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Effects of climate change on the distribution of indigenous species in oceanic islands (Azores)

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Abstract Oceanic islands host a high proportion of the world's endemic species. Many such species are at risk of extinction owing to habitat degradation and loss, biological invasions and other threats, but little is known about the effects of climate change on island native biodiversity. The Azorean archipelago provides a unique opportunity to study species-climate-change relationships. We used ensemble forecasting to evaluate the current and future distribution of well-studied endemic and native bryophytes (19 species), endemic vascular plants (59 species) and endemic arthropods (128 species), for two of the largest Azorean Islands, Terceira and São Miguel. Using a Regional Climate Model (CIELO), and assuming the

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extreme scenario RCP8.5, we examined changes in the potential distributions of the species and possible loss of climate space for them. Models projected that 23 species (11 %) could lose all adequate climate on either one or both islands. Five additional species were projected to lose ≥90 % of climate space. In total, 90 % of the species were projected to lose climate space: 79 % of bryophytes, 93 % of vascular plants and 91 % of arthropods. We also found for vascular plants and arthropods a tendency for upward shift in altitude in their suitable climate space, while for bryophytes the shift was towards the coastal areas. Our results have profound implications for future conservation priorities on islands, such as for the redrawing of conservation borders of current protected areas.

Keywords Climate change · Azores · Oceanic Islands · Ensemble modelling · Species distribution

1 Introduction

Oceanic islands host a high proportion of the world's endemic species, many of which are threatened with extinction as a consequence of human intervention (Cardoso et al. 2010; Triantis et al. 2010; Terzopoulou et al. 2015). Islands are thus places where the 'biodiversity crisis' is ominous and requires most urgent action (e.g. Whittaker and Fernández-Palacios 2007). Species diversity in small islands is very vulnerable to climate change because of the space limitation, along with the human pressure on the existing limited resources (Heller and Zavaleta 2009; Maharaj and New 2013). In terms of large-scale climatic changes and the comparably small spatial extent of islands, the opportunities for island species to shift their ranges in climate-relevant latitudinal (or longitudinal) extents and to maintain population size and genetic variability are restricted (Harter et al. 2015). Oceanic islands generally have lower overall species numbers per unit area (Whittaker and Fernández-Palacios 2007) but show higher percentages of endemism than mainland areas (Kier et al. 2009). Consequently, the limited insular areas host a high fraction of global biodiversity (Kreft et al. 2008; Kier et al. 2009). Biodiversity has been identified as a key determinant for the quality and functioning of ecosystems. Therefore, research efforts are necessary to set the scientific base for robust assessments of ecological climate change impacts on islands (biodiversity hotspots) to enable knowledge-based prioritisation of conservation and mitigation measures (Harter et al. 2015).

Reported threats to island biodiversity tend to ignore climate change effects, and their synergies with other threatening factors (but see Hortal et al. 2005; Jiménez-Valverde et al. 2009). One reason for this is that global circulation models (GCMs), the main tool for generating climate change scenarios, cannot simulate the small scale topographic and coastal features of those islands, which are nevertheless responsible for most of their observed microclimate variation. Current GCMs typically have a horizontal resolution of 100–500 km. This type of scale is too large for small islands and so it renders the task of applying climate change models difficult. The fitting of regional climate Models (RCM's) and further statistical (empirical or dynamical) downscaling techniques are, therefore, required to produce more detailed and realistic representations of climate features, including orographic precipitation and other sub-regional variations not captured by the GCMs (Fowler et al. 2007; Spak et al. 2007). The CIELO (Clima Insular à Escala LOcal) model is an example of a RCM that has already been used for modelling current species distributions in islands (e.g. Hortal et al. 2005, 2010; Jiménez-Valverde et al. 2009; Aranda et al. 2011; Fattorini et al. 2012). It has also been successful in studies of diversity patterns (e.g. Borges et al. 2006;

Boieiro et al. 2013; Florencio et al. 2013) for arthropods, bryophytes and vascular plants in both Azores and Madeira archipelagos.

The Azores archipelago, a set of nine medium-small islands in the North Atlantic Ocean, has a few striking natural features (like laurisilva forest, hot springs, lagoons, volcanic peaks), combining a high relative humid and temperate climate with volcanic shaped geomorphology, which allowed the development of a characteristic diversity of species. The single greatest estimated impact of global climate change for the Azores may be the change in annual precipitation distribution, with wetter winters while the other seasons become drier (Santos et al. 2004). This could have a significant impact on the islands' water resources.

Most studies of climate change impact on biodiversity have focused mainly on mammals, birds, reptiles, amphibians and seed plants (e.g. Bellard et al. 2012; Pacifici et al. 2015). Some studies focused or included invertebrates (e.g. Wilson et al. 2005; Jiménez-Valverde and Lobo 2007; Leroy et al. 2013; Martin et al. 2013; Moo-Llanes et al. 2013) and only a few have studied bryophytes (e.g. Bates and Preston 2011; Sérgio et al. 2011). Bryophytes are a potentially informative group to consider in climate change studies, since their physiology and ecology are distinct from vascular plants (ability to withstand drought – poikilohidry – while being dependent of environmental conditions due to the lack of a root system). We are not aware of any studies that have used arthropods, bryophytes and vascular plants together, and even separate there have been very few studies involving small islands. These groups are important biodiversity and environmental quality indicators (e.g. Gaspar et al. 2011; Aranda et al. 2014) because they reflect disturbances, human impacts, and environmental or global changes to the environment, and are therefore an excellent choice for studying the effects of climate change on biodiversity in small islands.

In this study we aim to quantify and analyse for the first time in a Macaronesian archipelago the potential effects of climate change on shifts of suitable climate space of well-studied indigenous species of three taxonomic groups—bryophytes, vascular plants and arthropods—for the islands of Terceira and São Miguel in the Azores archipelago, using regional climatic models, adapted to the topography and climate of the islands.

2 Materials and methods

2.1 Study area

The Azorean archipelago stretches out over 615 km in the North Atlantic Ocean (37–40 °N, 25–31 °W), 1584 km west of southern Europe and 2150 km east of the North American continent (Online Resource 1). It comprises nine main islands of recent volcanic origin, distributed in three groups: the western group of Corvo and Flores; the central group of Faial, Pico, Graciosa, São Jorge, and Terceira; and the eastern group of São Miguel and Santa Maria. Distribution data were collected from all the islands in the archipelago. The climatic projections were applied to the islands of Terceira and São Miguel, two of the largest, better studied, more populated, and economically, the most important islands of the archipelago.

2.2 Species data

Records of the species presence on islands were collected from a range of sources using ATLANTIS 3.1. This is a database purposefully built for biodiversity data storage in islands (see Borges et al. 2010), including a thorough review of the literature and field work done in the Azores (see http://www.atlantis.angra.uac.pt/atlantis). The database stores detailed information about the taxonomy and the distribution of all species on the geographical areas of interest. Data input is complex and implies validation by taxonomic experts. The biological data is available at 500 m ×500 m cells. We assembled data from all the islands of the archipelago in order to get the largest possible range of climatic conditions where the species were shown to occur.

We analysed bryophytes (Divisions Bryophyta and Marchantiophyta), vascular plants (Divisions Lycopodiophyta, Pteridophyta and Magnoliophyta) and arthropods (mostly from the orders Araneae, Diptera, Lepidoptera, and Coleoptera) since their records were acquired through extensive sampling. A total of 19 species of bryophytes, 59 species of vascular plants, and 128 species of arthropods were used for the analysis (Online Resource 2). The chosen species were indigenous (native and endemic) species. These were the most abundant species on the islands, as only 1 % of all bryophyte, vascular plant and arthropod species in the ATLANTIS data base had four or more occurrences (out of approximately 100,000 number of records).

2.3 Climate data

To produce a downscaled climatology of the Azores region we used the CIELO Model (Azevedo 1996; Azevedo et al. 1998, 1999) to obtain the climatic data. This model allowed us to obtain a high number of climatic variables related with temperature, rainfall, relative humidity and solar radiation. The CIELO model (Azevedo et al. 1998, 1999) is a simple layer model, based on the transformations experienced by an air mass crossing over a mountain, and simulates the evolution of an air parcel's physical properties starting from the sea level up to the mountain. This model has already been used to downscale climate change scenarios for the twenty-first century over islands (e.g. in the Azores, Terceira and São Miguel Islands) (Miranda et al. 2002; Santos et al. 2004). For this work, the CIELO model ran based on the Representative Concentration Pathways (RCPs) scenarios from the fifth Assessment Report (IPCC-AR5 2014). In this work we chose deliberately the "worst case scenario" RCP8.5 as a precaution strategy based on the historical and still actual trend on the greenhouse emissions which follows the scenario that leads to a radiative forcing of 8.5 W/m2 by the year 2100 (Peters et al. 2013; IPCC-AR5 2014). The spatial resolution of the climatic model is of 100 m × 100 m that comes from the Digital Elevation Model used as territory boundary, later resampled at 500 × 500 m to match species data.

2.4 Bioclimatic modelling

Bioclimatic envelope models use associations between aspects of climate and species' occurrences to estimate the conditions that are suitable to maintain viable populations. Once bioclimatic envelopes are characterized, they can be applied to a variety of questions in ecology, evolution, and conservation (Araújo and Peterson 2012). An ensemble of bioclimatic envelope models (BEM) (Araújo and New 2007) were generated for each species considered (14 models per species, to maximize the number of projections). The ensemble included projections from the following methods: 1) Mahalanobis distance (Mahalanobis 1936); 2) Euclidean distance; 3) Gower distance; 4) Ecological Niche Factor Analysis (Hirzel et al. 2002); 5) BIOCLIM (Kriticos et al. 2012); 6) Maximum Entropy (Phillips et al. 2006); 7)

Genetic Algorithm for Rule Prediction (Stockwell and Peters 1999); 8) Generalised Linear Models; 9) Generalised Additive Models; 10) Generalized Boosting Models; 11) Random Forests (Breiman 2001); 12) Multiple Additive Regression Splines (Friedman 1991); 13) Artificial Neural Networks; and 14) Flexible Discriminant Analysis (Hastie et al. 1994).

For each species, data were randomly divided into calibration and validation sets comprising 80 and 20 % of the species' range, respectively, and the procedure was repeated 10 times, maintaining the observed prevalence of species in each partition (i.e. for presence/absence methods the analyses were conducted using a random sample of 80 % of cells both inside and outside species' range). Thus, each calibration dataset was used to project species suitable climate space, according to the 14 BEM models. We fitted the 14 BEM's and projected species suitable climate spaces for baseline and future climates. The computer software - BioEnsembles - in which all these methods were implemented was used. This software was designed to optimize and take advantage of high-speed parallel processing, both within (multi-processors computers) and between (grid architecture) computers (Diniz-Filho et al. 2009). The True Skill Statistics (TSS) (Allouche et al. 2006), varying between −1 and 1, was used as a fit statistic. It was calculated for each model based on the confusion matrix expressing matches and mismatches of observed and predicted occurrences in the validation data set. This matrix was computed after using Receiver Operation Characteristic curves and the Area Under the Curve to convert continuous predictions into presence-absence. Models with TSS smaller than zero were discarded. Finally, this combination of models generates an ensemble-based frequency of species climate space and species are considered to occur in a given cell if at least 50 % of the models predict its occurrence there (i.e. a majority consensus rule) (Araújo et al. 2005, 2006). The range of uncertainties obtained with the fourteen modelling techniques was calculated and community patterns derived from the models were explored using geographical information systems (GIS).

2.5 Assessing climate change impacts on species' projected distributions

The maps of distribution obtained from the BIOENSEMBLES software were for two time periods: 1961–1990 and 2080–2099. For each species these were analysed to ascertain of the shifts in climate space. The grid maps were then overlaid using the DIVA-GIS software (Hijmans et al. 2004), creating maps of cumulative number of species per cell, for each taxonomic group and for each time period. The grids of all species were summed to yield a 'total count' grid for the time periods – within which the value of each cell represented the total number of species for which climate was projected to be suitable within the island. A difference map was created to determine the change in diversity per cell.

3 Results

A total of 206 species from the different taxonomic groups were analysed. Of these, 23 species (11 %) were projected to completely lose climate space on either one or both of the islands (Table 1) and five species are projected to lose ≥90 % of their climate space. In total 90 % of the species decrease their climate space, including 79 % of bryophytes, 93 % of vascular plants, and 91 % of arthropods. On the other hand, according to model projections, eight species increased their climate space on one or both islands in over 40 % of the distribution area (Table 2).

For both islands there is a decrease in the number of species per cell from the 1961–90 to the 2080–99 time period (Figs. 1 and 3). Across taxa, species richness increases as you go upslope towards the centre of the islands (Figs. 1 and 3). The highest decrease occurs on the coastal areas for vascular plants (Fig. 2) and arthropods (Fig. 3). An increase in number of species per cell is much less common, though seen in a few cases on São Miguel (e.g., coastal areas for bryophytes dark pink shading in Fig. 1).

For bryophytes, in São Miguel there is an increase of the number of species per cell in the coastal area (Fig. 1). In this island, 54 % of the cells have a decrease between 10 to 30 % in number of bryophyte species, while 11 % of the cells have no change, and 13 % see an increase (Fig. 1). In Terceira Island, a comparable proportion (62 % of the cells) is predicted to lose the same number of species (Fig. 1). Nevertheless, only 1 % of the cells will experience an increase of the number of species, while 6 % should present no change, which means a larger

Table 1 Table of species whose suitable climate space diminishes over 90 % or disappear between the 1961–90 and 2080–99 time periods for the three taxonomic groups

		Percentage of suitable climate space loss	
Taxonomic group	Species/Island	Terceira	São Miguel
Bryophytes	*Leucodon canariensis*	0	100
	Leucodon treleasei	100	100
	Sphagnum nitidulum	90	0
Vascular plants	*Azorina vidalii*	100	100
	Daucus carota	12	96
	Euphorbia azorica	100	100
	Euphrasia grandiflora	100	0
	Gaudinia coarctata	100	100
	Myosotis maritima	100	0
	Tolpis succulenta	100	100
Arthropods	*Aeolus melliculus moreleti*	28	96
	Agyneta rugosa	0	100
	Aphaniosoma azoricum	100	89
	Aphrosylus argyreatus	100	100
	Azorastia minutissima	0	100
	Coenosia testacea azorica	100	85
	Conocephalus chavesi	100	88
	Drouetius oceanicus oceanicus	100	0
	Ensina azorica	21	100
	Euconnus azoricus	100	0
	Eudarcia atlantica	100	0
	Graphania granti	98	59
	Microcreagrella caeca caeca	100	100
	Neomariania oecophorella	98	64
	Orchestia chevreuxi	100	13
	Philygria cedercreutzi	100	0
	Sciapus glaucescens brioni	0	100
	Sepsis nephodes	100	0

Table 2 Table of species whose suitable climate space increases over 40 % from the 1961–90 to the 2080–99 time period for the three taxonomic groups

		Percentage of suitable climate space gain	
Taxonomic group	Species	Terceira	S. Miguel
Bryophytes	*Trematodon perssoniorum*	0	40
Vascular Plants	*Laurus azorica*	46	8
	Pericallis malvifolia	142	114
Arthropods	*Atlantocis gillerforsi*	315	104
	Jaera nordmanni	0	192
	Polydesmus ribeiraensis	0	276
	Scaptomyza impunctata	43	46
	Simulium azorense	62	46

number of cells will lose species, corresponding to 93 % of the island's area versus 54 % in São Miguel.

For vascular plants, the pattern of species diversity loss is clearer with a large number of cells, 56 %, decreasing in number of species between 10 and 45 % for São Miguel and 73 % for Terceira (Fig. 2). In both islands only 2 % of the cells are expected to show an increase in the number of species, mostly in the central areas of the islands. For São Miguel 4 % of the cells have no change in number of species, while for Terceira only 1 % of cells have no change.

The arthropods show a clear decrease in the number of species per cell in the coastal area of São Miguel. In this island 53 % of the cells are expected to decrease between 10 and 45 % in number of species, while 34 % of the cells decrease in species between 0 and 10 %. There is an increase of richness in 10 % of the cells of São Miguel. (Fig. 3). For Terceira Island the diversity loss occurs mainly in the range of 10 to 20 % (in 37 % of the cells) and 20 to 45 % (in

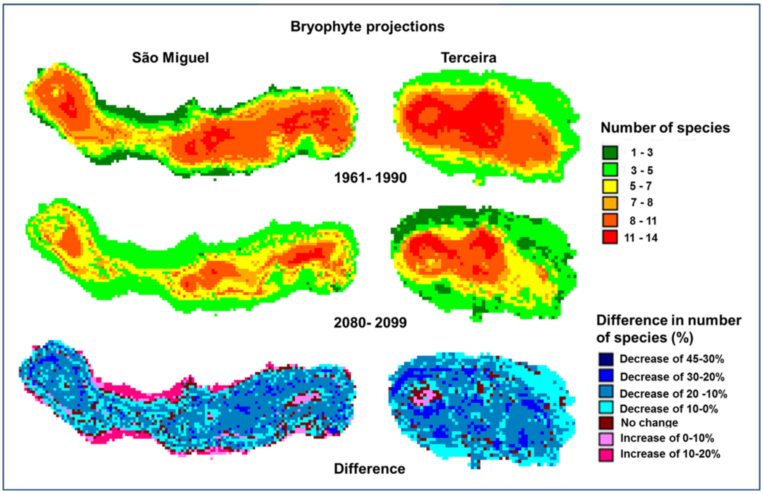

Fig. 1 Projected suitable climate space maps of bryophyte species for the period 1961–1990 and 2080–2099 and the calculated differences for São Miguel and Terceira Islands. Each cell represents the total number of species in that 500 m × 500 m cell. In the difference map each cell represents the difference in the number of species per cell in percentage

32 % of the cells) of species per cell (69 % of the cells in total), and mostly in the coastal area (Fig. 3). An increase of species is expected only in 4 % of the cells (Fig. 3).

4 Discussion

In the case of the Azorean species studied, we showed that of the 206 investigated indigenous species, 23 (11 %) might lose suitable climate in at least one of the islands within a relatively short period of time (≈ 80 years), and many others might experience a reduction of their suitable climate space. Actually, while some endemic beetle and spider species are already considered extinct due to human activities on Azorean islands (Cardoso et al. 2010; Terzopoulou et al. 2015), Triantis et al. (2010) have furthermore estimated that more than half of the extant native forest-dependent arthropod endemic species might eventually be driven to extinction due to major past and current land-use changes, fragmentation and forest loss. Climate change might act synergistically with other threats with the effect of speeding the extinction debt predicted by Triantis et al. (2010), as suggested by Malcolm et al. (2006) analysing endemic species in hotspots of biodiversity throughout the world.

Interestingly, a few species are predicted to increase their distribution significantly, e.g. the beetle *Atlantocis gillerforsi* (with a threefold increase – Table 2). The predicted climatic changes, regardless of land use, seem to provide a climatic niche that is more adequate for the survival and spread of this species. However, all of the studied species need to be further investigated to ascertain what their role in the ecosystem is, how they interact with other indigenous or exotic species, and how this will in turn affect their future distribution. Moreover, the changes expected on the forest cover may have unknown negative cascading effects on diversity, the so-called "cumulative biodiversity lags-framework" sensu Essl et al. (2015).

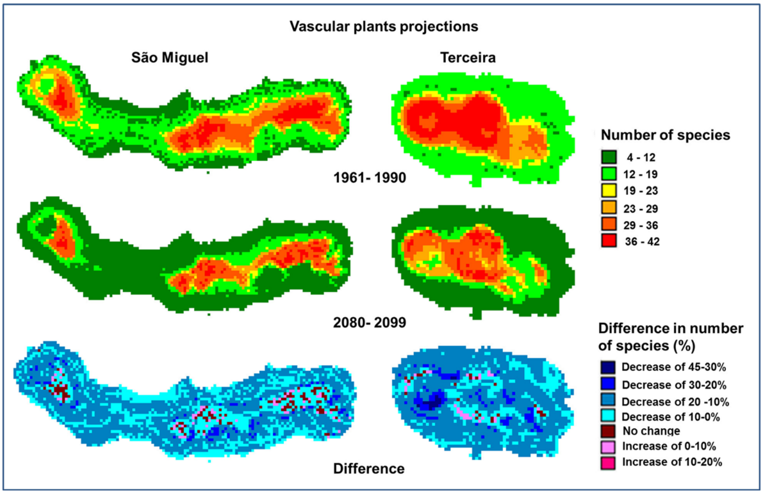

Fig. 2 Projected suitable climate space maps of vascular plant species for the period 1961–1990 and 2080–2099 and the calculated differences for São Miguel and Terceira Islands. Each cell represents the total number of species in that 500 m × 500 m cell. In the difference map each cell represents the difference in the number of species per cell in percentage

For oceanic/volcanic islands, due to the small area available, especially in higher altitudes, distribution shifting is expected to occur only in terms of altitudinal gradients. For the three taxonomic groups studied, the tendency was to shift towards the higher-elevation centre of the islands (Figs. 1 and 3). However there are differences between taxonomic groups. The arthropods and vascular plants for example differ from each other most markedly in the coastal areas, where the reduction of number of species per cell is clear (Figs. 2 and 3) with the projections for the future period indicating that the species range will shift towards the higher altitudes. However, bryophytes show a different pattern where the species range tend to shift towards the coastal areas (Fig. 1), in São Miguel, areas where habitat suitability may be quite scarce. Alatalo et al. (2014) found that some species of bryophytes survive climate change warming simulations which can account for this different projected response from the bryophyte group. However, Azorean bryophytes are located mainly in the evergreen (sub)tropical laurel forests (Gabriel and Bates 2005; Gabriel et al. 2011) and this implies that changes in the tree cover will have major impacts on bryophyte communities. This shows that there is still much to be done in terms of applied studies of the consequences of climate change to the different inter-specific interactions within ecosystems.

This study indicates that there are shifts of biodiversity under climate change. This should be considered in future conservation management. The projected shifts in biodiversity hotspots are a challenge for static conservation areas. In this regard, overlapping hotspots under current and expected future conditions highlight priority areas for robust conservation management Furthermore, addressing a wide range of species groups is important for conservation management to identify biota particularly at risk from climate change (Thom et al. 2016). This multi-species and multi-taxa approach provides more information about the impacts of climate change and allows an understanding of how the different groups that co-exist in the natural ecosystems of oceanic islands will have different responses to the incoming climatic changes. Not knowing what species contribute to what ecosystem services means that the full consequences of species extinctions may be extremely hard to predict (Cardoso et al. 2011).

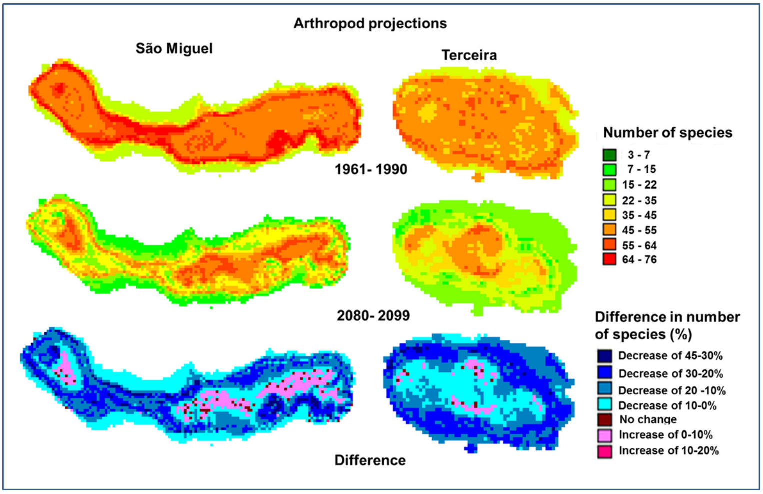

Fig. 3 Projected suitable climate space maps of arthropod species for the period 1961–1990 and 2080–2099 and the calculated differences for São Miguel and Terceira Islands. Each cell represents the total number of species in that 500 m × 500 m cell. In the difference map each cell represents the difference in the number of species per cell in percentage

In Azores, landscapes outside of protected areas are often hostile to the survival of species due to human infrastructure, fragmentation of habitats by way of intensive cattle agriculture, and associated stressors (Cardoso et al. 2009; Florencio et al. 2013). Such fragmentation can directly limit species migration and gene flow (Heller and Zavaleta 2009). There might be many cases where the future climatic conditions will be suitable for species to survive, but these will not be able to do so due to conflicts with human activities, particularly agriculture and forestry activities. The case of the bryophytes where we see a projected increase of diversity in the coastal area of São Miguel is a clear example of how this can in the future be a problem for conservation purposes, as the coastal areas of islands are usually densely populated. Current protected areas in the Azores are located mostly inland, where the predicted climate space suitability is generally higher. However, boundaries of these protected areas may be altered, and/or improved when considering these results. Further studies into prioritization of protected areas based on future suitable climate space are needed (Ferreira et al. in prep).

Ours is one of the first studies investigating climate change effects on island biodiversity, using three different taxonomic groups. Climate change was projected to have important impacts with species losing their entire suitable climate space in almost one eighth of the cases. This study is an important step towards application of regional models to specific situations like the unique case of oceanic islands. This has important implications for conservation purposes, where a holistic approach using multi-species and multi-taxa analysis along with adapted regional climate models should be the future direction of studies that can be used to support protected areas decisions.

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