.3 software (QGIS.org, 2021).

Statistical analysis

The effects of land-use type and altitude on Madeira Island bats were assessed at three different focal scales using Poisson general linear mixed-effects models (GLMMs). Prior to the analysis, all variables were standardized to a mean of zero and a standard deviation of one. Spearman's rank correlation coefficient and variance inflation factors (VIF) were calculated to test for multicollinearity (Dormann et al 2013), whereby we considered variables with VIF ≥ 3 and/or with a Spearman correlation >0.7 to be collinear, justifying their exclusion from the analysis. We therefore excluded the DTTS, which was negatively correlated with Altitude, and Built-up areas, which was negatively correlated with Laurisilva. Different sets of models were defined for each species and spatial-scale, using bat activity (number of bat passes per night) as a dependent variable. In addition to containing all non-correlated land-use categories mentioned above, full models also contained interaction terms between altitude and land-use category, to compensate for possible within-habitat altitudinal differences in abiotic conditions. Models included a random effect term accounting for the nested sampling design (i.e., sampling site within grid) and an offset with a site's total recording hours. We performed backwards model selection using Likelihood Ratio Tests on fully nested models (LRTs, cut-off probability $P > 0.1$). We used minimal adequate models (i.e., models containing only the variables and interactions which removed led to a significant decrease in explained variation) to estimate coefficients. Models were evaluated for overdispersion, zero-inflation and spatial autocorrelation using the package DHARMa (Hartig 2020). All GLMMs were run using the package glmmTMB (Brooks et al. 2017) in R v4.0.3 software (R Core Team 2020).

Results

From a total of 151,380 sound files, we identified 63,669 bat passes. Bats were recorded in all 75 grids, and in 212 of the 216 sampling sites. *Pipistrellus maderensis* was the most recorded species

(55,788 bat passes in 210 sampling sites) and *Plecotus austriacus* had the lowest number of detections (418 bat passes in 51 sampling sites) (Table 1; Figure A.2). For all three species, activity peaked within the first two hours after sunset (Figure A.3).

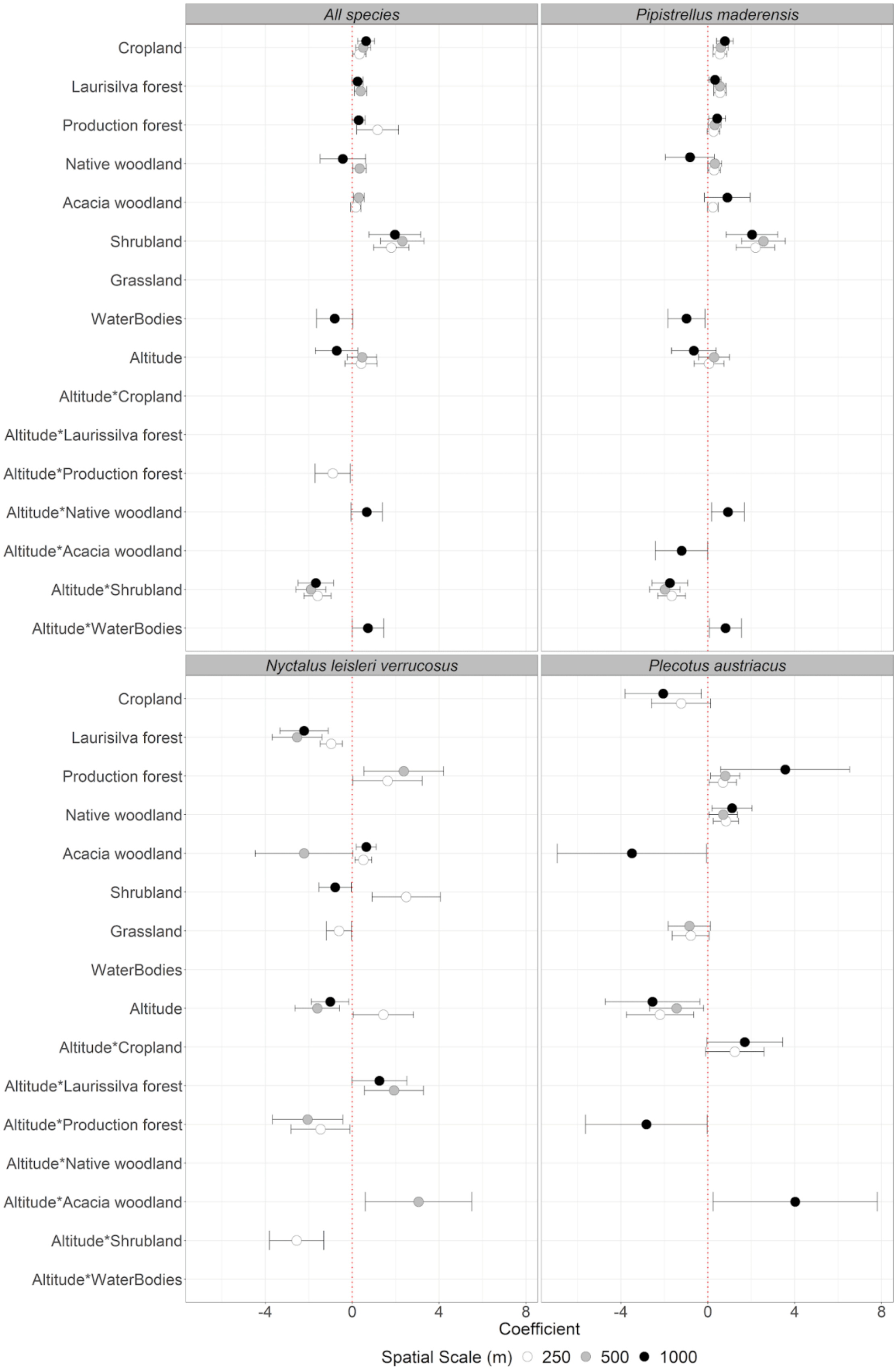
Table 1 – Echolocation call characteristics, foraging guild and numbers of bat passes and sampling sites where detected, for the three bat species recorded.

Species	**Call type**[1]	**FMaxE (kHz)**	**Duration (ms)**	**Foraging guild**	**Nº of bat passes (%)**	**Nº of sampling sites (%)**
Pipistrellus maderensis	QCF or FM-QCF	41-52	2.1-9.5	Edge space forager	55,788 (87.7%)	210 (97%)
Nyctalus leisleri verrucosus	QCF or FM-QCF	20-37	2.9-13.6	Open space forager	7,388 (11.6%)	147 (68%)
Plecotus austriacus	FM	24-39	1.7-6.5	Narrow space forager	418 (0.7%)	51 (24%)

[1] FMaxE = Frequency of Maximum Energy; FM = Frequency modulated; QCF = Quasi-constant Frequency.

Responses to land-use cover were scale-sensitive and varied according to the species analysed (Figure 2; Figure A.4-A.7 and Table A.2). Although results were scale-dependent, when a given predictor was included in the minimum adequate model of different scales for any of the three considered species, it normally indicated consistent associations between the predictor and activity level across scales. GLMMs residuals were not significantly spatially autocorrelated for 16 models out of 24 (based on Moran's *I* p-value < 0.05; Table A.3), and none of the models were overdispersed or zero-inflated (Table A.4 and A.5).

The activity of *Pipistrellus maderensis* was largely consistent across scales and showed a strong positive association with shrubland, cropland and Laurisilva cover (Figure 2; Figure A.5 and Table A.2). However, the response of *P. maderensis* to shrubland was highly sensitive to altitude, with the number of recorded bat passes decreasing with increasing altitude. To a lesser extent, the activity of *P. maderensis* was also positively associated to native woodland at the 250 m scale, and positively associated with production forest at larger scales (500 and 1000 m). Contrary to *P. maderensis*, the response of the activity of *Nyctalus leisleri verrucosus* to landscape features was very sensitive to the spatial scale, exhibiting a strong negative association with the cover of Laurisilva. However, this association was altitude-dependent and exhibited contrasting patterns with scale, with the number of recorded bat passes interacting negatively with altitude for the 250 m spatial scale but positively at the two larger scales (500 and 1000 m) (Figure 2; Figure A.6 and Table A.2). Furthermore, the activity of *N. l. verrucosus* was positively associated with shrubland at the smallest scale but negatively associated at the largest spatial scale. The response to *Acacia* woodland cover was particularly variable with scale, with the direction of the relation changing between all three spatial scales analysed. Lastly, production forest was positively associated with the activity of *N. l. verrucosus* at the two smallest scales, with the responses to this predictor being influenced by altitude. For *Plecotus austriacus* the low number of detections made it difficult to unequivocally evaluate the influence of the considered predictors. However, the species' activity displayed a positive association with native woodland and production forest cover for all three considered scales and a negative association with *Acacia* woodland and cropland cover at the 1000 m spatial scale. Although the activity of *P. austriacus* decreased with altitude for all the spatial scales considered, it interacted positively with *Acacia* woodland at the largest spatial scale (1000 m) (Figure 2; Figure A.7 and Table A.2).


All species
Pipistrellus maderensis
Nyctalus leisleri verrucosus
Plecotus austriacus
Cropland
Laurisilva forest
Production forest
Native woodland
Acacia woodland
Shrubland
Grassland
WaterBodies
Altitude
Altitude*Cropland
Altitude*Laurissilva forest
Altitude*Production forest
Altitude*Native woodland
Altitude*Acacia woodland
Altitude*Shrubland
Altitude*WaterBodies
-4
0
4
8
Coefficient
Spatial Scale (m) ○ 250 ● 500 ● 1000

269

Figure 2 – Poisson regression coefficients for the effects of the landscape cover, altitude, and their interactions on the bat activity of *Pipistrellus maderensis, Nyctalus leisleri verrucosus* and *Plecotus austriacus* in Madeira Island, Portugal. Points represent standardized conditional estimates from predictors presented in minimum adequate models. Error bars represent 95% confidence intervals. For more details on the models' results see Table A.2.

Discussion

Given an increasing human population, a key question is how bat biodiversity can be safeguarded in expanding human-modified landscapes. Owing to their reduced landmass, isolation and high degree of endemic species and subspecies, this challenge is particularly acute in oceanic islands (Conenna et al. 2017). Here, we provide the first insights into the responses of Macaronesian bats to human-induced land-use change. Our results revealed that although all three Madeiran bats can be found across the island's natural and anthropogenic habitats, they exhibit species-specific and scale-dependent responses to altitude and landscape-scale land-use cover.

The adaptability of aerial insectivorous bats to land-use change is largely mediated by functional traits such as echolocation call structure and wing morphology (Davies et al 2016; Jung & Threlfall 2016; Núñez et al 2019; Huang et al 2019). Edge space foragers such as *Pipistrellus maderensis* normally echolocate between 30-60 kHz and have calls with a frequency-modulated beginning followed by a constant-frequency component. They tend to forage along forest edges and meadows, locating their prey against the background. On the other hand, open space foragers such as *Nyctalus leisleri verrucosus* tend to have low frequency, far-reaching calls and narrow wings, thus being well-equipped to capturing prey in open air space. In contrast, narrow space foragers such as *Plecotus austriacus* have broad wings and tendentially hunt in cluttered spaces, capturing prey directly from the vegetation surface (Dietz & Kiefer 2016). Considering these distinct adaptations, it is somewhat unsurprising that the three bat species found in Madeira displayed distinct responses to landscape-scale habitat composition. Our results indicate that the activity of *P. maderensis* is positively associated with forest and shrubland habitats, whereas the activity of *N. l. verrucosus* is negatively associated with Laurisilva and, at least at some spatial scales, positively associated with the less densely vegetated production forest and shrubland habitats. This is largely in agreement with what would be expected based on the species' foraging guilds. Partly due to the reduced number of bat passes (< 1% of the total recorded), the results to *P. austriacus* are not as clear. Nonetheless, the positive association between the species activity and native woodland also agrees with the expectations based on the species' foraging guild.

Pipistrellus maderensis is restricted to the oceanic archipelagos of Madeira, the Canary Islands and possibly Azores (Portugal) (Rocha *in press*). Despite being one of Europe's most threatened bats and exhibiting synanthropic habits, little is known about its ecology and natural history. Our results revealed that the species is widespread throughout Madeira, being particularly associated with shrubland cover. The species' activity was also positively influenced by the cover of cropland across all three spatial scales considered, and with the cover of Laurisilva for the spatial scales of 250 and 500 m. Although no additional studies are available regarding the habitat associations of *P. maderensis,* these results are largely in agreement with findings for other *Pipistrellus* species (e.g., Russo & Jones (2003) and Mendes et al (2017) found *Pipistrellus* spp. to explore a wide array of woodland and open habitats, and Puig-Montserrat et al (2015) found *Pipistrellus pygmaeus* to be highly associated with cropland (rice paddies); but see e.g., Fuentes-Montemayor et al (2011) for an example of a negative association between the activity of *Pipistrellus pipistrellus* and farmland cover). Interestingly, although mounting evidence suggests that *P. kuhlii,* the sister taxa of *P. maderensis*, benefits from urbanization (Ancillotto et al 2016), our results indicate that the activity of *P. maderensis* is likely to be negatively influenced by the landscape-level coverage of built-up areas (for all three spatial scales considered, the activity of *P. maderensis* increased with the percentage coverage Laurisilva, which was negatively correlated with the percentage coverage of built-up areas). This seems to suggest that although *P. maderensis* exhibits synurbic characteristics – e.g., it often forages at streetlights (Rocha *in press*) – its tolerance to urban environments might not be as considerable as that of *P. kuhlii*.

Although the Leisler's bat is distributed across most of mainland Europe, the Near East, and North Africa, the subspecies *Nyctalus leisleri verrucosus* is restricted to Madeira (Boston et al *in press*). *Nyctalus leisleri* has a fast flight but poor maneuverability (aspect ratio 7.0; Norberg & Rayner 1987), and despite typically associated with deciduous and coniferous woodlands, it can also be found in a wide array of natural and anthropogenic open habitats (e.g., water bodies and urban areas) (Boston et al *in press*). Our results indicate that *N. l. verrucosus* is positively associated with production forest but negatively associated with evergreen Laurisilva habitats. Laurisilva has a high density of old trees, a feature typically favoured by the species (Ibáñez et al. 1992). However, its understory might be too cluttered for a species with relatively low maneuverability, which might prefer to forage in more open habitats.

Plecotus austriacus is widespread throughout Europe and has successfully colonized several islands, including the Balearic Islands, Sardinia, Corsica and Madeira (Razgour *in press*). The habitat selection of *P. austriacus* seems to vary throughout its range in mainland Europe, being closely associated with urban areas in Central Europe, but not so much in Southern Europe, where it favours more open landscapes (Gaisler & Bauerova 1985; Horácek et al 2004; Razgour *in press*). In Madeira, we have found that the activity of *P. austriacus* was negatively affected by the landscape-scale coverage of cropland, while being positively influenced by the coverage of production forest and native woodland. This somewhat contrasts to results from Switzerland, in which the species was found to be associated with cropland (orchards and vineyards), while being negatively associated with forest habitats (Rutishauser et al. 2012). However, it is in line with findings from Germany, Belgium, and Catalonia, in which radio-tracked *P. austriacus* positively selected deciduous woodlands and conifer woods (Kiefer 1996; Motte 2011; López-Baucells et al 2021).

Agriculture can affect insectivorous bats through a diversity of pathways, including direct and indirect changes in prey availability and reductions to roosting habitat (Treitler et al 2016; Williams-Guillén et al 2016; Kemp et al 2019). Agriculture-induced shifts to arthropod prey diversity and abundance are largely dictated by pest management regimes and the physical structure of the agricultural habitats that replace native vegetation (Fuentes-Montemayor et al 2011, 2013; Puig-Montserrat et al 2021). Unfortunately, due to the absence of data describing pesticide use and the physical structure of local-scale vegetation structure (e.g., tree density, canopy cover and vegetation clutter), we were unable to investigate how these might have affected the responses of bat activity to landscape-scale habitat composition. As previous studies suggest that vegetation structure might mediate or even act as a better predictor of the activity of forest-dwelling aerial insectivorous bats than landscape-level characteristics (Erickson & West 2003; Charbonnier et al. 2016; Froidevaux et al 2021 but see Froidevaux et al 2017), future studies assessing how the activity of island bats is affected by land-use features should aim to disentangle the effects of local- and landscape-scale characteristics.

Altitude had a negative influence on the activity of *Plecotus austriacus* and *Nyctalus leisleri verrucosus* but, contrary to our expectations, it displayed a less pronounced effect on the activity of *Pipistrellus maderensis*. Numerous taxa are predicted to shift their distributional ranges to higher elevations in response to climate change (Freeman et al 2021) and, for many bats species, climate and land-use change are anticipated to act synergistically, leading to a considerable reduction of environmental suitability across the species' range (Zamora-Gutierrez et al 2018). The contrasting responses of the three Madeiran bat species to altitude may thus suggest that the different species might react differently to future environmental shifts associated with climate change in Madeira.

It is important to note that the fieldwork for this study spanned a short period of time (ca. two months). We recognize that bat activity may change substantially with lunar phase, season and within years (Barlow et al 2015; Ferreira et al 2017; Rocha et al 2017b; Appel et al 2021) and as such our research does not capture any temporal variability in the response of bat activity to land-use. Furthermore, sound propagation can be attenuated by vegetation and aerial insectivorous bats - including the species found in Madeira - emit lower intensity echolocation calls in cluttered environments (Teixeira and Jesus 2009). The interpretation of our results should therefore consider that we have not tested differences in ultrasound attenuation between the sites in which the recorders where deployed and thus it is possible that the strength of the relationships detected may be either overestimated (in open habitats) or underestimated (in cluttered habitats). Nonetheless, most of the significant relationships detected are ecologically relevant and fit with expectations of the species echolocation and morphological characteristics. Additionally, our analyses did not account for eventual differences in detectability between the three species considered. Here, we highlight that *Plecotus austriacus* produces low intensity echolocation calls*,* which can only be detected from short (ca. < 5 m) distances (Russ 2012; Razgour *in press*). As such, our results should not be used to compare the three species occurring in Madeira in terms of their rarity.

Conclusions

Most island endemic bats suffer from a chronic lack of knowledge that can support evidence-based conservation (Conenna et al 2017; Oleksy et al 2018). However, the growing availability of affordable autonomous ultrasound recorders is considerably expanding our ability to conduct bat ecological research (Hill et al. 2018; Gibb et al. 2019). Low-cost, open-source sensors such as AudioMoths allow for efficient, non-invasive acoustic surveys and are particularly well-suited to investigate aerial insectivorous bats that commonly evade capture (Gibb et al. 2019). Here, we show that such detectors can effectively survey insular bat communities and provide valuable information about poorly known island endemic bats. The use of passive acoustic methods to survey bats in oceanic islands such as Madeira further benefits from the typically low number of echolocating bat species found in islands, when compared to mainland ecosystems. This will hopefully facilitate the use and development of classifiers for acoustic identification of insular bats (e.g., Walters et al 2012; Stathopoulos et al 2018; Mac Aodha et al 2018; López-Baucells et al 2019), which combined with low-cost autonomous ultrasound recorders can be used to monitor temporal changes in the activity and distribution of island bat species.

Appendices

Figure A.1 Photos demonstrating how Audiomoths were deployed during fieldwork.

Figure A.2 Total bat activity recorded for each bat species per sampling grid cell.

Figure A.3 Variation in bat activity throughout the night for all species.

Figure A.4 Scatter plot with regression line for all bat species.

Figure A.5 Scatter plot with regression line for Pipistrellus maderensis.

Figure A.6 Scatter plot with regression line for Nyctalus leisleri verrucosus.

Figure A.7 Scatter plot with regression line for Plecotus austriacus.

Table A.1 Description of land-use categories

Table A.2 Summary results of the minimum adequate models investigating relationships between bat activity and landscape cover.

Table A.3 Results of Moran's I test for the residuals of the full and minimal adequate models

Table A.4 Results of overdispersion test for the residuals of the full and minimal adequate models.

Table A.5 Results of zero-Inflation test for the residuals of the full and minimal adequate models.

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References

Ancillotto, L., Tomassini, A., & Russo, D. (2016). The fancy city life: Kuhl's pipistrelle, *Pipistrellus kuhlii*, benefits from urbanisation. *Wildlife Research, 42*, 598-606.

Appel, G., López-Baucells, A., Rocha, R., Meyer, C. F. J., & Bobrowiec, P.E.D. (2021). Habitat disturbance trumps moonlight effects on the activity of tropical insectivorous bats. *Animal Conservation*.

Barlow, K. E., Briggs, P. A., Haysom, K. A., Hutson, A. M., Lechiara, N. L., Racey, P. A., Walsh, A. L., & Langton, S. D. (2015). Citizen science reveals trends in bat populations: The National Bat Monitoring Programme in Great Britain. *Biological Conservation, 182*, 14-26.

Boston E. S. M., Dechmann, D. K. N & Ruczynski, I. (*in press*) Leisler's Noctule *Nyctalus leisleri* (Kuhl, 1817) in: K. Hackländer & F.E. Zachos (eds) Handbook of the Mammals of Europe. Springer International Publishing.

Brooks M. E., Kristensen K., van Benthem K. J., Magnusson A., Berg C. W., Nielsen A., Skaug H.J., Maechler M., & Bolker B.M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, 9, 378–400.

Carvalho, A. M. & Brandão, J. M. (1991). Geologia do Arquipélago da Madeira. Museu Nacional de História Natural da Universidade de Lisboa, Lisboa, 170 pp.

Charbonnier, Y., Gaüzère, P., van Halder, I., Nezan, J., Barnagaud, J.-Y., Jactel, H., & Barbaro, L. (2016). Deciduous trees increase bat diversity at stand and landscape scales in mosaic pine plantations. *Landscape Ecology, 31*, 291-300.

Claudino-Sales, V. (2019). Laurisilva of Madeira, Portugal. In Coastal World Heritage Sites (pp. 243-249). Springer, Dordrecht.

Clarin, B.-M., Bitzilekis, E., Siemers, B. M., Goerlitz, H. R. (2014). Personal messages reduce vandalism and theft of unattended scientific equipment. *Methods Ecology and Evolution* 5, 125–131.

Conenna, I., Rocha, R., Russo, D., & Cabeza, M. (2017). Insular bats and research effort: a review of global patterns and priorities. *Mammal Review* 47, 169–182.

Davies, T. E., Ruzicka, F., Lavery, T., Walters, C. L., & Pettorelli, N. (2016). Ultrasonic monitoring to assess the impacts of forest conversion on Solomon Island bats. *Remote Sensing in Ecology and Conservation, 2*, 107-118.

Denzinger, A., & Schnitzler, H.-U. (2013). Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology, 4*.

Dietz, C., & Kiefer, A. (2016). *Bats of Britain and Europe*: Bloomsbury Publishing.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitao, P. J., & Münkemüller, T. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*, 27-46.

Erickson, J. L., & West, S. D. (2003). Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. *Biological Conservation, 109*, 95-102.

Ferreira, D. F., Rocha, R., López-Baucells, A., Farneda, F. Z., Carreiras, J. M. B., Palmeirim, J. M., & Meyer, C. F. J. (2017). Season-modulated responses of Neotropical bats to forest fragmentation. *Ecology and Evolution*, 1-13.

Fleming, T. H., & Racey, P. A. (2009). *Island bats: evolution, ecology, and conservation*: University of Chicago Press.

Florencio, M., Patiño, J., Nogué, S., Traveset, A., Borges, P. A. V., Schaefer, H., Amorim, I. R., Arnedo, M., Ávila, S. P., Cardoso, P., de Nascimento, L., Fernández-Palacios, J. M., Gabriel, S. I., Gil, A., Gonçalves, V., Haroun, R., Illera, J. C., López-Darias, M., Martínez, A., Martins, G. M., Neto, A. I., Nogales, M., Oromí, P., Rando, J. C., Raposeiro, P. M., Rigal, F., Romeiras, M. M., Silva, L., Valido, A., Vanderpoorten, A., Vasconcelos, R., & Santos, A. M.

C. (2021). Macaronesia as a Fruitful Arena for Ecology, Evolution, and Conservation Biology. *Frontiers in Ecology and Evolution*, *9*.

Florens, F. B. V., Baider, C., Marday, V., Martin, G. M. N., Zmanay, Z., Oleksy, R., Krivek, G., Vincenot, C. E., Strasberg, D., & Kingston, T. (2017). Disproportionately large ecological role of a recently mass-culled flying fox in native forests of an oceanic island. *Journal for Nature Conservation, 40*, 85-93.

Freeman, B. G., Song, Y., Feeley, K. J., & Zhu, K. (2021). Montane species track rising temperatures better in the tropics than in the temperate zone. *Ecology letters, 24,* 1697-1708.

Froidevaux, J. S., Barbaro, L., Vinet, O., Larrieu, L., Bas, Y., Molina, J., Calatayud, F., & Brin, A., (2021). Bat responses to changes in forest composition and prey abundance depend on landscape matrix and stand structure. *Scientific Reports*, *11*, 1-13.

Froidevaux, J. S., Louboutin, B., & Jones, G., (2017). Does organic farming enhance biodiversity in Mediterranean vineyards? A case study with bats and arachnids. *Agriculture, Ecosystems & Environment*, *249*, 112-122.

Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J. M., & Park, K. J. (2013). Fragmented woodlands in agricultural landscapes: The influence of woodland character and landscape context on bats and their insect prey. *Agriculture, Ecosystems & Environment, 172*, 6-15.

Fuentes-Montemayor, E., Goulson, D., & Park, K. J. (2011). Pipistrelle bats and their prey do not benefit from four widely applied agri-environment management prescriptions. *Biological Conservation, 144*, 2233-2246.

Fuentes-Montemayor, E., Watts, K., Macgregor, N. A., Lopez-Gallego, Z., & Park, K. J. (2017). Species mobility and landscape context determine the importance of local and landscape-level attributes. *Ecological Applications*, *27*, 1541-1554.

Gaisler. J., & Bauerova, Z. (1985). The life of bats in a city. *Myotis* 23:209–215

Gibb, R., Browning, E., Glover-Kapfer, P., & Jones, K. E. (2019). Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods in Ecology and Evolution, 10*, 169-185.

Hartig, F. (2020). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.3.3.0. https://CRAN.R-project.org/package=DHARMa

Heim, O., Treitler, J. T., Tschapka, M., Knörnschild, M., & Jung, K. (2015). The importance of landscape elements for bat activity and species richness in agricultural areas. *PloS One*, *10*, e0134443.

Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K. and Nowosad, J. (2019). landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography*, *42*, 1648-1657.

Hill, A. P., Prince, P., Piña Covarrubias, E., Doncaster, C. P., Snaddon, J. L., & Rogers, A. (2018). AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods in Ecology and Evolution, 9*, 1199-1211.

Hijmans, R. J., L. Guarino, C. Bussink, P. Mathur, M. Cruz, Barrentes I., & Rojas E. (2004). DIVA-GIS. Vsn. 5.0. A geographic information system for the analysis of species distribution data. Manual available at http://www.diva-gis.org

Horácek, I., Bogdanowicz, W., & Dulid, B. (2004). *Plecotus austriacus* (Fischer, 1829) — Graues 1281 36. Langohr. In: Krapp F (ed) Handbuch der Säugetiere Europas, 4th edn. Wiebesheim: 1282 Aula-Verlag, pp 1001–1049.

Huang, J. C.-C., Rustiati, E. L., Nusalawo, M., & Kingston, T. (2019). Echolocation and roosting ecology determine sensitivity of forest-dependent bats to coffee agriculture. *Biotropica, 51,* 757–768.

Ibáñez, C., Guillén, A., Fernández, R., Pérez, J. L., & Guerrero, S. (1992). Iberian distribution of some little known bat species.

IUCN (2021). The IUCN Red List of Threatened Species. http://www.iucnredlist.org

Jesus, J., Teixeira, S., Teixeira, D., Freitas, T., & Russo, D. (2009). Vertebrados terrestres autóctones dos Arquipélagos da Madeira e Selvagens. Direcção Regional de Ambiente. Funchal.

Jones, G., & Teeling, E. C. (2006). The evolution of echolocation in bats. *Trends in Ecology & Evolution, 21*, 149-156.

Jones, K. E., Mickleburgh, S. P., Sechrest, W., & Walsh, A. L. (2010). 16. Global Overview of the Conservation of Island Bats: Importance, Challenges, and Opportunities. *Island Bats*, 496-530.

Jung, K., & Threlfall, C. G. (2016). Urbanisation and its effects on bats—a global meta-analysis. In *Bats in the Anthropocene: conservation of bats in a changing world* (pp. 13-33): Springer, Cham.

Kemp, J., López-Baucells, A., Rocha, R., Wangensteen, O. S., Andriatafika, Z., Nair, A., & Cabeza, M. (2019). Bats as potential suppressors of multiple agricultural pests: A case study from Madagascar. *Agriculture, Ecosystems & Environment, 269*, 88-96.

Kiefer A (1996) Untersuchungen zu Raumbedarf und lnteraktionen von Populationen des Grauen Langohrs (*Plecotus austriacus* Fischer, 1829) im Naheland. Johannes Gutenberg Universitat Mainz

López-Baucells, A., Flaquer, C., Mas, M., Pons, P., & Puig-Montserrat, X. (2021). Recurring fires in Mediterranean habitats and their impact on bats. *Biodiversity and Conservation*. 30, 385–402.

López-Baucells, A., Torrent, L., Rocha, R., Bobrowiec, P. E. D., Palmeirim, J. M-, & Meyer, C. F. J. (2019). Stronger together: Combining automated classifiers with manual post-validation optimizes the workload vs reliability trade-off of species identification in bat acoustic surveys. *Ecological Informatics, 49*, 45-53.

López-Bosch, D., Rocha, R., López-Baucells, A., Wang, Y., Si, X., Ding, P., Gibson, L. & Palmeirim, A. F. (2021). Passive acoustic monitoring reveals the role of habitat affinity in sensitivity of sub-tropical East Asian bats to fragmentation. *Remote Sensing in Ecology and Conservation*.

Mac Aodha, O., Gibb, R., Barlow, K. E., Browning, E., Firman, M., Freeman, R., Harder, B., Kinsey, L., Mead, G. R., Newson, S. E., Pandourski, I., Parsons, S., Russ, J., Szodoray-Paradi, A., Szodoray-Paradi, F., Tilova, E., Girolami, M., Brostow, G., & Jones, K. E. (2018). Bat detective—Deep learning tools for bat acoustic signal detection. *PLOS Computational Biology, 14*, e1005995.

Massetti, A., Sequeira, M. M., Pupo, A., Figueiredo, A., Guiomar, N., & Gil, A. (2016). Assessing the effectiveness of RapidEye multispectral imagery for vegetation mapping in Madeira Island (Portugal). European Journal of Remote Sensing, *49*, 643–672.

McGill, B. (2015). Biodiversity: Land use matters. *Nature, 520*, 38-39.

Mendes, E. S., Fonseca, C., Marques, S. F., Maia, D., & Ramos Pereira, M. J. (2017). Bat richness and activity in heterogeneous landscapes: guild-specific and scale-dependent? *Landscape Ecology, 32*, 295-311.

Motte, G. (2011). Etude comparée de l'écologie de deux espèces jumelles de Chiroptères (Mammalia : Chiroptera) en Belgique: l'oreillard roux (*Plecotus auritus*) (Linn., 1758) et l'oreillard gris (*Plecotus austriacus*) (Fischer, 1829). University of Liège

Newson, S.E., Evans, H.E., & Gillings, S. (2015). A novel citizen science approach for large-scale standardised monitoring of bat activity and distribution, evaluated in eastern England. Biological Conservation, *191*, 38-49.

Nogué, S., Santos, A. M. C., Birks, H. J. B., Björck, S., Castilla-Beltrán, A., Connor, S., de Boer, E. J., de Nascimento, L., Felde, V. A., Fernández-Palacios, J. M., Froyd, C. A., Haberle, S. G., Hooghiemstra, H., Ljung, K., Norder, S. J., Peñuelas, J., Prebble, M., Stevenson, J., Whittaker, R. J., Willis, K. J., Wilmshurst, J. M., & Steinbauer, M. J. (2021). The human dimension of biodiversity changes on islands. *Science, 372*, 488.

Norberg, U. M., Rayner, J. M. V., & Lighthill, M. J. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 316*, 335-427.

Norder, S. J., de Lima, R. F., de Nascimento, L., Lim, J. Y., Fernández-Palacios, J. M., Romeiras, M. M., Elias, R. B., Cabezas, F. J., Catarino, L., Ceríaco, L. M. P., Castilla-Beltrán, A., Gabriel, R., de Sequeira, M. M., Rijsdijk, K. F., Nogué, S., Kissling, W. D., van Loon, E. E., Hall, M., Matos, M., & Borges, P. A. V. (2020). Global change in microcosms: environmental and societal predictors of land cover change on the Atlantic Ocean Islands. *Anthropocene*, *100242*.

Núñez, S. F., López-Baucells, A., Rocha, R., Farneda, F. Z., Bobrowiec, P. E. D., Palmeirim, J. M., & Meyer, C. F. J. (2019). Echolocation and Stratum Preference: Key Trait Correlates of Vulnerability of Insectivorous Bats to Tropical Forest Fragmentation. *Frontiers in Ecology and Evolution, 7*.

Oleksy, R. Z., Ayady, C. L., Tatayah, V., Jones, C., Froidevaux, J. S. P., Racey, P. A., & Jones, G. (2018). The impact of the Endangered Mauritian flying fox Pteropus niger on commercial fruit farms and the efficacy of mitigation. *Oryx, 55*, 114-121.

Perry, R. W., Thill, R. E., & Leslie Jr, D. M. (2008). Scale-dependent effects of landscape structure and composition on diurnal roost selection by forest bats. *The Journal of Wildlife Management, 72*, 913-925.

Pinto, N., & Keitt, T. H. (2008). Scale-dependent responses to forest cover displayed by frugivore bats. *Oikos, 117*, 1725-1731.

Puig-Montserrat, X., Flaquer, C., Gómez-Aguilera, N., Burgas, A., Mas, M., Tuneu, C., Marquès, E., & López-Baucells, A (2015). Bats actively prey upon mosquitoes and other deleterious insects in rice paddies: Potential impact on human health and agriculture. *Pest Management Science*, *76*, 3759-3769.

Puig-Montserrat, X., Mas, M., Flaquer, C., Tuneu-Corral, C., & López-Baucells, A. (2021). Benefits of organic olive farming for the conservation of gleaning bats. *Agriculture, Ecosystems & Environment, 313*, 107361.

Put, J. E., Fahrig, L., & Mitchell, G. W. (2019). Bats respond negatively to increases in the amount and homogenization of agricultural land cover. *Landscape Ecology, 34*, 1889-1903.

QGIS.org (2021). QGIS Geographic Information System. QGIS Association. http://www.qgis.org

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Razgour, O. (*in press*) Grey long-eared bat, *Plecotus austriacus*, Fischer, 1829 in: K. Hackländer & F.E. Zachos (eds) Handbook of the Mammals of Europe. Springer International Publishing

Rocha, R. (*in press*) Madeiran pipistrelle *Pipistrellus maderensis* (Dobson, 1878) in: K. Hackländer & F.E. Zachos (eds) Handbook of the Mammals of Europe. Springer International Publishing

Rocha, R., López-Baucells, A., Farneda, F. Z., Groenenberg, M., Bobrowiec, P. E. D., Cabeza, M., Palmeirim, J. M., & Meyer, C. F. J. (2017a). Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects. *Landscape Ecology, 32*, 31-45.

Rocha, R., Ovaskainen, O., López-Baucells, A., Farneda, F. Z., Ferreira, D. F., Bobrowiec, P. E., Cabeza, M., Palmeirim, J. M. & Meyer, C. F. (2017b). Design matters: an evaluation of the impact of small man-made forest clearings on tropical bats using a before-after-control-impact design. *Forest Ecology and Management*, *401*, 8-16.

Russ, J. (2012). British Bat Calls. A Guide to Species Identification. Pelagic Publishing, Exeter

Russell, J. C., & Kueffer, C. (2019). Island Biodiversity in the Anthropocene. *Annual Review of Environment and Resources, 44*, 31-60.

Russo, D. and Jones, G. (2003), Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. *Ecography*, *26*, 197-209.

Rutishauser, M. D., Bontadina, F., Braunisch, V., Ashrafi, S., & Arlettaz, R. (2012). The challenge posed by newly discovered cryptic species: disentangling the environmental niches of long-eared bats. *Diversity and Distributions, 18*, 1107-1119.

Spatz, D. R., Zilliacus, K. M., Holmes, N. D., Butchart, S. H. M., Genovesi, P., Ceballos, G., Tershy, B. R., & Croll, D. A. (2017). Globally threatened vertebrates on islands with invasive species. *Science Advances, 3*.

Stathopoulos, V., Zamora-Gutierrez, V., Jones, K. E., & Girolami, M. (2018). Bat echolocation call identification for biodiversity monitoring: a probabilistic approach. *Journal of the Royal Statistical Society: Series C (Applied Statistics), 67*, 165-183.

Teixeira, S., & Jesus, J. (2009). Echolocation calls of bats from Madeira Island: acoustic characterization and implications for surveys. *Acta Chiropterologica, 11*, 183-190.

Tershy, B. R., Shen, K.-W., Newton, K. M., Holmes, N. D., & Croll, D. A. (2015). The Importance of Islands for the Protection of Biological and Linguistic Diversity. *Bioscience, 65*, 592-597.

Torrent, L., López-Baucells, A., Rocha, R., Bobrowiec, P.E.D. & Meyer, C.F.J. (2018). The importance of lakes for bat conservation in Amazonian rainforests: an assessment using autonomous recorders. Remote Sens Ecol Conserv, 4: 339-351.

Treitler, J.T., Heim, O., Tschapka, M., & Jung, K. (2016). The effect of local land use and loss of forests on bats and nocturnal insects. *Ecology and Evolution*, *6*, 4289-4297

Tuneu-Corral, C., Puig-Montserrat, X., Flaquer, C., Mas, M., Budinski, I., & López-Baucells, A. (2020). Ecological indices in long-term acoustic bat surveys for assessing and monitoring bats' responses to climatic and land-cover changes. *Ecological Indicators*, *110*, 105849.

Walters, C. L., Freeman, R., Collen, A., Dietz, C., Brock Fenton, M., Jones, G., Obrist, M. K., Puechmaille, S. J., Sattler, T., Siemers, B. M., Parsons, S., & Jones, K. E. (2012). A continental-scale tool for acoustic identification of European bats. *Journal of Applied Ecology, 49*, 1064-1074.

Whittaker, R. J., & Fernández-Palacios, J. M. (2007). *Island biogeography: ecology, evolution, and conservation*: Oxford University Press.

Williams-Guillén, K., Olimpi, E., Maas, B., Taylor, P. J., & Arlettaz, R. (2016). Bats in the Anthropogenic Matrix: Challenges and Opportunities for the Conservation of Chiroptera and Their Ecosystem Services in Agricultural Landscapes. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 151-186). Cham: Springer International Publishing.

Zamora-Gutierrez, V., Pearson, R. G., Green, R. E., & Jones, K. E. (2018). Forecasting the combined effects of climate and land use change on Mexican bats. *Diversity and Distributions, 24*, 363-374.