Endemism increases species' risk to climate change in areas of global biodiversity importance

Abstract

Climate change affects life at global scales and across systems but is of special concern in areas that are disproportionately rich in biological diversity and uniqueness. Using a meta-analytical approach, we analysed >8,000 risk projections of the projected impact of climate change on 273 areas of exceptional biodiversity, including terrestrial and marine environments. We found that climate change is projected to negatively impact all assessed areas, but endemic species are consistently more adversely impacted. Terrestrial endemics are projected to be 2.7 and 10 times more impacted than non-endemic natives and introduced species respectively, the latter being overall unaffected by climate change. We defined a high risk of extinction as a loss of >80% due to climate change alone. Of endemic species, 34% and 46% in terrestrial and marine ecosystems, and 100% and 84% of island and mountain species were projected to face high extinction risk respectively. A doubling of warming is projected to disproportionately increase extinction risks for endemic and non-endemic native species. Thus, reducing extinction risks requires both adaptation responses in biodiversity rich-spots and enhanced climate change mitigation.

Keywords: Extinction Risk, Biodiversity Hotspots, Global-200 Ecoregions, Introduced Species

1. Introduction

Climate change is already impacting biodiversity and is likely to intensify over the next few decades unless substantive mitigation efforts are implemented (IPCC 2018). Both modelling and field observations suggest non-uniform extinction risks of wild species across geographic regions and between taxa, even at low levels of warming (e.g. Urban 2015; Román-Palacios & Wiens, 2020). This spatial variation in impacts shapes global biodiversity responses to climate change. Despite the publication of many hundreds of studies on projected impacts of climate change on species and ecological communities, it remains challenging to synthesize clear patterns of risk across different levels of ecological organization (e.g. species and community levels), between ecological realms (terrestrial, freshwater and marine), as a function of ecological uniqueness (i.e. level of endemicity), and as a function of policy-relevant climate scenarios (low to high projected rates of climate change). Analysis to tease out the importance of such factors would be valuable in informing our understanding of climate risks to biodiversity, and in prioritising and developing adaptive responses.

Previous work suggests a range of expectations relevant to the factors mentioned above. With respect to projected vulnerabilities across ecological realms, global level assessments are rare. Marine communities are expected to show greater sensitivity to climate change than terrestrial communities because the distribution of marine species is more strongly governed by their thermal tolerances (Sunday et al. 2012) and thermal safety margins are lower (Pinsky et al. 2019). As isotherms shift most strongly in marine equatorial regions (Burrows et al. 2011) the combination of vulnerability and exposure predicts the largest impacts there. In addition, there is a positive correlation between climatic and non-climatic stressors in marine environments, whereas on land regions of strong climate change tend to be those with low non-climatic impacts (Bowler et al. 2020). On land, subtropical to temperate flatlands are projected to have the greatest climate velocities (Loarie et al. 2009, Burrows et al. 2011), and are thus expected to show the greatest projected impacts.

Geographic range shifts, expansions and contractions are among the most common responses of species to climate change (Poloczanska et al. 2013; Molinos et al. 2016; Saeedi et al. 2017; Chaudhary et al. 2020; Yasuhara et al. 2020). Species with large geographic ranges are expected to be less vulnerable, as they may find refugia in parts of their range (Lucas et al. 2019). Introduced species that become invasive are expected to be less vulnerable due to their adaptability to new environments (Oduor et al. 2016). In contrast, the more restricted ranges of endemic species means that they are often at greater risk of extinction from local impacts, including habitat loss and interactions with introduced species; the effects of which are being exacerbated by changes in climate (Catford et al. 2012; IPCC 2019). Endemics have restricted geographic ranges, sometimes associated with a specialized environmental niche, limited dispersal abilities, and reduced population size and adaptive capacity (Chichorro et al. 2019; Staude et al. 2020). Therefore, areas of high endemism are likely to be particularly vulnerable to climate change at both species- and community-levels (Malcolm et al. 2006; Dirnböck et al. 2011; Enquist et al. 2019).

Biodiversity is unevenly distributed across the globe, and areas with exceptional biodiversity are prioritized in conservation efforts (Brooks et al. 2006; Asaad et al. 2018; Zhao et al. 2020). Biodiversity hotspots (Myers et al. 2000) and the Global-200 ecoregions (Olson and Dinerstein 2002) together comprise 273 irreplaceable terrestrial, freshwater and marine areas, with notable endemism, richness and/or unusual ecological or evolutionary phenomena, hereafter called 'rich-spots'. These areas are expected to experience severe climatic change in the future (Beaumont et al. 2011; Bellard et al. 2014). If exceptional biodiversity is due to long-term climatic stability (Dynesius and Jansson 2014; Senior et al. 2018), then endemic species of such areas may be particularly at risk of adverse impacts even under less extreme climate scenarios.

The vulnerability of these rich-spots to climate change has been previously investigated using coarse estimations based on modelling species-area relationships (*e.g.* Brooks et al. 2002; Malcolm et al. 2006; Bellard et al. 2014; Habel et al. 2019). For example, Malcolm et al. (2006) assessed the climate change impact on 25 rich-spots by modelling the change in habitat area, and corresponding changes in biodiversity, likely as a result of future biome distributions projected by global vegetation models. Similarly, Bellard et al. (2014) modelled the effect of projected climate change on 34 rich-spots to examine the extent to which they would experience novel climates and the proportion of endemic species affected by this change, as well as the potential expansion of invasive species. However, such previous studies have tended to produce approximations of the number of species that would be adversely affected as climatic niche space is lost. Estimates based solely on area lack the necessary sensitivity of species-specific parameters and do not incorporate the local context of each different rich-spot, possibly biasing vulnerabilities towards larger areas (Brooks et al. 2006). A species-specific and community-level examination of vulnerability to climate change would provide more robust evidence from which to estimate risks and on which to base adaptation strategies.

We assessed over 8,000 projections of climate change impacts in 232 studies for endemic, non-endemic native and introduced species and communities across terrestrial, freshwater and marine environments, based on papers that account for their identity and local context of different rich-spots. Through this extensive systematic review of the literature, we aimed to test for differences in projected responses between endemic, non-endemic native and introduced species; differences in projected responses of species and communities of terrestrial and marine ecosystems; and how vulnerability is projected to vary among climate zones, geographic regions, and across a representative range of climate change scenarios for this century.

2. Methods

2.1. Literature Search

We performed an extensive literature search for papers that investigated the impacts of climate change on biodiversity in global priority conservation areas. We considered two conservation schemes: “Biodiversity Hotspots” (Myers et al. 2000, extended by Mittermeier et al. 2004; Mittermeier et al. 2011; Williams et al. 2011; Noss et al. 2015), including 35 terrestrial regions; and “Global-200 Ecoregions” (Olson and Dinerstein 2002), including 195 terrestrial and freshwater regions and 43 marine regions (Supplementary Figure 2, Supplementary Table 1). The Global-200 (Olson and Dinerstein 2002) are a set of irreplaceable and distinctive ecoregions, which comprise areas of high endemism and/or species richness, and/or unusual ecological or evolutionary phenomena. While biodiversity hotspots represent a substantive fraction of global species richness on less than 16% of the terrestrial surface area, the Global-200 ecoregions extend well beyond this area and are more representative of all environments. The rich-spots included in this study comprise 48% and 17% of the world’s terrestrial and marine surfaces, respectively (Supplementary Table 1). There is some overlap of approximately 14% between both conservation schemes on land (Supplementary Figure 2). We searched for papers published since 2012 using “climate change” AND “biodiversity” AND the names of each of the rich-spots. We aimed to understand whether recent trends in biodiversity research have changed since the latest reviews (IPCC 2014a; Urban 2015). We directed the search at peer-reviewed journal articles, but included 10 scientific reports from research institutions where there were data gaps.

We found 395 publications that evaluated climate change on some aspect of biodiversity in these rich-spots. From these, we only used 232 papers that established future projections of climate change impacts with quantifiable risks upon biodiversity. According to the IPCC WGII-AR5, risk is “the potential for consequences where something of value is at stake and where the outcome is uncertain” (IPCC 2014b); i.e., any consequence brought about by climate change for biodiversity (IPCC 2014c). If a paper provided risk projections for several species or used several climate change scenarios, we gathered the information for all of them as multiple data entries. Thus, we gathered risks for individual species or mean values for species assemblages reported, compiling 8,158 risk projections (Supplementary Table 2).

2.2. Data Analysis

For each study, we classified the biodiversity rich-spots by (a) ecosystem, geographic region and climatic zone; (b) major taxonomic group; (c) whether endemic (only present within the rich-spot area), non-endemic native, or introduced species; and (d) type of impact on biodiversity according to five commonly cited measures of species-level impacts, namely i) population abundance (and catch potential of fisheries as a proxy for abundance), ii) physiology and iii) increase or decrease in spatial range in species distribution; and of community-level impacts, namely iv) diversity (species and taxonomic richness) and v) habitat change (Supplementary Table 3). For conciseness, hereafter we use the term native for non-endemic native species. We also classified climate change scenarios by their projected warming levels (Supplementary Table 3), using IPCC (2018) thresholds, which conclude that limiting global surface air temperature (Gsat) increase to 1.5ºC above the pre-industrial level would have a relatively muted (milder) impact on biodiversity, with successively more adverse impacts projected with warming between 1.5-2ºC (moderate), 2-3ºC (high) and increases in warming of >3ºC (very high). For each study, we categorised impacts by scenario used, and time frame over which impacts were projected. In cases in which results were presented as mean values of multiple scenarios, these were categorised as 'ensemble'. In cases where authors did not follow recognised scenarios, and scenarios described could not be placed within one of these categories (e.g. some studies applied idiosyncratic, extreme scenarios or ad-hoc temperature and/or rainfall changes), these were classified as 'ambiguous' and excluded from our main analysis (17 papers corresponding to 790 risk projections; Supplementary Table 2). Due to insufficient data, we excluded introduced species in the marine ecosystem from this part of the analysis.

We determined an effect size quantified as the percent magnitude of change between current and future time periods. Positive effect sizes represented increases in biodiversity impact categories in the future whereas negative effect sizes represented decreases. For example, a spatial change of 100% meant that a species was projected to double its distribution area within the projected period. Neutral effect sizes indicated that no change in biodiversity was projected to occur.

Because effect sizes were based on comparisons between varying time periods, we standardised the effect size by dividing it by the number of years between the periods, obtaining a projected annual incremental change. This standardized effect size allows direct comparisons between studies (it cannot be inferred as an indication of actual change occurring *per year)*. Some of the papers did not explicitly specify the baseline current year of the projections, and in these cases we extracted this information from the raw data used in the model described in each paper's methods (*e.g.,* WorldClim database). We excluded studies covering time spans of more than 150 years, because the calculated relative rates of change are biased by time spans of observation. For instance, the negative power law relationship between observed rates and time spans of observation leads to lower rate estimates when time spans are long (Kemp et al. 2015).

We calculated extinction risks as the projected likelihood of extinction (i.e., disappearance of the species within the rich-spot) in each geographic restriction and taxonomic group. We used the International Union for Conservation of Nature (IUCN) criteria of ≥ 80% abundance loss characterizing critical endangerment, with extremely high risk of extinction (criteria A4, IUCN 2012). For spatial change, we adopted the extinction risk criteria from Urban (2015) of ≥ 80% loss of geographic range. We also considered data that explicitly referred to extirpation or extinction. For the extinction risk calculation, we only considered data that presented risk projections for single species (6162 effect sizes for single species), since the mean values presented for species assemblages could bias results. Therefore, we calculated the number and proportion of species projected to have a positive response to climate change, as well as those projected to be at risk of extinction.

All statistical analysis was performed in R version 4.0.3 (R Core Team 2020). Because the different impact categories involve very different responses of either species, communities or habitats, we decided to run separate generalised linear mixed-effects models (GLMMs) to determine the significant ($\alpha = 0.05$) drivers of the standardised effect sizes of each impact. The data were therefore subset into five groups, namely species-level impacts: i) abundance, ii) physiology, iii) spatial change; and community-level impacts: iv) diversity, v) habitat change. Because the standardised effect sizes clustered around the mean with higher kurtosis than the Gaussian distribution for all data subsets, we corrected the distribution using the LambertW package (Goerg 2016) thus reducing the effect of extreme outliers (Goerg 2011). These transformations were done individually for each effect group rather than overall for the full dataset. The transformed standardised effect sizes were used in all GLMMs and inferences are made using these. All GLMMs were run using the lmer function in the lme4 package (Bates et al. 2015) with Gaussian-identity distribution-links.

Saturated models for each impact category were built with the following predictor variables included as fixed effects: ecosystem, climatic zone, taxonomic group, species geographic restriction and warming level. Predictor variables were omitted from saturated models if there was only one sub-category for that impact category (e.g., species' distribution as endemic, native and introduced species was omitted from the physiology GLMM as there were only native species in this impact category). The transformed standardised effect size was included in all models as the response variable and the study's unique identity (DOI) was included as a random effect. Once saturated models were constructed, a step-down model-building approach was followed to simplify the models using the step function of the lmerTest package (Kuznetsova et al. 2017). This approach requires the construction of a saturated model followed by the automated removal of fixed effects and random effects that do not contribute significantly ($\alpha = 0.05$ for fixed effects and $\alpha = 0.1$ for random effects) to the intercept and slope of the model (Kuznetsova et al. 2017).

Once the final, simplified models (Table 1) for each impact category were obtained from the step-down approach, the summary function of the lmerTest package was used to obtain output tables for the GLMMs, with the model estimates and degrees of freedom using the Satterthwaite's (Kenward-Roger's) approximations for the t test and the corresponding p values (Kuznetsova et al. 2017). In addition to the summary tables, the emmeans function of the emmeans package (Lenth 2019), which uses the Tukey post-hoc method, was used to obtain pairwise comparisons of the sub-categories for each significant predictor variable in the final model. From the summary tables and pairwise comparisons, inferences could be made about the significance of each predictor variable in driving the respective impacts, as well as the difference in the standardised effect sizes between the sub-categories for each significant predictor variable.

We created the graphs using GraphPad Prism software version 8.0.1 (GraphPad Software, San Diego, California USA, www.graphpad.com). We created the maps using *tidyverse* and *sf* packages in R software (R Core Team 2019; Wickham et al. 2019; Pebesma et al. 2018).

3. Results

3.1. Study biases

Literature on quantifiable climate impacts on biodiversity was unevenly distributed worldwide. Some rich-spots appear very well assessed, with > 250 effect sizes each, namely the Brazilian Atlantic Forest, Mesoamerica, Maputaland-Pondoland-Albany, Cape Floristic Province and California Floristic Province, which together comprise 59 % of our data for terrestrial effect sizes; and the Mediterranean Sea, which comprises 50 % of marine effect sizes (Supplementary Figure 1; Supplementary Table 1). Despite our extensive literature survey, we found no data for 49 % of the 273 rich-spots (Supplementary Figure 1; Supplementary Table 1).

In our review, over 200 studies estimated climate change impacts on terrestrial ecosystems, whereas only 34 studies focused on marine ecosystems, suggesting that the ecological literature is biased towards biodiversity from terrestrial ecosystems. Only 14 studies assessed impacts over freshwater species, which were analysed within terrestrial due to lack of data. We also found taxonomic bias in the literature towards birds and plants, with over 1400 species each (Figure 4). Most studies considered a few selected threatened or ecologically important species, some assessed only endemic species, and fewer studies modelled all the species (> 100) within a taxonomic group, which reflects an inherent bias towards local endemics in the global biota (e.g. Enquist et al. 2019). Of the species reviewed in our analysis, 73% of the effect sizes referred to non-endemic natives, 17% endemics and 5% introduced species (plus <5% unclassified). Because this may under or overestimate their proportions within each and overall study areas we have limited our interpretation to the general direction of effects.

3.2. Overall impacts

Climate change is projected to have negative impacts on virtually all terrestrial species in all rich-spots, with the exception of introduced species. This is in accordance with our previous expectations that introduced species would be the least impacted by climate change (Figure 1). While this was also generally the case for marine endemic and native (i.e., non-endemic) species, Arctic species were projected to increase their abundance and/or range (Figure 2). When grouping species into climatic zones, and those inhabiting mainland, islands, mountains and in the ocean (Figure 3), all impact categories projected negative effects due to climate change, except in the case of introduced species. Biological measures of response were also projected to be negatively affected, namely species abundance, diversity (including of introduced species), spatial area, habitat area and physiology (Figure 3). Introduced terrestrial species were projected to be significantly positively affected by climate change in the subtropics, mountains and in terms of spatial change (Figure 3). There were insufficient data on marine introduced species for analysis. Species of all groups of organisms and in almost all geographic regions were negatively affected by climate change (Supplementary Figure 3). Only non-endemic native amphibians in Central and South America were projected to benefit from climate change, an unexpected result.

3.3. Taxa

All taxonomic groups, except for introduced species and non-endemic native amphibia, were projected to be negatively affected by climate change both overall (Figure 4), and within continents (Supplementary Figures 3, 4). Although amphibians had the highest average effect size increase, meaning an overall positive impact, this average was elevated by a number of native species with very high projected increases (Figure 4). At the same time, amphibians were the group with one of the greatest number of species at risk of extinction (Figure 4). A high number of native terrestrial plants may also face high extinction risk, even though endemics were projected to be significantly more impacted (Figure 4, Table 1). Terrestrial endemic birds were projected to be the most significantly impacted taxa (Figure 4, Table 1). In marine ecosystems, the most impacted taxa appear to be seabed organisms, coral reefs, fish and plants. Endemic marine fishes were projected to be significantly more impacted than non-endemic native fishes (Table 1). Introduced species were positively impacted by climate change, but the species evaluated were restricted to terrestrial plants and a few species of freshwater benthos. Increased climate warming from 1.5 to 3ºC increased the risk of species extinctions except in the case of introduced species (Figure 5).

3.4. Endemicity

Terrestrial endemic species were projected to be significantly more adversely impacted by climate change than terrestrial non-endemic native and introduced species (Figure 1). Terrestrial endemic species were projected to be 2.7 times more impacted than native species (negative mean standardised effect size of 0.34 % vs 0.92 %) and 10 times more impacted than introduced species. Note that these values refer to the standardised effect sizes, which when considering the time periods of these constant rates, a negative change of 1% can be translated into losses of 80% by 2100. Introduced species were projected to be unresponsive to or benefit from climate change overall. As in terrestrial regions, overall marine endemic species were significantly more impacted than marine native species.

Endemic species were projected to be more impacted than natives in almost all assessed rich-spots (with the exception of Cerrado, New Caledonia, Sundaland, Wallacea, Polynesia-Micronesia and Himalaya for terrestrial ecosystems and Humboldt current for marine ecosystems), while introduced species were projected to have either neutral or positive impacts (Figure 1). This finding was supported by the GLMMs, where endemic species were found to be significantly more affected than native and introduced species in abundance, spatial change and diversity models (Table 1). The most prominent negative impacts for endemic species were in South America, Africa and Oceania. In comparison, native species were generally less negatively impacted than endemics, with a few native species even showing small positive impacts (Supplementary Table 1; Table 1). Introduced species were either neutrally or positively impacted, with only slight decreases in some rich-spots (Figure 1, Figure 3, Supplementary Table 1, Table 1).

The greater adverse impact of projected climate change on endemic species was evident across climatic zones and geographic regions (Figure 3). Endemic species were projected to be the most sensitive to climate change in all climatic regions, showing higher negative impacts than native or introduced species in tropical, subtropical and temperate regions (Figure 3). Marine endemic species were projected to be more impacted than native species in temperate regions, but not in tropical regions (Figure 3).

The five defined impact categories had different magnitudes of impacts on species. Endemics were more impacted in terms of the abundance category than other categories, and compared to native species in land and oceans (Figure 3, Table 1). Diversity was consistently projected to be negatively impacted irrespective of species distribution. It was the only impact category where introduced species were negatively impacted. In contrast, endemics were the most significantly impacted (Table 1). Spatial area impacts were significantly greater for terrestrial and marine endemics than natives and introduced species (Table 1). These spatial area impacts were more prominent for marine species, whereas introduced species are increasing their distributions despite climate change. Loss of habitat area for terrestrial endemic and native species was similar, however marine habitat was more affected for native species. Changes in physiology were more pronounced for marine species than terrestrial.

Endemics were consistently projected to be more impacted than native and introduced species under different warming intensities (Figure 5, Table 1). Although the average projected negative mean impacts were constant with climate change intensification, the proportion of species facing extremely high extinction risk increased considerably with warming. The proportion of endemic species at risk of extinction rose tenfold, from 2 % to 20 % and 32 % in terrestrial and marine ecosystems, respectively, with a doubling of warming from mild to very high (i.e., from below 1.5 to above 3 ºC). Although the magnitude of impact within the standardised time frames is higher for terrestrial than marine endemics (i.e., they reach high impacts within shorter time frames), the higher proportion of marine endemics in the studies eventually amounts to projected impacts higher than an 80% loss, i.e., they face extinction risks (Figure 5).

3.5. Extinction risk

More than 60 % of tropical terrestrial endemic species were projected to be at risk of extinction due to climate change alone. Endemic species from islands and mountain regions had extremely high extinction risk (100 and 84 % of species, respectively), which was over six times more than in mainland regions (12 %) (Figure 3). Of marine endemic species 54% were at risk of extinction, and while most of these occurred in temperate regions note the Mediterranean bias and paucity of tropical data in available studies (Figures 3, 4).

Overall, 92 % of terrestrial endemics were projected to be negatively affected as a result of climate change, in comparison to 80 % and 48 % for terrestrial native and introduced species, respectively. At the same time, 34 % of terrestrial endemic species were estimated to be at extremely high risk of extinction, whereas this risk was 20 % for native and 0 % for introduced species (Figures 3, 4). For marine species, 95 % of endemics and 87% of natives were projected to be negatively impacted by climate change (Figure 4). We found significant statistical differences between marine endemic and native species (Table 1). The proportion of marine species at risk of extinction was more than twice as high for endemics (54 %) than for natives (26 %) (Figure 3).

Most species assessed for risk of extinction were in Central and South America for terrestrial (2,782), and the Mediterranean for marine ecosystems (576) (Supplementary Figures 5, 6). However, Oceania, with its islands of high endemicity, had the greatest proportion (50 %) of terrestrial species projected to be threatened with extinction by climate change, followed by 30 % in the Americas, Europe and Asia (Supplementary Figure 5). In contrast, Oceania had no marine species projected to be at risk of extinction (Supplemental Figure 6). In marine systems, the Mediterranean, an enclosed sea with high endemicity, had the highest number of marine species (25%) projected to have a high risk of extinction with climate change (Supplemental Figure 6).

4. Discussion

4.1. Key findings

Our results demonstrate that endemic and native (i.e. indigenous non-endemics) species are consistently more at risk from the adverse effects of climate change than introduced species across both terrestrial and marine environments, geographic areas, climatic zones, taxonomic groups and impact types, with endemics by far the most at-risk group. In contrast, introduced species are projected to experience either neutral or beneficial impacts from changing climate conditions. That introduced species are projected to increase despite climate change is an additional concern within rich-spots. Because rich-spots have high diversity, uniqueness and endemism, our findings are a cause for concern on a global scale.

Although the biodiversity rich-spots have been selected qualitatively based on a mixture of criteria on data available at the time, recent analyses of plants support the locations of terrestrial endemism and rarity (Enquist et al. 2019). Additional areas have been proposed and/or protected for nature conservation and there exist many studies on the effects of climate change on species outside these rich-spots that we have excluded from our analysis. A quantitative biogeographic mapping across all biodiversity measures would provide a more robust delimitation of rich-spots, as recently conducted for land plants (Enquist et al. 2019) and the oceans (Zhao et al. 2020). In our analysis, we also found great geographic bias in the sampling of rich-spots, which is a limitation that could skew results. It is also important to note that climate change is one of several, often synergistic, threats to these rich-spots, including habitat loss, overexploitation and pollution (Brook et al. 2008; Albano et al. 2021), which were not considered here. However, the consistent projections of a loss of biodiversity across geographic, taxonomic, and climate impact categories suggests current knowledge is adequate to indicate the general risk of species extinctions, particularly of endemic species.

4.2. Introduced species

Areas with high distinctiveness and endemism may be particularly vulnerable to invasion by human introduced species (Ricciardi and Atkinson 2004; Berglund et al. 2009; Bellard et al. 2014), notably when native species are naive to introduced predators (Urban 2020). By compressing the range of native species, invasive species may become a source of additional pressure (Vila and Weiner 2004, Catford et al. 2012). Ultimately, the replacement of endemic species by fewer, generalist and widespread opportunists would lead to homogenisation in biodiversity rich-spots, causing ecosystem simplification (McKinney and Lockwood 1999). This phenomenon could be masked initially by relatively unchanged local richness associated with species turnover, but yet still contributing to a pattern of declining global biodiversity (Thomas et al. 2013).

In our analysis, plants comprised the majority of introduced species within rich-spots. Plants are some of the world's most proficient invasive species (Lowe et al. 2000). Future climate change may exacerbate such invasions (Liu et al. 2016; Wang et al. 2019). Invasive plants can outcompete native species under increased temperature and carbon dioxide conditions (Van Kleunen et al. 2010; Davidson et al. 2011; Liu et al. 2016). Coastal and high latitude regions have been identified to be most at risk from introduced plants as a result of climate change (Wang et al. 2019). This is supported by our findings that introduced species consistently responded positively to climate change in mountain and island systems. Similarly, Bellard et al. (2014) projected that the biodiversity rich-spots most at risk from invasive species are mainly islands or groups of islands, including Polynesia–Micronesia, New Zealand and the Philippines.

4.3. Endemic species

Species adaptation can be enhanced by distributional shifts to habitats in suitable climatic conditions, but this is less likely for endemic than for native species. Greater extinction risks have already been associated with restricted range (rare and often endemic) species (Staude et al. 2020) in multiple taxonomic groups worldwide (Newbold et al. 2018). Bellard et al. (2014) predicted that biodiversity rich-spots would experience an average 31% loss of current climatic conditions by the 2080s, which would negatively impact an average of 25% of endemic species per hotspot. We found that terrestrial endemic species from island and mountain rich-spots were projected to be at much greater risk of climate change impacts than mainland areas. Both are centres of endemicity due to their geographic and environmental isolation (Kier et al. 2009; Noroozi et al. 2018) and are more prone to species invasions than mainlands (Bellard et al. 2014; Elsen and Tingley 2015). These areas have been projected to experience proportionately higher rates of climate-induced range expansions of introduced species (Lamsal et al. 2018, Wiens et al. 2019). Within mountain regions, upward shifts in species elevational ranges (Chen et al. 2011) imply that many montane species will be limited by future altitudinal space, although species responses depend on topographic complexity (Elsen and Tingley 2015). Such consistent extinctions of endemics could disrupt the ecological interactions that buffer ecosystems against disturbances (Mouillot et al. 2013; Pires et al. 2018). Islands of the Caribbean, Madagascar, Indian Ocean Islands, Philippines, Western Ghats and Sri Lanka, could lose all their endemic plants due to climate change by 2050, and African mountain rich-spots were also at risk of endemic plant loss (Habel et al. 2019).

4.4. Island biota

The very high extinction risk we discerned for islands reflects the geographic isolation, high levels of endemicity, narrow ranges and small population sizes of many insular species. These factors limit range shifts and increase vulnerability to both stochastic and deterministic threats (Manne et al. 1999). Old oceanic islands generally host orders of magnitude higher levels of endemism (i.e., a higher percentage of all species are endemic) than continental regions due to the greater levels of speciation arising from long periods of insular isolation (Gallagher et al. 2020). However, lower genetic variation can be associated with this greater degree of speciation, leading to poor adaptive, dispersal and defensive capacities and a high vulnerability to extrinsic disturbances (Harter et al. 2015, Kumar and Taylor 2015). Extinction risk of island endemics is further intensified when continuing loss, degradation and fragmentation of habitats across already limited terrain are combined with a changing climate, sea-level rise, extreme weather events and disproportionate prevalence of invasive species (Bellard et al. 2014, Petzold and Magnan 2019). Given the high levels of endemism on islands (Bellard et al. 2014, Petzold and Magnan 2019), the high extinction risk for insular endemics found in our analyses indicates disproportionate risks for future global biodiversity.

4.5. Adaptation

This synthesis reveals that climate change is a widespread potential threat to biodiversity rich-spots, regardless of climatic zone, geography or taxonomic grouping. Because biodiversity rich-spots contain disproportionately more global biodiversity per unit area than less rich regions, they are a priority for nature conservation. Importantly, their concentration of endemic species implies particular vulnerability to the effects of climate change, based on results presented here. Whereas a global synthesis also has suggested that endemism increases species risk to climate change, the magnitude of this vulnerability was 6 % higher for endemics than for non-endemics (Urban, 2015). Notably, our results indicate that endemic species from rich-spots are at much higher vulnerability than non-endemics compared to global averages, which reinforces their priority for conservation actions. The local extinctions projected for non-endemic natives within rich-spots could be buffered by more heterogeneous climate change impacts in other parts of their larger ranges. Additionally, they might be able to disperse more readily than endemics, and track suitable climatic conditions, especially in marine ecosystems (Lenoir et al. 2020).

The intensity and velocity of climate change can hinder species' ability to adapt to such change (Visser 2008; Brito-Morales et al. 2020). Several measures hold promise for reducing the species extinctions projected. These include implementing globally-networked fully-protected areas on land and sea that are representative of habitats and environmental conditions (Klein et al. 2015; Gray et al. 2016; Zhao et al. 2020). Addressing concomitant stressors to biodiversity may also aid climate change adaptation by increasing resilience of species and natural habitats subjected to degradation and disturbance (Bowler et al. 2019; Travis 2003). For example, sustainable land and sea-use practices aid species persistence and movement between natural habitats, such as provided by habitat connectivity through less-transformed corridors, including multi-use landscapes and restricted seabed trawling. Extending protected areas networks to include such biodiversity rich-spots, managing the intensity of land and sea-use in their surroundings and addressing habitat degradation would enhance their resilience (Bates et al. 2019). However, such protected areas would require careful design to protect biodiversity at the present and under future conditions of climate change (Vale et al. 2018; Hannah et al. 2007, Hannah et al. 2020), in order to facilitate species range migration in response to climate change. Our analysis suggests that the design and implementation of expanded protected area networks (e.g. Vale et al. 2018; Hannah et al. 2007, 2020) that prioritise endemic species would increase their efficacy under future conditions of climate change. Focussed monitoring of endemic species' populations and associated habitats would enable the early detection of negative trends in wild populations and provide motivation for active interventions such as active habitat restoration and translocation of populations (Segan et al. 2016).

The particular vulnerability of endemic species identified here suggests that even with effective conservation, biodiversity rich-spots might remain at high extinction risk due to increasing climate change alone (Bruno et al. 2018). Apart from our finding that mean effect sizes are consistently negative regardless of warming level, the proportion of species at extremely high risk of extinction increases considerably with temperature. Our results show that even with successful conservation efforts, there remains still an extinction risk for 20 %

and 32 % of the terrestrial and marine endemics in biodiversity rich-spots at > 3 ºC warming without mitigating climate change. This finding supports previous studies that quantified the benefits of mitigation (i.e., limiting warming) for biodiversity at the global scale (e.g., Warren et al. 2018, Nunez et al. 2019, Hannah et al. 2020, Hoegh-Guldberg et al. 2019). Therefore, alongside enhanced conservation actions, efforts to mitigate climate change would reduce risks to biodiversity considerably.

5. References

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Figure 1. Climate change impacts on species within terrestrial rich-spots. Mean standardised effect sizes of (a) all species, (b) endemic species, (c) native species and (d) introduced species. The colour scale is standardised for all maps and ranges from Positive (greater than 2%, blue) to Negative (less than -2%, red). Maximum and minimum values for mean projected standardised effect sizes range from 3.2% (Non-endemic native - Drakensberg Montane Woodlands and Grasslands) to -2.2% (Endemic - Caribbean Islands) (Supplementary Table 1).

Figure 2. Climate change impacts on species within marine rich-spots. Mean standardised effect sizes of (a) all species, (b) endemic species, (c) native species. The colour scale is standardised for all maps and ranges from Positive (greater than 2%, blue) to Negative (less than -2%, red). Maximum and minimum values for mean projected standardised effect sizes range from 3.2% (Native - Drakensberg Montane Woodlands and Grasslands) to -2.2% (Endemic - Caribbean Islands) (Supplementary Table 1).

Figure 3. Climate change effects on species classified by climatic, geographic and biological impact categories. (a) Mean standardised effect sizes (mean ± 95 % CI) represent increases and decreases in impact categories. Comparisons between species with different geographic distributions within impact categories are described in Table 1. (b) The proportion of species that are positively or negatively impacted by climate change. Species groups with risk projections higher than 80 % losses are considered at extremely high extinction risk (endemics) and local extinction risk (non-endemic natives) within the rich-spots.

Figure 4. Climate change effects on species with different geographic distributions within different taxonomic groups. (a) Mean standardised effect sizes (mean ± 95 % CI) representing increases and decreases. Comparisons between species with different geographic distributions within impact categories are described in Table 1. (b) The number of species that are positively or negatively impacted by climate change. Species with risk projections higher than 80 % losses are considered at extremely high extinction risk (endemics) and local extinction risk (non-endemic natives) within the rich-spots.

Figure 5. The impact of warming level on species. (a) Mean standardised effect sizes with different warming levels where mild, moderate, high and very high levels correspond to <1.5 °C, 1.5-2 °C, 2-3 °C and >3 °C, respectively. (b) Diagram indicating the relative proportions of species at extremely high extinction risk for each of the different warming levels. Species with risk projections higher than 80 % losses are considered at extremely high extinction risk (endemics) and local extinction risk (non-endemic natives) within the rich-spots.

Table 1. Summary of the generalised linear mixed-effects models for the standardised effect sizes for the projected impacts of climate change on species and communities in terrestrial and marine rich-spots globally. Models were run separately for each impact category. Response variables and predictor variables included in the models are indicated. All predictor variables were included in the models as fixed effects and the unique identity (DOI) of each journal article was included in each model as a random effect. Parameter estimates, standard errors (SE), degrees of freedom (df), t values and p values (computed using Satterthwaite's method of approximation) for the models are given. Significant predictor variables indicated in bold with significance given as *$p<0.05$, **$p<0.01$ and ***$p<0.001$.