Title: Assessing the vulnerability of freshwater crayfish to climate change

Running title: Vulnerability of crayfish to climate change

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ABSTRACT

Aim: Climate change is a major threat to the persistence of biodiversity. Global assessments highlight the most climate-vulnerable species and geographic regions based on species traits and measures of exposure to climate change. Yet the majority of climate-change vulnerability assessments have focused on terrestrial and marine vertebrates and largely ignored the less-well known freshwater species and invertebrates. We present the first global analysis of 574 species of freshwater crayfish (Families: Astacidae, Parastacidae and Cambaridae) using IUCN's trait-based vulnerability assessment protocol.

Location: Global.

Methods: We collected species-specific information on sensitivity (eight traits), adaptive capacity (four traits) and exposure (five traits) to climate change and combined those dimensions to assess overall species vulnerability.

Results: Our results predicted that 87% of freshwater crayfish species are highly sensitive to climate change (primarily due to habitat specialization), 35% have low adaptive capacity and 57% are highly exposed (based on an ensemble mean of four general circulation models for a moderate IPCC scenario, RCP6.0). Combining sensitivity, low adaptive capacity, and exposure, we assessed 87 species (15%) as vulnerable to climate change. These species are distributed globally with high concentrations in the south-eastern USA (36 species), south-eastern Australia (21 species) and Mexico (10 species), reflecting global patterns of crayfish species richness. Of the 91 species listed as threatened by climate change in the IUCN Red List, we predicted 18 species to be climate-change vulnerable.

Main conclusions: We identified hotspots of species vulnerable to climate change that require further conservation attention. The IUCN trait-based protocol can help identify data gaps and key traits that should be investigated further and thus can help overcome knowledge shortfalls on the effects of climate change. Our study provides key insights for the application of climate-change vulnerability assessment to data-poor invertebrates, which remain underrepresented in global conservation priorities.

KEYWORDS: Climate change, vulnerability, sensitivity, exposure, adaptive capacity, freshwater crayfish, traits, freshwater biodiversity.

INTRODUCTION

Freshwater ecosystems are some of the most threatened on earth and contain disproportionate numbers of threatened species (Collen et al., 2014), yet they remain largely neglected in global conservation priority-setting. Over the past centuries, humans have modified land and aquatic areas through overexploitation, habitat destruction/degradation, flow modification, pollution and the introduction of exotic species (Dudgeon et al., 2006). The Intergovernmental Panel on Climate Change (IPCC) estimates that 20–30% of the world's species are likely to be at high risk of extinction from climate change this century (IPCC, 2014), while the combined effects of climate change and increasing water consumption are predicted to cause the loss of 75% of local fish diversity by 2070 (Xenopoulos et al., 2005).

Climate is the predominant environmental driver that shapes the biogeography of freshwater organisms at large spatial scales and affects their thermal ecology, growth, and performance (Poff, Pyne, Bledsoe, Cuhaciyan, & Carlisle, 2010). Species may be highly sensitive to climate change due to their rarity (i.e. abundance), narrow environmental tolerance (e.g. intolerance to changes in temperature, precipitation and dissolved oxygen; Bone *et al.* 2014, Nussey *et al.* 2005), dependence on specialized habitats or changes in interspecific interactions (Rahel & Olden, 2008). Species may also be exposed to sea-level rise and temperature and precipitation changes (J. M. Furse, Coughran, & Wild, 2012). Changes in precipitation and flow regime due to climate change have been observed in the ranges of crayfish and these changes are expected to continue under future climate change scenarios (Hughes, 2003; Karmalkar & Bradley, 2017). Some species may have low adaptive capacity to climate change due to poor dispersability (e.g. low dispersal capability, limited habitat availability and dispersal barriers) and/or poor evolvability (e.g. small reproductive output and long-life span) (Foden et al., 2013).

Because the impacts of climate change on species are diverse, multiple methods have been developed to assess species' vulnerability to climate change. For example, correlative distribution models are used to estimate species' realized niches and are applied to a wide range of taxa at various spatial scales, although the approach requires adequate species occurrence data (Wiens, Stralberg, Jongsomjit, Howell, & Snyder, 2009). Mechanistic models can be developed from field studies and laboratory experiments on a particular taxon, but they are not applicable to species lacking detailed physiological or life-history data (Moore, DiStefano, & Larson, 2013; Pacifici et al., 2015). The IUCN Red List of Threatened Species^{TM} protocol, on the other hand, has been criticized for under-representing slow-acting threats (e.g. climate change; Keith *et al.* 2014, but see Pearson *et al.* 2014). Trait-based approaches have become a popular tool to assess poorly-known species and to complement IUCN Red List assessments (Böhm et al., 2016).

Trait-based vulnerability assessments integrate species' biological and ecological characteristics (i.e. sensitivity and adaptive capacity) with exposure to climate change impacts (Foden et al., 2013). Trait-based approaches are increasingly used in the scientific literature with a wide range of taxa including regional populations of plants (Still, Frances, Treher, & Oliver, 2015), insects (Conti, Schmidt-Kloiber, Grenouillet, & Graf, 2014), freshwater fish (Carr, Hughes, & Foden, 2014) and mammals (Dickinson, Orme, Suttle, & Mace, 2014) and global populations of corals, amphibians, birds (Foden et al., 2013) and reptiles (Böhm et al., 2016). The lack of data on species occurrences, demography and thermal tolerance for many invertebrates and freshwater species precludes the use of data-hungry distribution and demographic models for assessing the effects of climate change (Moore et al., 2013; Westhoff et al., 2006). For poorly known species, accounting for biological traits and exposure to climate change may be the only feasible approach (Foden et al., 2013).

To assess species vulnerability to climate change, trait-based protocols such as the IUCN climate-change vulnerability assessment (Foden et al., 2013) use Boolean coding (i.e. yes or no) for categorical variables and set thresholds for continuous variables. For example, a species within the lowest 25% of the distribution of range size values are commonly classified as rare and hence having low adaptive capacity to respond to climate change. The use of arbitrary thresholds for continuous variables introduces a degree of subjectivity to estimates of species responses to climate change. Both the selection of traits and their values are derived from unstructured expert elicitation, thereby increasing uncertainty. Because traits influencing responses to climate change differ among taxa (Böhm et al., 2016; Foden et al., 2013), comparing climate vulnerability among taxa is difficult. Owing to the limited data on species' current responses to climate change, the trait-based approach has not yet been validated for global populations of amphibians, reptiles, or birds (Böhm et al., 2016; Foden et al., 2013). In groups where mechanistic models and species distribution models are lacking, the IUCN Red List threat classification provides the only means of comparing the outputs of multiple protocols.

Freshwater crayfish (Families: Astacidae, Parastacidae and Cambaridae) are a useful case study for assessing the vulnerability of freshwater species to climate change because they are economically important (K. Crandall & Buhay, 2008) and 32% of species are globally threatened (Richman et al., 2015), a higher percentage than birds (13%) and mammals (25%), but lower than amphibians (41%) and reptiles (35%) (IUCN, 2018). Freshwater crayfish are a diverse group of crustaceans with 669 species identified globally (K. A. Crandall & De Grave, 2017) and divided into two superfamilies: Astacoidea (in the Northern Hemisphere) and Parastacoidea (in the Southern Hemisphere). Crayfish are distributed in 60 countries with high species diversity in the south-eastern USA (~ 500 spp.) and in south-eastern Australia (150 spp.). A few species are found in East Asia, Europe, Madagascar, and South America.

In this study, we use a trait-based vulnerability assessment to predict the climate change vulnerability of 574 species of freshwater crayfish assessed on the global IUCN Red List (Richman et al., 2015). We ask three questions: i) Which freshwater crayfish species are vulnerable to climate change and what are the implications for their conservation?, ii) How does uncertainty in trait selection and data quality affect the assessment?, and iii) How do the results of the assessment compare with species already identified as threatened by climate change in the IUCN Red List? We conduct the first global vulnerability assessment for a freshwater invertebrate taxon, extensively test the IUCN climate-change vulnerability assessment protocol and provide key recommendations for its robust application in data-poor taxa.

METHODS

Dataset

The IUCN lists 590 species of freshwater crayfish including four extinct species as of 2009 (species discovered after 2009 are not included; Richman *et al.,* 2015). We excluded 12 species from the analysis due to the absence of range maps and four species with no biological information, resulting in a global dataset of 574 species. Trait information was collected from species descriptions, field guides and morphological measurements obtained from >1,700 field and museum specimens, reported in Bland *et al.* (2015). We collated additional data focusing on dissolved oxygen dependency, extrinsic barriers to dispersal, environmental tolerance to temperature and precipitation changes, dependence on habitats which are prone to sea-level rise, exposure to changes in mean temperature and precipitation, and changes in temperature and precipitation variability (see the Supplementary Material).

We followed the IUCN climate-change vulnerability assessment protocol that combines three key dimensions of climate change vulnerability: sensitivity, exposure, and adaptive capacity (Foden et al., 2013). For each dimension, we selected key traits and used thresholds for continuous traits to determine whether a species scored *low* or *high* for that trait. Species with a *high* score on any trait of sensitivity, adaptive capacity or exposure were considered to be highly sensitive, have low adaptive potential or be highly exposed, respectively. Species that were highly sensitive and had low adaptive potential were considered *biologically susceptible* to climate change. Species that were highly sensitive, had low adaptive potential and were highly exposed to climate change (i.e. scored high on all three dimensions) were considered *climate change vulnerable*. The traits and thresholds used to determine species' positions along these dimensions are summarized in Table 1 (see the Supplementary Material).

Sensitivity

We defined sensitivity as a species' inability to persist in its habitat under climate change. We collected data on the following traits: habitat specialization, microhabitat specialization, narrow tolerance to temperature and precipitation changes, dependence on high dissolved oxygen, dependence on interspecific interactions, rarity within populations and fragmented population ranges. We considered all habitat and microhabitat specialists to be highly sensitive to climate change (Table 1 and Supplementary Material). Any species known to depend on only one habitat type listed in the IUCN habitat classification (**Table S1**; Richman *et al.* 2015) was considered a habitat specialist.

Similarly, if a species was known to depend on a microhabitat (e.g. burrows or caves), it was considered a microhabitat specialist. Burrowers are particularly dependent on predictable water levels and water seasonality (Horwitz & Richardson, 1986). The increased frequency and duration of droughts due to climate change may result in reduced flow regime and habitat connectivity (Dhungel, Tarboton, Jin, & Hawkins, 2016) and may affect the survival of burrow-dependent crayfish (Acosta & Perry, 2001). While some burrowers are currently able to withstand annual droughts (DiStefano, Magoulick, Imhoff, & Larson, 2009), others have been found to be negatively impacted by droughts (Kouba, Buřič, & Kozák, 2010). We precautionarily considered burrowers as sensitive to climate change.

Theoretical models (Badino, 2010; Covington & Perne, 2015) and direct field observations (Dominguez-Villar, Lojen, Krklec, Baker, & Fairchild, 2015) have revealed that climate change can influence and modify underground climate and threaten invertebrate ectotherms. Based on observation for cave-dwelling spiders (Mammola, Goodacre, & Isaia, 2018), species that depend on caves may be as vulnerable to climate change, if not more, than species depending on other habitats. Previous studies have shown that 75% (out of 28 spp.) of North American cave-dependent crayfish are threatened (Adamowicz & Purvis, 2006). Species that depend on cave habitats globally are also at high risk of extinction (Bland, 2017). Following the approach taken by Foden et al. (2013), Carr et al. (2014) and Böhm et al. (2016), we considered cave-dependent species as highly sensitive to climate change. Other studies suggest that burrows and caves provide refuges from climate change impacts (Adamowicz & Purvis, 2006; DiStefano et al., 2009). We analysed the sensitivity of our results to the listing of burrow- and cave-dependent crayfish as sensitive to climate change.

Due to the lack of empirical data on species' environmental tolerances (Westhoff & Rosenberger, 2016), we used the average absolute deviation (AAD) of temperature and precipitation across species' ranges as a proxy (Böhm et al., 2016; Foden et al., 2013). Using the Worldclim global dataset (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), we extracted the monthly mean temperature and precipitation for 1975 (average of 1961–1990) across each species' range. The AAD for a given dataset: $x_1, x_2, \dots x_n$ is defined as $\mathrm{AAD} = \frac{1}{n}\sum_{i=1}^{n}|x_i - \bar{x}|$, where x is the monthly mean of temperature or precipitation in the species' range, $\bar{x}$ is the monthly mean of temperature or precipitation of all months over the whole period and n is the number of months.

Following Foden *et al*. (2013), we selected the 25% of species with the lowest values (i.e. species occurring naturally across the smallest range of temperature and precipitation) as highly sensitive. We also used dissolved oxygen (DO) as a proxy for environmental tolerance as DO plays a crucial role in the growth and survival of aquatic species (Dean & Richardson, 1999). Because burrowers and cave dwellers can switch from water to air as their oxygen source when waters become oxygen-depleted, DO is not a limiting factor for their survival (McMahon, 2002), so we considered all burrowers and cave dwellers as tolerant to low DO content. We classified species as dependent on high DO concentrations based on the literature and qualitative assessments by experts in the IUCN Red List, and these species were considered sensitive to climate change.

Climate change may favour dispersal of some invasive species (Rahel & Olden, 2008). Due to the antagonistic behaviour of crayfish, smaller body-sized species can be susceptible to large-bodied or aggressive invaders (Adamowicz & Purvis, 2006). Local extinction of *Faxonius virilis* and *F. propinquus* have been documented due to competition with larger, invasive *F. rusticus* (Lodge, Taylor, Holdich, & Skurdal, 2000). We considered body size as a proxy for the impacts of competition with invasive species; the 25% of species with the smallest body size were considered sensitive to climate change.

Some freshwater crayfish are slow growing, late maturing, long lived and/or rare (J. M. Furse & Coughran, 2011), and may face risks from Allee effects, stochastic events, and reduced recovery capacity. Because data on population size is lacking for most crayfish, we assessed species rarity as low species abundance or high range fragmentation based on qualitative data recorded in the IUCN Red List.

Adaptive capacity

Adaptive capacity is defined as the degree to which a species is able to reduce or avoid the adverse effects of climate change through dispersal and colonization of climatically suitable areas and/or evolutionary responses (Foden et al., 2013). We collected data on range restriction, extrinsic barriers to dispersal, declining population trends and clutch size to assess adaptive capacity. Shifts in distribution may be difficult for species with narrow distribution ranges and slow dispersal rates or for species occurring in high altitudes or in areas limited by dispersal barriers (Reynolds & Soutty-Grosset, 2012).

Dispersal barriers, whether natural (e.g. arid zones, oceans, and mountain ridges) or anthropogenic (e.g. roads and areas converted by humans) can prevent species from dispersing to climatically suitable areas, limiting their ability to adapt to climate change. Dispersal barriers also hamper gene flow among populations, which may increase susceptibility to environmental disturbances (Whiterod, Zukowski, Asmus, Gilligan, & Miller, 2017). Any species exclusively occurring at ≥1000 m above sea level was considered dispersal limited, as were species for which the IUCN Red List explicitly identified dispersal barriers.

Global species extinctions result from a sequence of population declines and local extinctions and many of the current, non-climatic threats to species do not appear to be slowing (Butchart et al., 2010). A population that is already declining because of other pressures is unlikely to have a similar capacity to adapt to new environmental changes as stable or increasing populations. In this study, we considered species with declining population trends as having low adaptive capacity to climate change. Species with already small range sizes may have low population sizes and less genetic variation (Ouborg, Vergeer, & Mix, 2006), hence low adaptive capacity to climate change. Similarly, species with low reproductive rates are less equipped to adapt to catastrophic events and environmental impacts (Beissinger, 2000). We considered the 25% of species with the lowest values for distribution range size and clutch size to have low adaptive capacity.

In summary, we defined species with restricted distributions, low intrinsic dispersal ability, declining population trends, barriers to dispersal or small clutch size as having low capacity to adapt to climate change (**Table 1**).

Exposure

We define exposure as the nature, rate and magnitude of environmental pressure experienced by a species from both climatic changes (e.g. temperature and precipitation) and associated factors (e.g. sea-level rise) (Foden *et al*., 2013). We collected data on species' dependence on habitats that are prone to sea-level inundation, exposure to changes in mean temperature and precipitation and their variability (Table 1). Any species with a range entirely within habitats susceptible to future sea-level rise was considered highly exposed to climate change.

For climatic change variables, we used climate-change projections at 30-s resolution (Hijmans et al., 2005) based on an ensemble of four General Circulation Models (BCC-CSM1-1, MIROC-ESM, MIROC-ESM-CHEM and MIROC5) and three representative concentration pathways for 2050 (average for 2041–2060) and 2070 (average for 2061–2080). These pathways represent low (RCP4.5), intermediate (RCP6.0) and high (RCP8.5) emission scenarios.

We assessed changes in mean temperature as the absolute change in mean temperature across species' ranges for all months between 1975 and 2050. We assessed changes in temperature variability as the absolute difference in AAD in temperature across species' ranges for all months between 1975 and 2050. To assess changes in mean precipitation we calculated the absolute ratio of changes in mean precipitation across species' ranges for all months between 1975 and 2050. For changes in precipitation variability, we calculated the absolute ratio of changes in AAD in precipitation across species' ranges for all months between 1975 and 2050. We considered the 25% of species with the highest values for climatic change variables to be highly exposed to climate change. We repeated the analyses for projections to 2070. We reported overall vulnerability using RCP6.0 for 2050 as an average projection compared to the pessimistic RCP8.5 and the optimistic RCP4.5 (see results in Supplementary Material).

Sensitivity analyses

The use of traits with missing information and the selection of arbitrary thresholds for continuous traits may affect the output of trait-based vulnerability assessments. We assessed the sensitivity of our results to missing data by first scoring all unknown trait values as *low* (treatment 1, described in the main results unless mentioned otherwise) and then considering these as *high* (treatment 2). We also repeated the analysis by excluding traits with more than 40% missing data or where alternative assumptions concerning the relationship of traits with climate change can be made (e.g. burrowers and cave dwellers) (treatment 3). We present detailed sensitivity analyses in the Supplementary Material. To investigate species' sensitivity to trait selection, we also removed each trait in turn from the analysis and identified the total number of species sensitive to the removal of that trait.

In most continuous variables, there are no ecological thresholds to classify species as vulnerable to climate change. To investigate the sensitivity of our results to arbitrary thresholds, we repeated the analyses with thresholds from 5% to 50% in 5% increasing intervals. The main result is described using the 25% threshold for continuous variables as used in Foden et al. 2013 and Böhm et al. 2016.

Comparison with the IUCN Red List

The IUCN Red List uses unstructured expert elicitation to identify key threatening processes affecting species based on the IUCN threat classification scheme (Salafsky et al., 2008). We compared which of our species assessed as vulnerable to climate change were threatened (Vulnerable, Endangered, or Critically Endangered) in the IUCN Red List. In addition, we recorded which of the climate change vulnerable species also had climate change listed as a threat in the IUCN Red List.

RESULTS

Overall vulnerability

Based on the first treatment of missing data (all unknown traits values set to *low*) and default climate change scenarios (RCP6.0 for 2050), we found that 15% of freshwater crayfish (87 species) were vulnerable to climate change (Fig. 1). Climate change-vulnerable species belonged to 19 of the 32 crayfish genera. Of these, *Procambarus* showed the highest number of climate change vulnerable species (14 spp.), followed by *Cambarus* (13 spp.), *Euastacus* (12 spp.), *Orconectes* (7 spp.; Table S2). The highest number of climate change-vulnerable species were located in the south-eastern USA (36 out of 346 spp.), Australia (22 out of 151 spp.), Mexico (10 out of 49 spp.) and Madagascar (6 out of 7 spp.) (Fig. 2a).

Combining sensitivity and low adaptive capacity alone, 196 species (34%) were biologically susceptible to climate change (Fig. 1). The application of different thresholds for quantitative traits showed a linear relationship between the threshold and the number of species vulnerable to climate change (Fig. 3). Excluding burrowers and cave dwellers from treatment 1 resulted in 85 species being vulnerable to climate change.

Climate-change vulnerability varied among climate-change scenarios, with most species vulnerable under scenario RCP8.5 (Fig. S1 and Table S3). The numbers of climate change-vulnerable species under the different missing data treatments and RCPs are summarised in Fig. 4 and Table S3 (see, Fig. S1 for species richness in 2050 and 2070).

When all unknown trait values were set to *high* (treatment 2), 249 (43%) species were identified as vulnerable (Fig. 2b). Here, hotspots of climate-vulnerable species were found in the USA (180 spp.), Australia (32 spp.), Mexico (13 spp.) and South American countries (9 spp.). The proportion of missing data ranged between 0.6% and 64.6% among traits, with large data gaps for clutch size (64.6% missing data), high DO dependency (63.6%), rarity (44%) and fragmented population ranges (41.6%; Table S4). Exclusion of these traits (treatment 3) resulted in 68 species assessed as vulnerable to climate change. Excluding burrowers and cave dwellers from treatment 3 (missing traits excluded) resulted in 66 species being vulnerable to climate change.

Sensitivity

Considering sensitivity alone, when missing data were assumed to lead to *low* vulnerability to climate change (treatment 1), 87% (502 spp.) of species were highly sensitive to climate change. High sensitivity was primarily triggered by habitat specialization (291 spp.), microhabitat specialization (173 spp.), tolerance to temperature and precipitation changes (143 spp.), and interspecific dependencies (142 spp.). Overall, 172 species scored high for sensitivity due to a high sensitivity score on a single trait, with the largest number of species (69 spp.) receiving a high score due to habitat specialization only. Removing habitat specialization and interspecific dependencies resulted in 433 and 475 species listed as highly sensitive to climate change, respectively. Removing other traits (dependence on high DO, rarity, and fragmented population ranges) had little effect on the results (Table S5).

In treatment 2 (missing traits values set to *high*), 570 species were scored as highly sensitive to climate change. Excluding traits with poor data quality (treatment 3) resulted in 490 species listed as highly sensitive. Excluding burrowers and cave dwellers from treatment 3 resulted in 462 species listed as highly sensitive. Of the 40 species that got dropped out moving from treatment 1 to treatment 3, nine were predicted to have climate change as a threat in the IUCN Red List and six were vulnerable in our main analysis (treatment 1).

Adaptive capacity

We found 204 species (36%) to have low adaptive capacity in treatment 1 (missing traits values set to *low*). Of the four traits assessed in this dimension, the largest number of species was found to have low adaptive capacity due to range restriction (143 spp.) and clutch size (50 spp.). Altogether, we scored 159 species as having low adaptive capacity due to the contribution of a single trait, mostly range restriction (100 spp.). Removing range restriction from the adaptive capacity dimension resulted in 104 species having low adaptive capacity. Extrinsic barriers to dispersal had the lowest effect on adaptive capacity and its removal resulted in the assessment of 198 species as having low adaptive capacity. Under treatment 2 (missing traits values set to *high*), 455 species were assessed as low adaptive capacity (Fig S3). Removing declining population trend and clutch size from the adaptive capacity dimension (treatment 3, missing traits excluded) resulted in 181 and 174 species being listed as having low adaptive capacity, respectively.

Exposure

Data were available for all variables in the exposure dimension. Overall, we scored 57% of species (325) as highly exposed to climate change based on an ensemble mean of four general circulation models for a moderate IPCC scenario, RCP6.0. For 142 species, this was due to exceeding the threshold value in a single variable. Changes in precipitation and temperature variability resulted in 65 and 33 species listed as highly exposed, respectively. Removing sea level rise habitats had the smallest impact (322 spp. out of 325), whereas changes in precipitation had the largest impact, resulting in 260 highly exposed species (out of 325 spp.). Removing changes in temperature variability, changes in precipitation variability and changes temperature changes resulted in 292, 297 and 311 species listed as highly exposed, respectively.

Comparison with the IUCN Red List

Of the 574 crayfish, assessed in this study 144 are listed as threatened in the IUCN Red List. Of these, 41 were predicted to be climate change vulnerable in this study (37 species based on treatment 3, missing traits excluded). The number of climate change-vulnerable species in each country or region differed from the number of species predicted to have climate-related threats in the IUCN Red List (Fig. 5a). Of the 91 species listed as threatened by climate change on the IUCN Red List (83 in Australia alone), 18 species were also predicted to be climate change-vulnerable in this study (Fig. 5b, Table S6). In Australia, 16 species were identified as vulnerable to climate change under both the IUCN Red List and the trait-based vulnerability protocol (Table S7).

DISCUSSION

We present the first global climate-change vulnerability assessment of freshwater crayfish, a highly imperilled group (32% threatened; Richman et al., 2015). We assessed 15% of crayfish (87 species) as vulnerable to climate change, with large variations in species identified as sensitive (87%), low adaptive (36%), or highly exposed (57%). Sensitivity analyses revealed wide variation in the contribution of different traits to the overall vulnerability assessment. Comparisons with species listed as threatened on the IUCN Red List showed that many of our climate change-vulnerable species (41 spp.) are also threatened on the IUCN Red List. However, there was little congruence between species identified as vulnerable to climate change by our protocol and species identified as threatened by climate change on the IUCN Red List. This implies that climate-change vulnerability assessments generate additional conservation priorities to those identified by the IUCN Red List.

One reason behind the differences found between the IUCN Red List and our analysis is the different objectives of the two protocols. While the IUCN Red List focuses on population and range symptoms to assess risks from a wide variety of threats, climate-change vulnerability assessments use risks from sensitivity, exposure, and low adaptive capacity to quantify overall climate-change vulnerability. The two protocols are likely to assess risk to species over different time scales for crayfish, which typically have small generation lengths (Bland, 2017; Moore et al., 2013). However, the two protocols may identify similar mechanisms of risk, with crayfish IUCN Red List assessments relying heavily on species' ranges (Bland, 2017), an important trait in our analysis.

A disproportionately high number of species from Australia (83 spp.) were deemed to have climate-related threats on the IUCN Red List compared to species from the USA (5 spp.), although the USA has more than twice the number of species than Australia (Richman et al., 2015). While the total number of vulnerable species changed with different trait selection, these patterns were robust, with both the USA and Australia always showing high numbers of vulnerable species. Climate-change modelling predicts that both south-eastern Australia (Hughes, 2003), and the USA (Karmalkar & Bradley, 2017) will experience extreme weather events in the future, suggesting that there are discrepancies between regions in the consideration of climate change as a threat on the IUCN Red List. We recommend that assessors should aim for consistency when listing climatic threats among regions. Ideally, the assessment of threats under the IUCN Red List should be based on empirical evidence such as climate scenarios for each region (i.e. threat mapping; Bland et al. 2017). This could contribute to increased transparency of threat listings and greater consistency in assessments among geographic regions.

Our results show that most crayfish are sensitive to climate change, although large numbers are also highly exposed or show low adaptive capacity. Sensitivity to climate change in freshwater crayfish is higher than in other terrestrial taxa to which the protocol has been applied (amphibians: 72%, reptiles: 81% and birds: 64%), but lower than in corals (99%). These differences between taxa can be due to differences in trait selection as well as the quality of the datasets used in each study (Böhm et al., 2016). Although we followed a standard IUCN approach (Foden et al., 2013), our assessment differed in terms of data collection, the climate datasets included and of its use of sensitivity analyses not previously conducted in trait-based vulnerability assessments.

Only six species of crayfish (out of 375) are protected under the Endangered Species Act in the USA (https://ecos.fws.gov/ecp0/pub/SpeciesReport.do?groups=K&listingType=L&mapstatus=1)

and 12 species (out of 148) are protected in Australia under the Environment Protection and Biodiversity Conservation (EPBC) Act (http://www.environment.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl), despite indications from the global IUCN Red List that many more species are at risk (Richman et al., 2015). As two major hotspots of climate-change vulnerability for crayfish are found in the USA and Australia, further analyses should be conducted to assess in-situ protection levels of vulnerable species. Although protected areas do not always protect species from climate change (Araujo, Alagador, Cabeza, Nogues-Bravo, & Thuiller, 2011), they can reduce impacts from cumulative threats. Climate change-vulnerable species should be brought to the attention of policy makers to ensure better statutory protections against harvesting and ecosystem modifications.

Assigning traits with no information a *high* score (treatment 2) rendered disproportionately large number of species (43%, 249 spp.) vulnerable to climate change compared to treatment 1 (15%, 87 spp.). This indicates the substantial data gaps for large numbers of species, as highlighted by Moore *et al.* (2013) and Westhoff *et al.* (2016). This finding underlines the importance of field data collection for species for which there is no information on certain traits. Sensitivity analyses for threshold selection for quantitative traits revealed a linear relationship between thresholds and the number of species at risk, making it difficult to select thresholds objectively (Fig. 3). The choice of a 25% threshold for treatment 1 is arbitrary but results in a manageable number of prioritised species.

Thirty-seven (43%) of our climate change-vulnerable species are not listed as threatened in the IUCN Red List and should be given increased attention in conservation planning and future IUCN Red List assessments. Species that are both climate change-vulnerable and threatened according to the IUCN Red List and regions where they are concentrated should be evaluated to reduce existing threats and create management plans for future mitigation interventions. The 16 Australian crayfish classified as vulnerable to climate change and included as threatened by climate change in the IUCN Red List (Table S6) should be the focus of immediate conservation action, followed by the establishment of monitoring programs and recovery plans. This would in part drive conservation recommendations in terms of whether there are areas that provide refugia from climate change. Special consideration for monitoring should be given to the 196 species that are not presently exposed but are biologically susceptible.

Climate change might enhance the rate of invasiveness in freshwater species (Rahel & Olden, 2008), with potential for significant alteration in macroinvertebrate communities (Mathers et al., 2016). Out of the 669 species of freshwater crayfish, 28 have established self-reproducing populations outside their native range after human translocation (Gherardi, 2010). Invasive crayfish threaten native species through competition for space and food (Lodge et al., 2000) or cause mortality as disease vectors (Capinha, Larson, Tricarico, Olden, & Gherardi, 2013). While range contraction may occur for some invasive species (Carreira, Segurado, Laurila, & Rebelo, 2017), climate change may favour range expansion for other invasive crayfish (Feria & Faulkes, 2011). Therefore, native species may have to confront challenges from both climate change related impacts and invasive crayfish.

Many species (433 spp.) were sensitive to climate change due to habitat specialization. A global study on crayfish found that habitat specialists are more at risk of extinction (Bland, 2017). Crayfish are extremely range-limited, with 25% of species with ranges smaller than 6,860 km^2. We found that range restriction alone is responsible for the assessment of 100 species as having low adaptive capacity. Small range size is typically associated with higher extinction risk in ecological theory (Bland *et al.* 2017). Range restriction leads to higher risk from spatially explicit stochastic threats that may result from climate change (Murray et al., 2017). However, the mechanisms through which climate change is likely to affect narrow-ranged crayfish is currently unclear, with some evidence suggesting high past resilience to prolonged droughts (DiStefano et al., 2009) or increased mortality (Wolff, Taylor, Heske, & Schooley, 2016).

A second important step is to assess whether species will be able to track shifting conditions through habitat connectivity. Our study showed that four out of five European freshwater crayfish are climate-change vulnerable, in agreement with a previous study that concluded that climate-suitable areas for native freshwater crayfish will decrease by 19–72%, with most future suitable areas being inaccessible (Capinha et al., 2013). Even if a species can move into new suitable locations, it may face competition with other crayfish species living in the area with uncertain consequences. Resolving these issues requires further research and is vital when considering future conservation translocations of crayfish threatened by climate change.

Our analyses relied on a number of assumptions relating species' traits to climate-change responses and considerable data gaps exist in some of the traits used (Table S4). Most of our assumptions may not suit every species due to the nature of our macro-ecological analysis. Some traits (e.g. high DO dependency, rarity within population and fragmented ranges) were derived as categorical variables based on expert opinion in the IUCN Red List, with unknown data sources and quality. Further quantitative data collection from field observations will reduce data gaps and improve data quality for these traits. Due to the paucity of information about the number of reproductive events per year for the majority of crayfish, we used maximum egg number as a proxy for clutch size. Although seasonality-dependent development (e.g. reproduction) is considered to be a major life-history trait likely to be impacted by climate change (Foden et al., 2013), lack of information prevented us from including this trait. A global review for thermal tolerance of freshwater crayfish concluded that thermal tolerance data are available for only 6% of species (Westhoff & Rosenberger, 2016). Field data collection, thermal tolerance experiments and data collation efforts through regional and global assessments should be a key research focus for data-poor crayfish (Bland, 2017; Moore et al., 2013; Westhoff et al., 2006).

An important caveat of our study is the quality of IUCN range maps, especially for freshwater species mapped at the watershed level. With only few species (62 spp. out of 574), known to have occurrence data in GBIF and ALA (Troja & McManamay, 2016), modelling the potential distributions of freshwater crayfish under climate change is challenging. Global climate projections improved substantially in CMIP5 models but those are still not free from biases and uncertainty (Wang, Zhang, Lee, Wu, & Mechoso, 2014). Our spatial metrics of sensitivity and exposure to climate change could be refined with habitat suitability models, which more accurately describe species distribution (Rondinini et al., 2011).

Species may respond to changes in climate at different rates and some may benefit from climate change through improved reproduction and/or range expansion (Gallardo & Aldridge, 2013). For example, the distribution of the Redclaw Crayfish, *Cherax quadricarinatus,* is restricted to tropical and subtropical climate and the species is unable to tolerate prolonged exposure to temperatures below 10°C (Reynolds & Soutty-Grosset, 2012). Climate warming is likely to facilitate range expansion for the species, but our protocol does not account for this.

This study provides a blueprint for the application of climate-change vulnerability assessment to data-poor invertebrates. Our key recommendations for applying this protocol in data-poor contexts are: i) conduct extensive sensitivity analysis on missing data, trait selection, thresholds, and the use of different climate models; and ii) assess similarities and differences with other tools and methods such as the IUCN Red List or if available, distribution models and mechanistic models. The strength of the trait-based protocol lies in its ability to identify data gaps and help direct research to overcome knowledge shortfalls that limit conservation efforts for climate-vulnerable species.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Table S1. List of crayfish habitats based on the IUCN habitat classification.

Table S2. List of crayfish species projected to be vulnerable to climate change.

Table S3. Summary of vulnerable species in different RCPs for 2050 and 2070.

Table S4. Total number of crayfish species scoring high and low for each trait under treatment 1 (missing traits values set to *low*).

Table S5. Summary of total number of species scoring high for a single trait only in sensitivity, adaptive capacity, and exposure.

Table S6. List of the species that were identified as vulnerable to climate change in this study that also have climate change mentioned as a threat in the IUCN Red List.

Table S7. Comparison of the numbers of crayfish species in Australia that were identified as vulnerable to climate change in this study and for which climate change is mentioned as a threat in the IUCN Red List.

Figure S1. Richness map of climate change vulnerability under treatment 1.

Figure S2. Species richness map (n = 68) of climate change vulnerability (for RCP6.0 and with 25% threshold of continuous traits) when traits of high unknown values are removed.

Figure S3. Richness map of climate change vulnerable species, when all species with unknown traits are set to *high* under treatment 2.

Table 1. Species traits and thresholds included in this study for the three dimensions of sensitivity, exposure, and adaptive capacity. Traits are annotated with S for sensitivity, A for adaptive capacity and E for exposure. See the Supplementary Material for further information on trait selection.

Sensitivity			
Traits	Explanation	Threshold	Hypotheses
Specialized habitat and/or microhabitat requirements			
S1. Habitat specialization	Total number of dependent habitats a species is known to live in	Low = > 1 habitat type High = 1 habitat type	Under climate change, generalists are likely to be able to shift distribution and resource use between habitat types, while habitat specialists may not.
S2. Microhabitat specialization	Species which is dependent on one or more microhabitats (e.g. burrows and caves)	Low = False High = True	Burrowers are dependent on predictable water levels and water seasonality. The frequency and duration of droughts and reduced flow regime due to climate change may affect the survival of burrow-dependent crayfish. Similarly, species dependent on caves may be vulnerable to climate change.
Narrow environmental tolerances that are likely to be exceeded due to climate change at any stage in the life cycle			
S3. Narrow tolerance to precipitation changes	Average Absolute Deviation (AAD) of precipitation change across species' ranges	Low = Highest 75% (> 16.82 mm) High = Lowest 25% (≤ 16.82 mm)	Species with narrow tolerance to precipitation changes are likely to be sensitive to reductions in flow regime (in both magnitude and seasonality).
S4. Narrow tolerance to temperature changes	AAD of temperature change across species' ranges	Low = Highest 75% (> 3.64°C) High = Lowest 25% (≤ 3.64°C)	Species with narrow temperature tolerances are likely to be sensitive to temperature changes.
S5. High dissolved oxygen dependency	Species has high dissolved oxygen dependency	Low = False High = True	Species dependent on high dissolved oxygen are likely to be sensitive to changes in dissolved oxygen due to climate change.

Dependence on interspecific interactions which are likely to be disrupted by climate change			
S6. Interspecific dependency	Smaller-bodied species are unable to persist with larger-bodied invasive species	Low = Highest 75 % (> 28.8 mm) High = Lowest 25 % (≤ 28.8 mm)	Smaller-bodied species will be susceptible to invasion and aggression by large crayfish shifting their distributions due to climate change.
Rarity			
S7. Rare within population	Species is rare within population	Low = False High = True	Species that are rare within populations will not be able to recover from population collapses after catastrophic events.
S8. Fragmented population ranges	Species has highly fragmented population ranges	Low = False High = True	Climate change may induce further range contraction for species that are already geographically fragmented.
Adaptive capacity			
Poor dispersability			
A1. Range restriction	Species with small distribution ranges	Low = highest 75% (> 6,860 km^2) High = lowest 25% (≤ 6,860 km^2)	Species with restricted geographic ranges may have low adaptive capacity to climate change impacts.
A2. Extrinsic barriers to dispersal	Species is surrounded by barriers such as mountains, oceans, or other anthropogenic developments	Low = False High = True	Species located in areas with extrinsic barriers that prevent species from dispersing to climatically suitable areas will be adversely impacted by climate change.
Poor evolvability			
A3. Declining population trends	Species has declining population trends	Low = False High = True	Species with declining population trends will be unable to maintain sustainable populations under climate change.
A4. Clutch size	Species is producing a small number of eggs	Low = highest 75% (> 56) High = lowest 25% (≤ 56)	Species with smaller clutch sizes are less equipped to adapt to climate change impacts.

Exposure			
Sea-level rise habitats			
E1. Exposure to sea-level rise	Species dependent only on habitats prone to sea-level rise	Low = False High = True	Habitats already prone to sea-level inundation are likely to become permanently unsuitable due to further sea-level rise.
Temperature changes			
E2. Changes in mean temperature	Changes in mean temperature across the species' range (measured as the absolute difference in mean temperature across the species' ranges for all months between 1975–2050 and 2070)	Low = lowest 75% (< 2.39°C) High = highest 25% (≥ 2.39°C)	Changes in mean temperature may exceed the upper tolerance limit of some species.
E3. Changes in temperature variability	Changes in temperature variability across the species' range (measured as the absolute difference in AAD in temperature across species' ranges for all months between 1975–2050 and 2070)	Low = lowest 75% (< 0.264°C) High = highest 25% (≥ 0.264°C)	Same as above.
Precipitation changes			
E4. Changes in mean precipitation	Changes in mean precipitation across the species' range (measured as absolute ratio of change in mean precipitation across the species' range for all months between 1975–2050 and 2070)	Low = lowest 75% (< 0.034 mm) High = highest 25% (≥ 0.034 mm)	Species experiencing severe changes in mean precipitation are likely to be highly exposed to climate change impacts, especially where species are currently occurring in areas of seasonal droughts or for species dependent on intermittent streams.

E5. Changes in precipitation variability	Changes in precipitation variability across the species' range (measured as absolute ratio of change in AAD in precipitation across the species' range for all months between 1975–2050 and 2070)	Low = lowest 75% (< 0.269 mm) High = highest 25% (≥ 0.269 mm)	Same as above.

FIGURE LEGENDS

Figure 1**.** Summary of climate-change vulnerability in freshwater crayfish using RCP6.0 for 2050. Using full trait variables, species with *high* score in all three dimensions of climate-change vulnerability (i.e., sensitivity, adaptive capacity, and exposure) were considered *climate change vulnerable.* Of the 574 species analysed in this study 502 species (87%) were found to be highly sensitive, 204 (35%) were low adaptive and 325 (57%) were highly exposed to climate change. Of these, 196 species (34%) were both sensitive and low adaptive, 282 (49%) were both sensitive and highly exposed and 90 (16%) were highly exposed and low adaptive to climate change. Overall, 87 species (15%) were predicted to be climate-change vulnerable and 24 species were scored to be immune to any climate-change impacts.

Figure 2. Species richness map of climate-change vulnerable species (87 spp.) using RCP6.0 in 2050, when species with missing traits values were set to (a) *low* or (b) *high* to climate change impacts or (c) when traits with high proportions of missing data were excluded.

Figure 3. Trait-based vulnerability scores broken down for the different dimensions under varying threshold values for quantitative traits, using RCP6.0 in 2050. Here species with missing trait values were set to *low*.

Figure 4. Climate-change vulnerability under different RCPs for 2050 and 2070. In treatment 1 species with unknown traits values were set to *low*, while in treatment 2 these were set to *high*.

Figure 5. (a) Richness map of species threatened by climate change in the IUCN Red List (n = 91) and (b) richness map of climate-vulnerable species which are also threatened by climate change in the IUCN Red List (n = 18).

Figure 1.

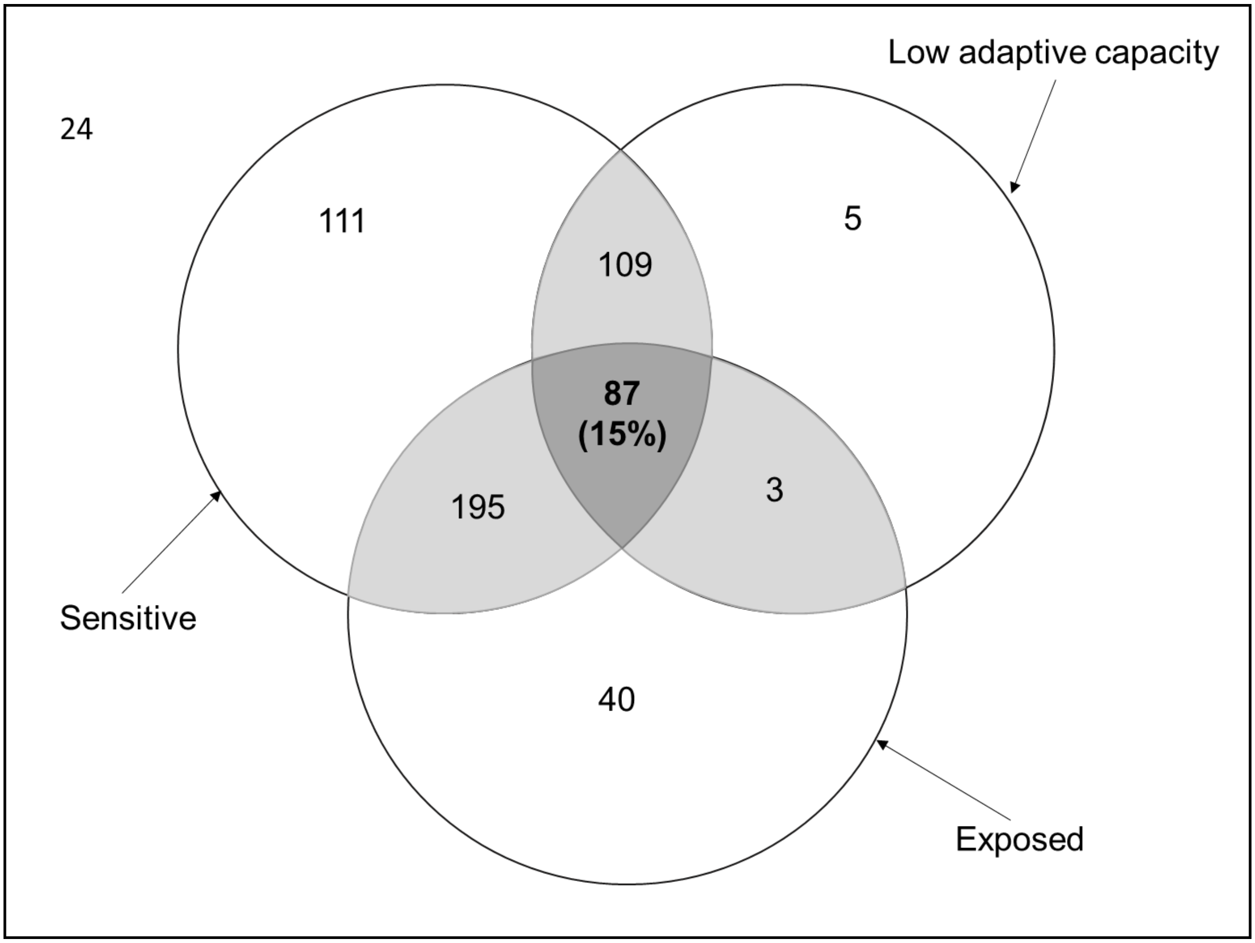

Low adaptive capacity
24
111
109
5
87
(15%)
195
3
Sensitive
40
Exposed

Figure 2.

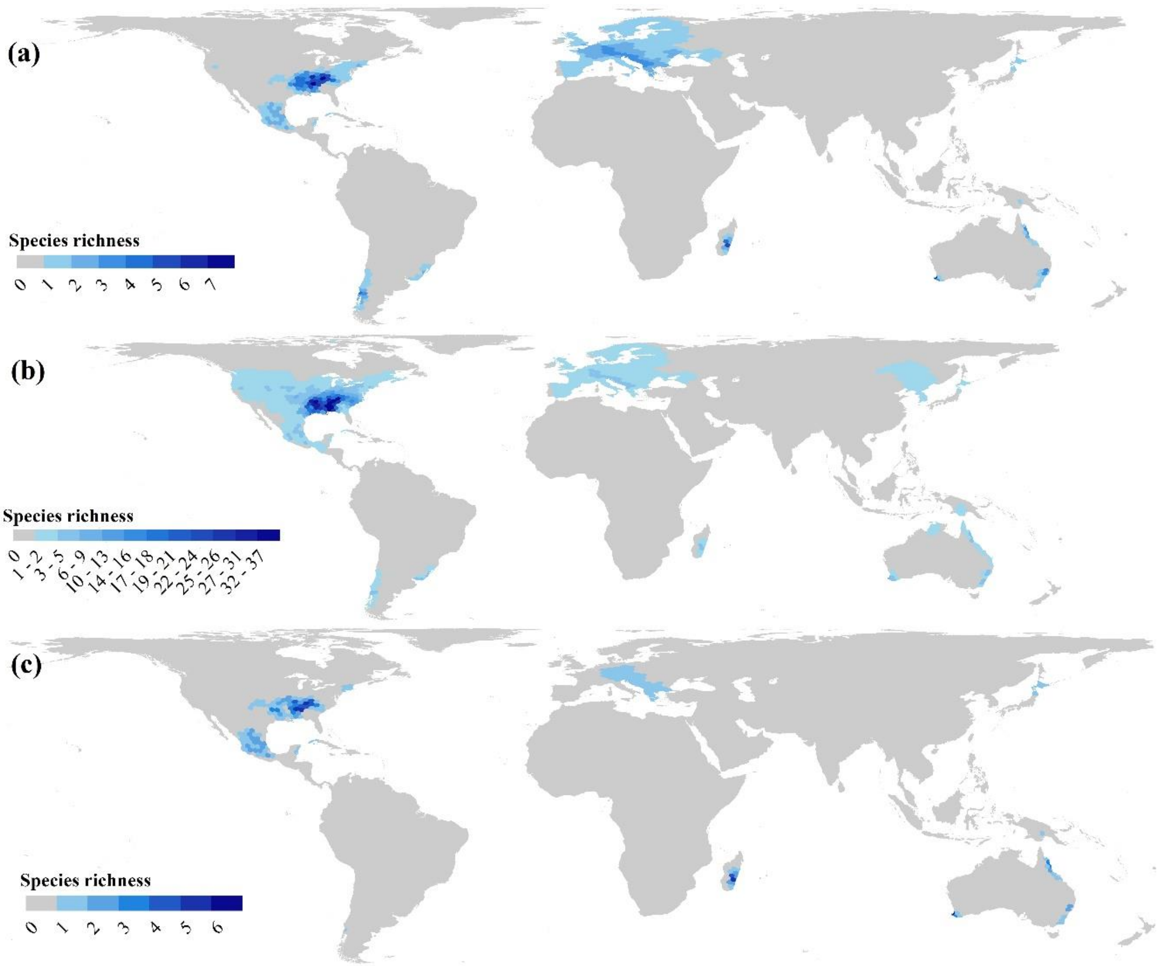

(a)
Species richness
0
1
2
3
4
5
6
7
(b)
Species richness
0
1 - 2
3 - 5
6 - 9
10 - 13
14 - 16
17 - 18
19 - 21
22 - 24
25 - 26
27 - 31
32 - 37
(c)
Species richness
0
1
2
3
4
5
6

Figure 3

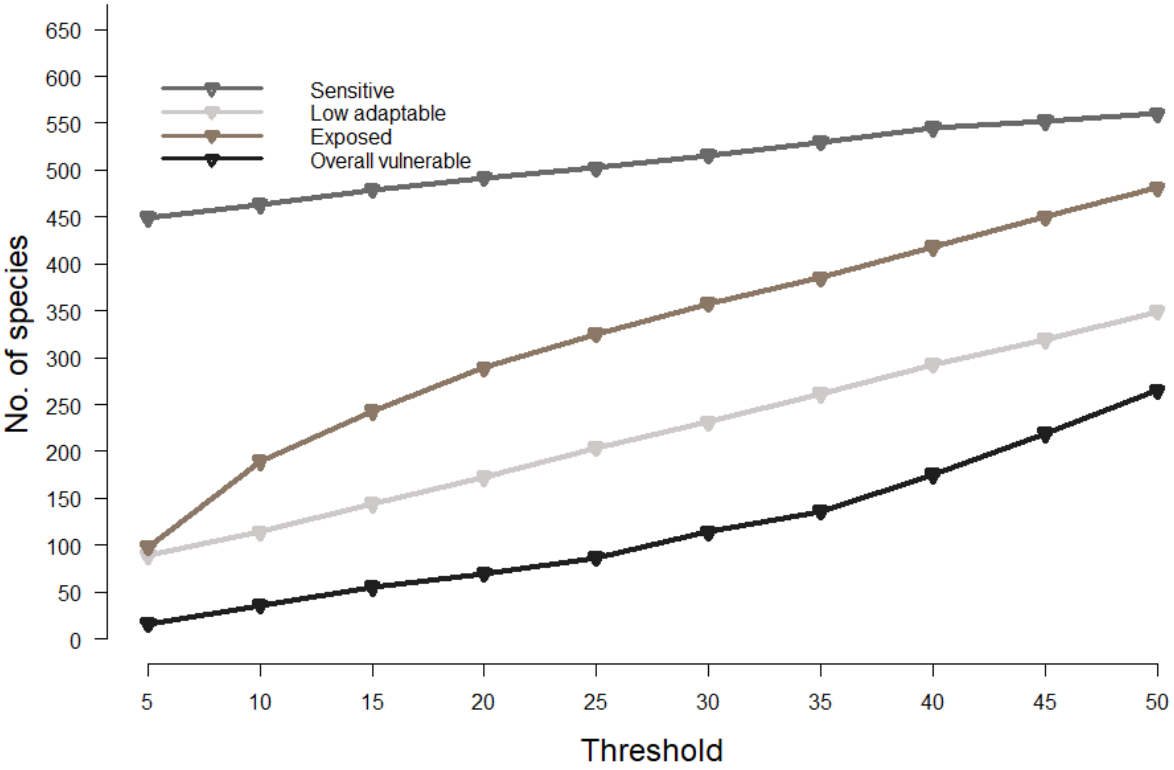

Sensitive
Low adaptable
Exposed
Overall vulnerable
No. of species
650
600
550
500
450
400
350
300
250
200
150
100
50
0
5
10
15
20
25
30
35
40
45
50
Threshold

Figure 4.

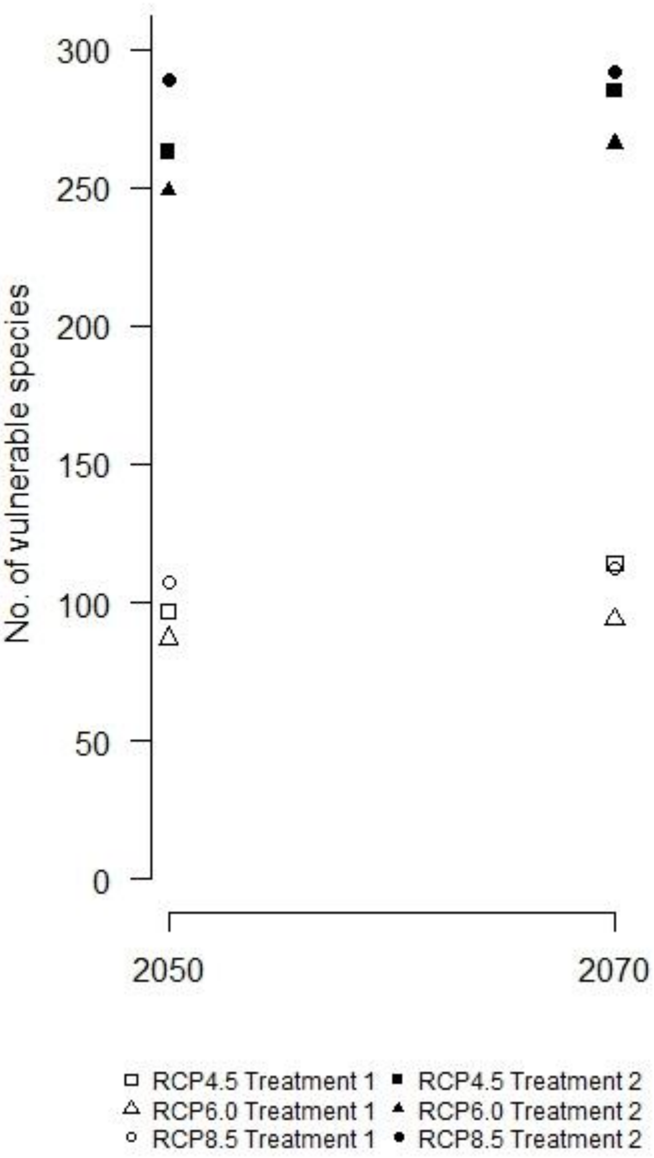
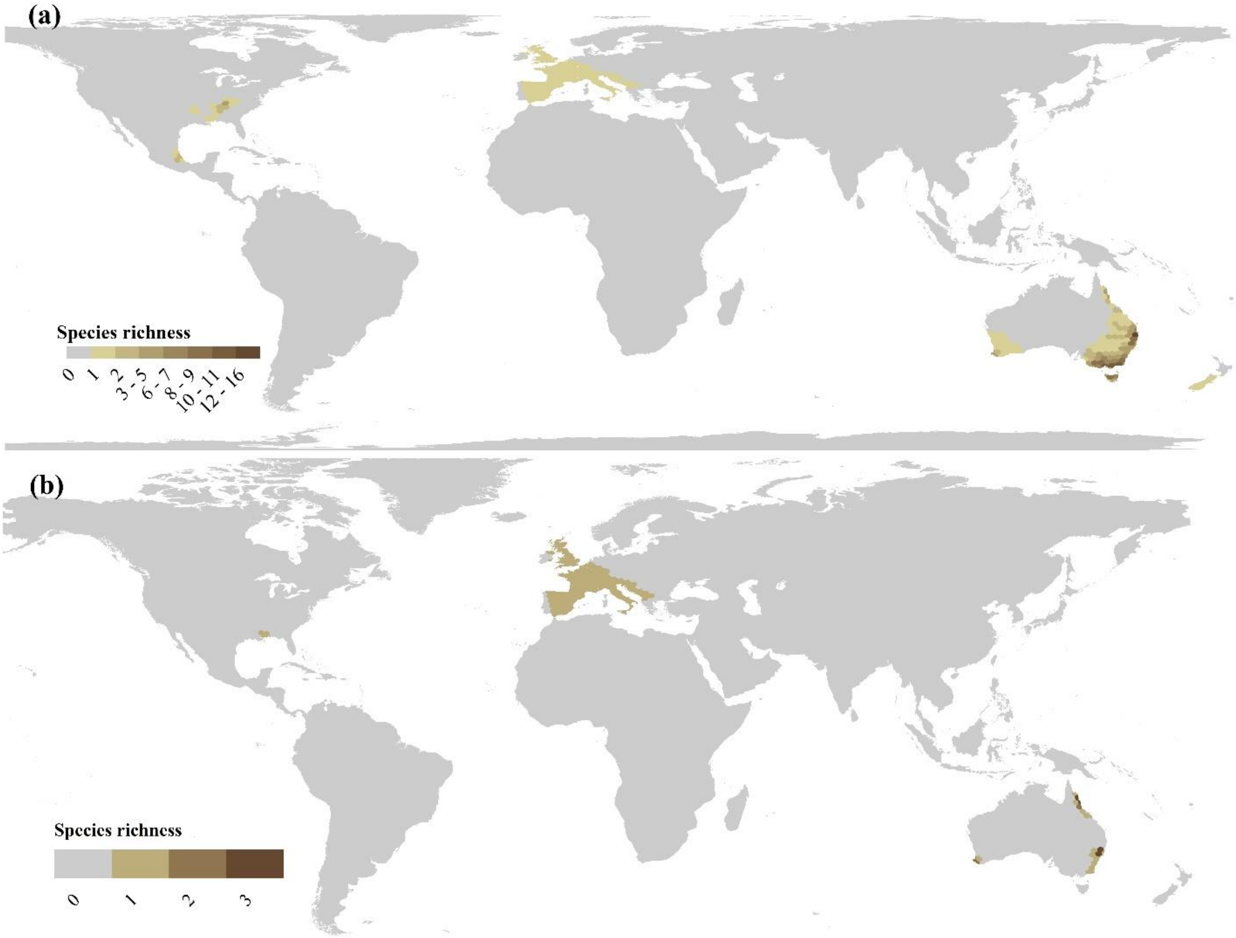

No. of vulnerable species
300
250
200
150
100
50
0
2050
2070
□ RCP4.5 Treatment 1
■ RCP4.5 Treatment 2
△ RCP6.0 Treatment 1
▲ RCP6.0 Treatment 2
○ RCP8.5 Treatment 1
● RCP8.5 Treatment 2

Figure 5.


(a)
Species richness
0
1
2
3 - 5
6 - 7
8 - 9
10 - 11
12 - 16
(b)
Species richness
0
1
2
3