UNIL | Université de Lausanne

Faculté de biologie et de médecine

Ecole de biologie

PHYSIOLOGICAL THERMAL LIMITS ALLOW ADDITIONAL INTERPRETATION OF SPECIES DISTRIBUTION MODELS

Travail de Maîtrise universitaire ès Sciences en comportement, évolution et conservation, spécialisation « Géosciences, Ecologie et Environnement »
Master Thesis of Science in Behaviour, Evolution and Conservation, specialisation «Geosciences, Ecology and Environment»

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Janvier 2022

Abstract (English)

Species distribution models (SDM) use the realised niche to predict the distribution of species. This subset of the fundamental niche defines the set of abiotic conditions where species can survive and reproduce but that is constrained by dispersal limitations and biotic interactions. SDM therefore consider certain parts of the geographic range to be unsuitable in the future, even though they might remain in the fundamental niche.

Here we use existing data on animals' physiological or field thermal limits to assess whether the fundamental thermal niche limits (hereafter FL) are expectedly less restrictive than the realized thermal niche limits (hereafter RL). We then evaluate how and to which extent these differences translate in the geographic space and what would be the effect of considering FL instead of RL for current and future predictions.

Our results show that FL is not always wider than RL but that the proportion of geographic range between RL and FL (hereafter "RF potential suitability" range) will increase at the upper bound. Our study shows that physiological data provides complementary interpretation to SDM's predictions by showing that animals can survive even when the macrohabitat exceeds their FL and that they will probably be able to exceed their RL in the future, at the upper thermal bound.

Abstract (Français)

Les modèles de distribution d'espèces (SDM) utilisent la niche réalisée pour prédire la distribution d'espèces. Ce sous-ensemble de la niche fondamentale définit un ensemble de conditions où une espèce peut survivre et se reproduire mais limité par les limites de dispersion et les interactions biotiques. Les SDM considèrent donc que certaines parties de l'aire géographique ne seront plus viables dans le futur, malgré le fait qu'elles pourraient rester dans la niche fondamentale.

Ici, nous utilisons les limites thermiques existantes d'animaux, physiologiques ou de terrain, pour évaluer si les limites thermiques de la niche fondamentale (ci-après FL) sont, comme attendu, plus larges que les limites thermiques de la niche réalisée (ci-après RL). Nous évaluons ensuite comment et dans quelle mesure ces différences se traduisent dans l'espace géographique et quel serait l'effet de considérer FL au lieu de RL pour les prédictions actuelles et futures.

Nos résultats montrent que FL n'est pas toujours plus large que RL mais que la proportion d'aire géographique entre RL et FL (ci-après "RF potential suitability" range) augmente à la limite supérieure. Notre étude montre que les données physiologiques fournissent une interprétation complémentaire aux prédictions des SDM, en montrant que les animaux peuvent survivre même lorsque le macro-habitat dépasse leurs FL et qu'ils seront probablement capables de dépasser leur RL à l'avenir, à la limite supérieure de températures.

Keywords

Fundamental niche, Realized niche, thermal limits, geographic range

Introduction

Species distribution models (SDM) are powerful tools to model the current and the future geographic distribution of species by coupling observed occurrence data with topo-climatic data (Guisan & Zimmermann, 2000; Elith & Leathwick, 2009). SDM are based on the environmental niche concept as introduced by Hutchinson (1957). Hutchinson distinguished two types of niches: the fundamental niche which defines the set of abiotic conditions allowing individuals to survive and reproduce (i.e. where the population growth rate is positive) and the realized niche which is the fundamental niche constrained by biotic interactions and, as added more recently, by dispersal limits. The realized niche is therefore expected to be more restrictive than the fundamental niche (Soberón & Arroyo-Peña, 2017). Nevertheless, Soberón and Arroyo-Peña (2017) hypothesize that a species may have a realised niche that is apparently larger than the fundamental niche (e.g. fitted by a model) if: 1) there are suitable microhabitats in non-viable macrohabitats, behavioural adaptations or facilitation mechanisms (Bruno et al., 2003); 2) There has been an evolution of the physiological limits of the species between the collection of the data and the current period; and 3) There are sink populations outside the fundamental niche (Pulliam, 2000).

Predictions from SDM rely on the realized environmental niche and consider that the environment is unsuitable beyond the niche limits (Veloz et al., 2012). These models are therefore unable to predict the distribution of the species if biotic interactions change (Wisz et al., 2013; Jiménez et al., 2019). However, under rapid climate change, evidence suggest that species are tracking suitable environmental conditions at different pace (Burrows et al., 2011; Santini et al., 2016), implying potential changes in biotic interactions (Montoya & Raffaelli, 2010; Blois et al., 2013). Such changes may lead species to occupy sites with new conditions previously not included within their realized niche e.g. if there is a release of the competition pressure that allow species to colonize and thrive in new abiotic conditions (Catullo et al., 2015). As a result, the use of the fundamental niche rather than or in addition to the realized niche in SDM is increasingly recognized as useful for the interpretation of distribution patterns (Pearson & Dawson, 2003; Hoffmann & Sgrò, 2011; McMahon et al., 2011). Some studies in particular have shown that using physiological data in models can reduce the impact of climate change on the distribution of species compared to models that do not use them (Bush et al., 2016; Gamliel et al., 2020). The major problem is that if such physiological data are supposed to reflect the limits of the fundamental niche, they are however difficult and costly to acquire, because they must be measured in the laboratory, under controlled conditions, considering many individuals (Sunday et al., 2012; Bennet et al., 2018).

Recently, the GlobTherm database containing the physiological thermal limits of hundreds of species of plants, fungi and animals collected from many studies was released (Bennet et al., 2018). Given that temperature is one of the main drivers of the distribution of animal species

(Merriam, 1894; Orton, 1920; Cossins & Bowler, 1987), this database represents a great opportunity for determining how and to which extent fundamental niche limits differ from realized niche limits. In our study, we used global geographic databases to estimate the observed realized niche thermal limits (hereafter RL) of 597 species belonging to five classes of animals: actinopterygians, amphibians, malacostracans, mammals and reptiles. We used the physiological data from the GlobTherm database as a proxy for the fundamental thermal niche limits (hereafter FL) of the same species. Using these two databases, we first tested the hypothesis that FL is indeed less restrictive than RL at both extremes of the gradient (lower and upper thermal limits). We then evaluated how and to which extent these changes translate in the geographical space and what would be the effect of considering FL instead of RL for future predictions. We expected that the proportion of geographic range of species currently predicted as "suitable" by both FL and RL would remain the same for lower thermal limits, as both FL and RL lower bounds theoretically consider the whole current geographic range as "suitable" and temperatures are expected to increase overall (see Figure 2). On the other hand, for the upper thermal limits, we expected that the proportion of species geographic ranges that is currently predicted as "suitable" would decrease by 2100. Furthermore, since FL is expected to be less restrictive than RL, we expected that part of the geographic range classically predicted by SDM as unsuitable (both under current and future environmental conditions) would be predicted as suitable based on FL. This study is important to pinpoint the differences in predictions between field data (limits of the realised thermal niche) and physiological data. In addition, this can make it possible to define a geographic range potentially suitable for species under specific physiological assumptions, which provides additional interpretation to SDM.

Method

Data acquisition

Distribution data for species belonging to five taxonomic groups (*Actinopterygii, Amphibia, Malacostraca, Mammalia, Reptilia*) were recovered from two databases: IUCN (International Union for Conservation of Nature; https://www.iucnredlist.org/en) and GBIF (Global Biodiversity Information Facility; https://www.gbif.org/en/). IUCN data are expert-based and come in the form of coarse polygons representing the global geographic distribution of a given species (Burgman & Fox, 2003; Herkt et al., 2017; Alhajeri & Fourcade, 2019). GBIF data, on the other hand, are citizen-science based and come in the form of point coordinates with a high resolution but whose spatial coverage is limited (Yesson et al., 2007; Chandler et al., 2017). GBIF data were cleaned by removing: empty elements, non-georeferenced occurrences, missing observations, duplicated coordinates for the same species and coordinates that had both a latitude and a longitude equal to zero.

Physiological thermal limits were retrieved from the "GlobTherm" dataset. This dataset compiles physiological thermal limits for plants, fungi and animals, based on 567 studies (Bennet et al., 2018). Several metrics were used to determine physiological thermal limits,

depending on the groups and studies present in the dataset. The most common metric was the "Critical Threshold" (CT) which is the temperature at which individuals can no longer perform basic functions, such as feeding or moving (59.5% of the species considered in our analyses at upper bound; 30.1% at lower bound). For some species (3.4% at lower bound; 4.8% at lower bound) "Lethal Temperatures" (LT50, when 50% of the individuals died; LT100, when 100% of the individuals died) were reported. For mammals (37.1% of the species considered at upper bound; 65.2% at lower bound), the thermal limit was measured as the "Thermal Neutral Zone" (TNZ) which is the limit above and below which an individual must actively regulate its body temperature to maintain a fixed internal temperature.

To recover the lower thermal limits and upper thermal limits within the realized niche of each species (RL), we used two different raster layers representing the "maximum temperature of the warmest month" and the "minimum temperature of the coldest month". For terrestrial species, we used "Worldclim" raster layers at a 2.5' resolution (WorldClim; https://worldclim.org/) whereas for marine species we used surface raster layers at a 5' resolution from "Bio-ORACLE" (Bio-ORACLE : Marine data layers for ecological modelling; https://www.bio-oracle.org/). These resolutions were the highest we could acquire.

Due to their low precision, IUCN polygons are often projected on rasters with a coarse resolution (Akçakaya et al., 2006). For our study, we wanted to keep as many pixels as possible, to calculate more precisely the proportion of "suitability" in the geographical range. The polygons of each species were therefore projected onto the maximum and minimum temperature rasters, at low resolution (1°) and highest available resolutions (2.5' for terrestrial and freshwater species, 5' for marine species). The trend of the different classes remains the same between the different resolutions (see Appendix 1). The high-resolution rasters were therefore kept for the entire study.

To study changes in "suitable" ranges in the future we used the same temperature layers as for the current period under two Representative Concentration Pathways (RCP): RCP2.6 and RCP8.5. RCPs are climate scenarios that include global temperature changes by 2100. RCP 2.6 predicts the weakest changes whereas RCP 8.5 is the scenario that predicts the most significant temperature changes (van Vuuren et al., 2011). For terrestrial environments, predictive rasters for the years 2081 to 2100 from the Climate System Model of Beijing Climate Center (BCC-CSM2-MR) were retrieved from the "WorldClim" website. For marine environments, rasters for the years 2090 to 2100 were recovered from the "Bio-ORACLE" website.

Determination of thermal limits

To determine RL from IUCN polygons, we extracted the values of pixels contained within the polygon of each species (thus assuming that the species is present everywhere within the polygon) for both the raster of minimum and maximum temperatures (see Figure 1), in the R software, version 4.0.4 (R Core Team, 2021), using the "raster" package, version 3.5 (Hijmans, 2020). For species at least partially terrestrial we used the Worldclim rasters while for marine

species we used the Bio-ORACLE rasters. For freshwater species, we used values for terrestrial rasters as surrogate for freshwater values (Morrill et al., 2005). The highest and lowest values were retrieved to determine the upper and lower bounds of RL, respectively (dashed blue lines in Figure 1). For GBIF data, RL were directly retrieved from values extracted from point coordinates. Species whose distribution contained less than 30 cells (either for GBIF or IUCN data; 123 species in all) were considered rare species. These species are more sensitive to climate change than common species (Foden et al., 2013). We therefore removed them to avoid potential confounding effects on "suitable" ranges changes, in the future. FL (dashed red lines in Figure 1) were extracted from the GlobTherm dataset. Species for which either the upper or lower FL was available were retained.
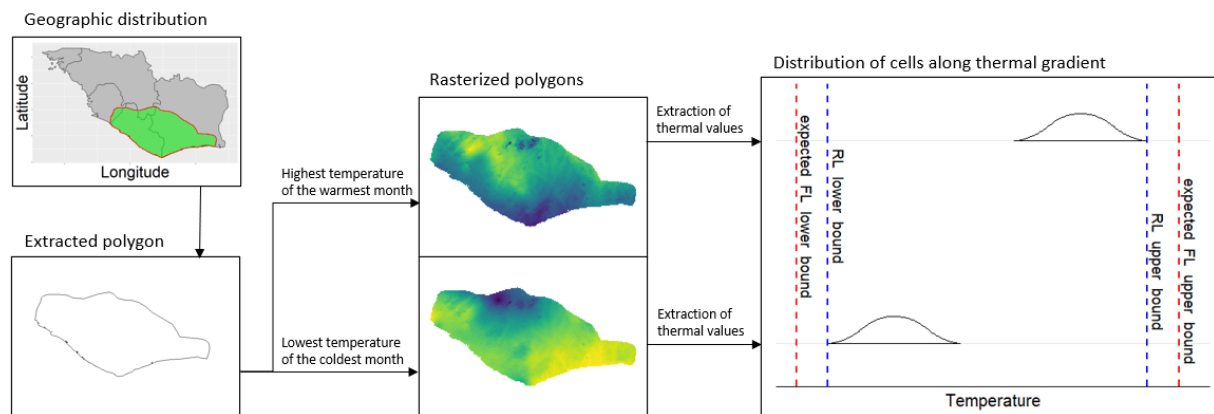

Figure 1. Realized thermal niche limits (RL) determination process for IUCN data. Physiological thermal limits considered as fundamental thermal niche limits (FL) were directly extracted from GlobTherm dataset.

Overall, data from 597 species were used in the study. 474 species (35 marine actinopterygians, 64 freshwater actinopterygians, 38 amphibians, 3 malacostracans, 176 mammals, 158 reptiles) had data on the upper limit while 419 species (15 marine actinopterygians, 8 freshwater actinopterygians, 17 amphibians, two malacostracans, 273 mammals, 104 reptiles) had data on the lower limit, for both RL and FL. Actinopterygians were separated into two groups owing to some species living in freshwater environments and other living in marine environments.

For each class of animals, we tested the difference between RL and FL using a paired Wilcoxon test. Upper and lower bounds were considered separately. Differences between RL and FL were tested separately depending on whether RL was estimated with GBIF or IUCN data.

Determination of the proportion of "suitable" and "potentially suitable" geographic ranges

In order to measure the changes in the proportion of cells "suitable" and "potentially suitable" over the geographic range for each species between the current period and the future, we computed these proportions for each projection (current, RCP 2.6 and RCP 8.5) and for each limit (lower or upper) separately. The proportion of geographic range considered "suitable" according to RL was called "RL suitability" range (green segments in Figure 2). The proportion of range "suitable" according to FL was called "FL suitability" range (light blue segments in

6

Figure 2). FL is expected to be higher than RL at upper bound (respectively lower than RL at lower bound), for all species (Figure 2, yellow segments of theoretical case "1)"). However, it is also possible, for some species, that RL is higher than FL at upper bound of lower than FL at lower bound (Figure 2, yellow segments of theoretical case "2)"). In the two cases, the yellow segments in Figure 2 show that some of the cells in the rasterised geographic range are "suitable" according to the least restrictive limit but are "unsuitable" according to the most restrictive limit. These cells were considered "potentially suitable". The proportion of "potentially suitable" cells in the geographical range was called "RF potential suitability" range. The "RF potential suitability" ranges that followed either the theoretical case "1)" or "2) were presented in the same way in the results, due to of the difficulty we had in separating the species within a group and the divergences that can exist for the same species between the lower bound and the upper bound (e.g. FL higher than RL at upper bound and higher than RL at lower bound). Nevertheless, the distinction between "RF potential suitability" ranges according to theoretical case "1)" or "2)" was done in the discussion.
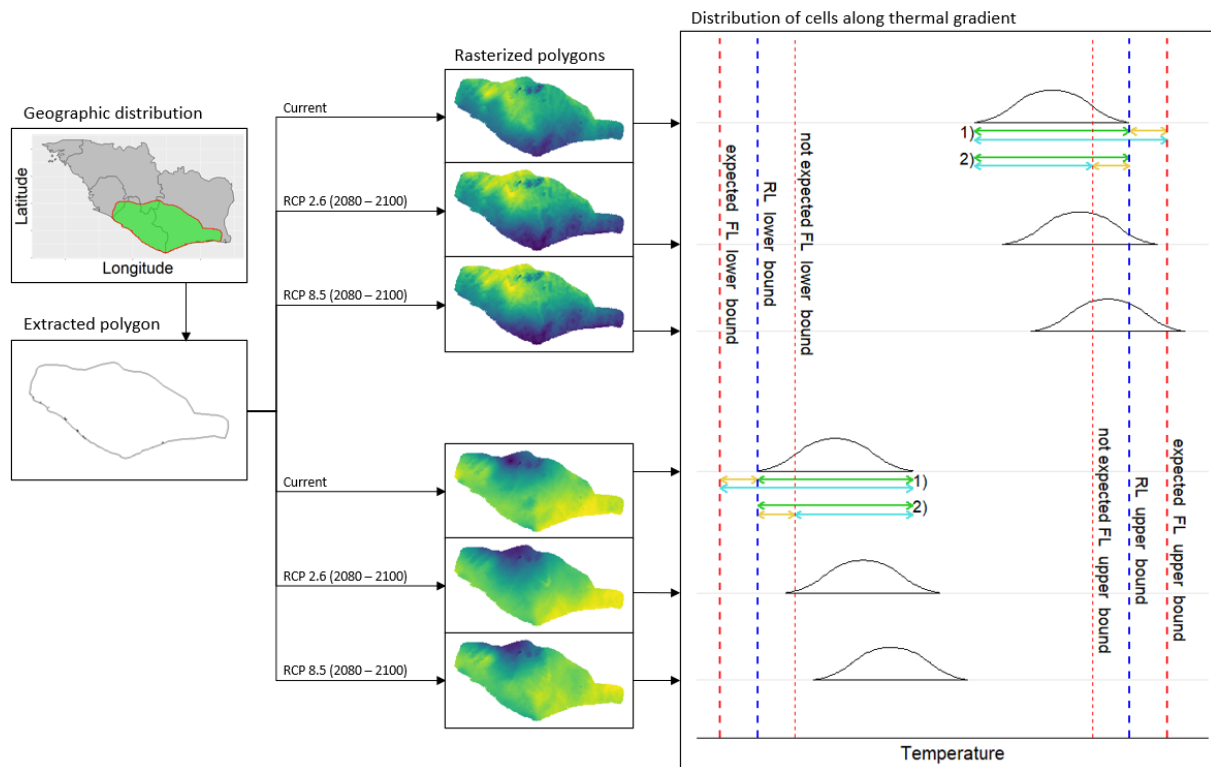

Figure 2. Determination process of "suitable" and "potentially suitable" ranges' proportions for IUCN data. Green segments show the thermal ranges used to measure the proportions of "suitable" range according to realized thermal niche limits (RL). Light blue segments show the thermal ranges used to measure the proportions of "suitable" range according to fundamental thermal niche limits (FL). Yellow segments show the thermal ranges used to measure the proportions of "potentially suitable" range. For both upper and lower bound, 2 theoretical cases are possible to measure the "potentially suitable" range, depending on whether FL is less restrictive than RL (case "1)") or if RL is less restrictive than FL (case "2)"). The same procedure was used for future projections, but the segments are not shown. See Figure 4.A,B,C for an example of geographic range subdivided following the theoretical case "1)" and Figure 5.A,B,C for an example of geographic range subdivided following the theoretical case "2)".

Specifically, for each projection and considering the upper (respectively lower) bound, we extracted the number of cells with a value lower (respectively higher) or equal relative to both

RL (considering both IUCN and GBIF data) and FL. These numbers were then divided by the total number of cells in the rasterized polygon to determine the proportion of the geographic range considered as "suitable" relative to RL and FL (respectively light green and light blue segments in Figure 2). To determine the proportion of the geographic range that is "potentially suitable", we subtracted the number of cells within RL from the number of cells within FL. The absolute value of this difference was then divided by the total number of cells in the rasterized polygon, to obtain the proportion of geographic range that is potentially suitable (yellow segment in Figure 2). Recovering the absolute value of the difference was necessary, as some species had RL less restrictive than FL.

Significant changes regarding the proportion of the geographic range considered "suitable" and "potentially suitable" between the current period and the future were tested separately for each taxonomic group using a Kruskal-Wallis non-parametric test.

Results

Thermal limits comparison

Regarding the upper bound (Figure 3.A), mammals and freshwater actinopterygians showed a tendency for RL to be higher than FL (paired Wilcoxon tests with both p-values < 0.001) whereas the opposite was found (i.e. FL higher than RL) for marine actinopterygians and reptiles (paired Wilcoxon test's with both p-values < 0.001). Amphibians and malacostracans showed no significant differences between RL and FL (paired Wilcoxon tests with both p-values > 0.05).
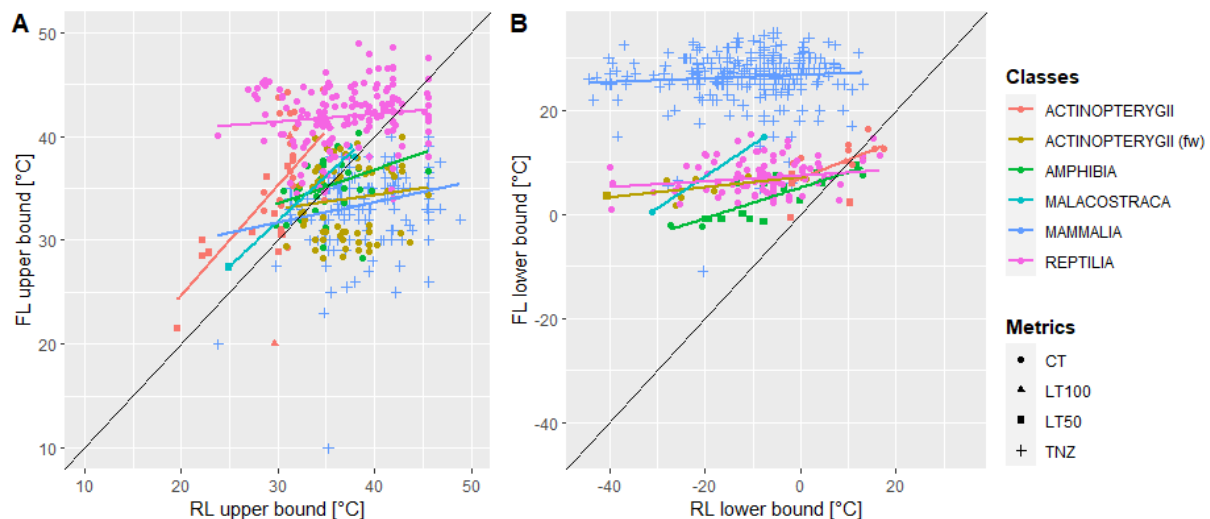

Figure 3. Comparison of species' FL and RL for both upper and lower bounds. A. Comparison for upper limits. **B.** Comparison for lower limits. CT: Critical Threshold; LT100: Lethal Temperature for 100% of individuals; LT50: Lethal Temperature for 50% of individuals; TNZ: Thermal Neutral Zone. RL was estimated from IUCN polygons. For a similar figure with RL estimated from GBIF data see Appendix 2.

For lower limits (Figure 3.B), FL of reptiles, mammals, amphibians and freshwater actinopterygians were higher than their RL (paired Wilcoxon tests with all p-values < 0.05).

The remainder of actinopterygians and malacostracans showed no significant differences between RL and FL (paired Wilcoxon tests with both p-values > 0.05).

Similar results were obtained when RL were estimated with GBIF data (Appendix 2).

Changes in the proportion of "suitable" and "potentially suitable" geographic ranges

Considering as an example the species *Pseudonaja textilis*, we illustrate how the geographic range is expected to change with respect to the upper bound between the current period and the future considering both RL and FL (Fig.4 left column). The species follows the theoretical case "1)" in Figure 2, at the upper bound. This means that FL is higher than RL at the upper bound. Because RL is defined based on the current geographic range, all pixels are included with RL and are therefore "suitable" in the current period. This proportion changes in the future owing to temperature in some pixels exceeding the upper bound of the RL. Under the scenario RCP 2.6 all these pixels are included within FL indicating that they would still be "potentially suitable". Under RCP 8.5 a larger proportion of the geographic range presents temperatures that exceed RL. However, contrary to RCP 2.6, the temperature in some pixels will increase to such an extent that it will also exceed FL upper bound indicating that these pixels would be unsuitable with regards to both niche limits.
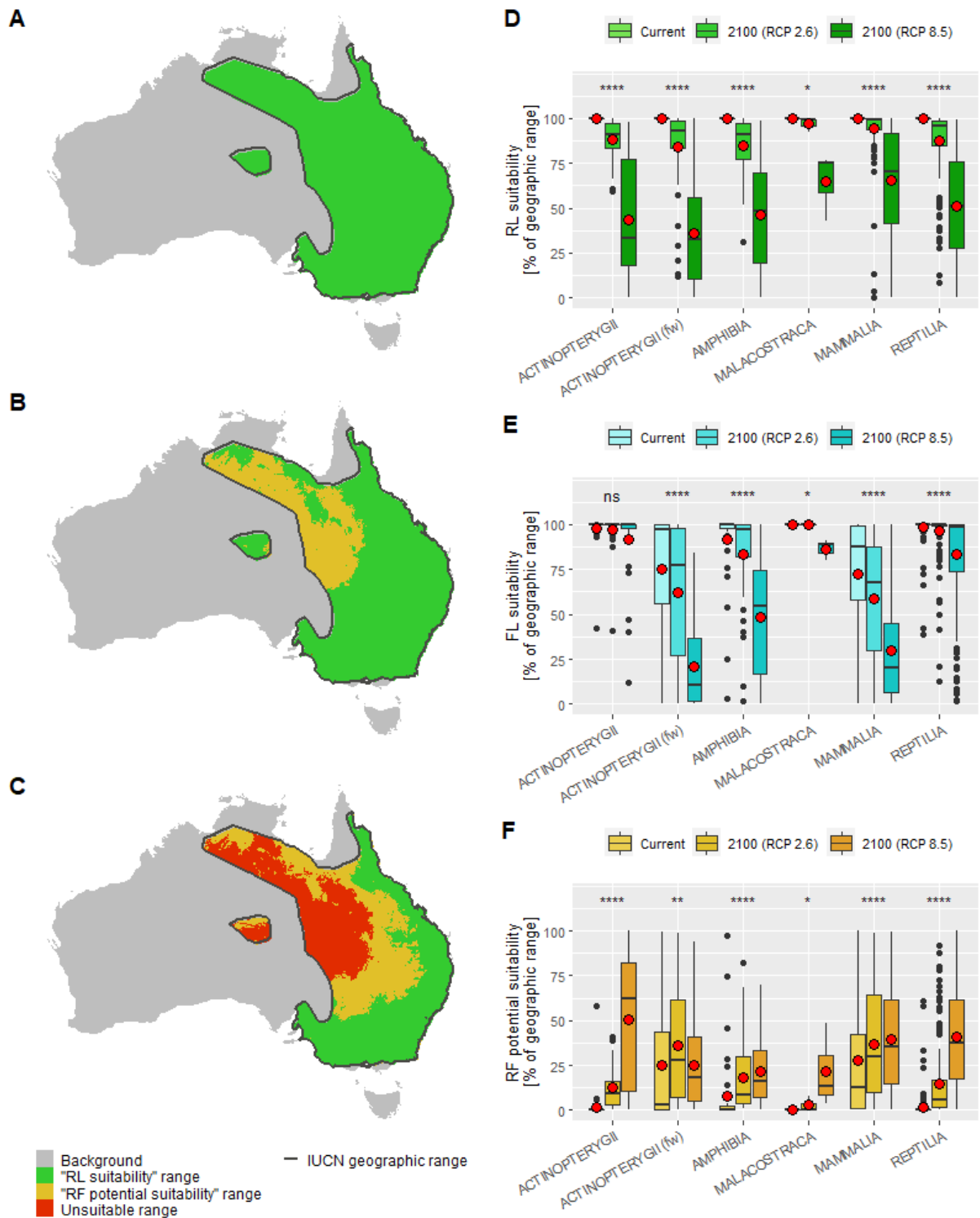
Figure 4. Changes in "suitable" and "potentially suitable" geographic ranges considering the upper bound. Panels (A) to (C): example of change in the suitable range for the species of *Pseudonaja textilis* for the current period (A) and for the future (2100) under the scenario RCP 2.6 (B) and the scenario RCP 8.5 (C). Panels (D) to (F): proportion of cells included within RL (D), within FL (E) and included within the highest limit (FL or RL, depending on the species) but excluded from the other limit (F) across all species for each taxonomic group under the three projections (current, RCP 2.6, RCP 8.5). RL suitability was estimated on the base of IUCN polygons. NS: Not Significant; *: p<0.5; **: p<0.1; ***: p<0.001; ****: p<0.0001.

More generally (i.e. considering all species), the proportion of the "RL suitability" range is predicted to decrease in the future for all taxonomic groups (Kruskal-Wallis test; all p-values

10

< 0.001)(Figure 4.D). Regarding FL, the proportion of the suitable range is also predicted to decrease (Kruskal-Wallis test; p-values < 0.001)(Figure 4.E) except for marine actinopterygians (p = 0.136). In each group (except malacostracans), some species have FL upper bound lower than RL upper bound. For this reason, some pixels are not "suitable" according to FL upper bound and the proportion of "FL suitability" is not 100% for the current time for those groups (Figure 4.E). This is more obvious for groups that have FL upper bound significantly lower than RL upper bound (i.e. freshwater actinopterygians and mammals). For all groups, the proportion of pixels categorized as "potentially suitable" is predicted to increase (Kruskal-Wallis test; all p-values < 0.001)(Figure 4.F) though to a different extent depending on taxonomic groups. For instance, under RCP 8.5, the proportion of the "potentially suitable" range for marine actinopterygians increased from 0% to 50% by 2100 and from 0% to 40% for reptiles. This increase is restricted to less than 25% for the other groups. Similar results were obtained when RL was measured with GBIF data (see Appendix 3).
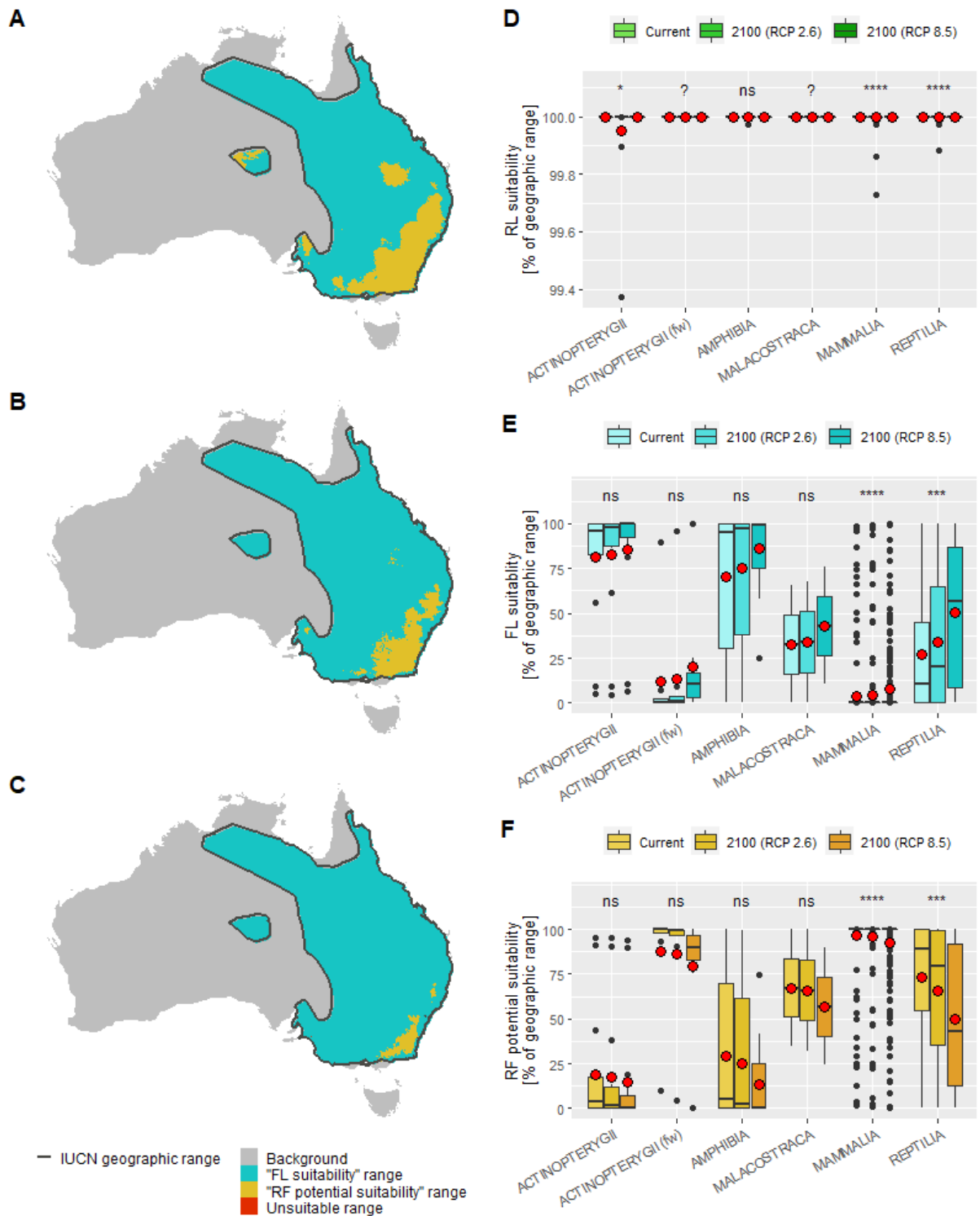
Figure 5. Changes in "suitable" and "potentially suitable" geographic ranges considering the lower bound. Left column: example of change in the suitable range for the species of *Pseudonaja textilis* for the current period (A) and for the future (2100) under the scenario RCP 2.6 (B) and the scenario RCP 8.5 (C). Right column: proportion of cells included within RL (D), within FL (E) and included within the lowest limit (FL or RL, depending on the species) but excluded from the other limit (F) across all species for each taxonomic group under the three projections (current, RCP 2.6, RCP 8.5). RL suitability was estimated on the base of IUCN polygons. NS: Not Significant; ?: no variation between the 3 projections; *: p<0.5; **: p<0.1; ***: p<0.001; ****: p<0.0001.

Similar to the upper bound, we illustrate here how the geographic range of *Pseudonaja textilis* is predicted to evolve in the future for both FL and RL this time considering the lower bound

12

of niche limits. Importantly, and contrary to the upper bound, we can see that not all pixels of the current geographic range are considered "suitable" with regards to FL. This is because some pixels with species occurrences (i.e. RL) have lower temperatures than FL of the species. Indeed, this species follows the theoretical case "2)" at the lower bound of Figure 2. This means that RL is lower than FL at the lower bound. These pixels are predicted to be less abundant in the future owing to an increase of temperature values.

More generally, although the proportion of the "RF suitability" range is predicted to significantly decrease in the future for some taxonomic groups (marine actinopterygians, mammals and reptiles) under the scenario RCP 2.6 (Kruskal-Wallis tests with p-values < 0.001), the tendency is not confirmed under the scenario RCP 8.5, and the difference is not significant for the other groups (Kruskal-Wallis tests with p-values > 0.05) (Figure 5.D). Regarding FL, only mammals and reptiles present a significant increase in the proportion of "suitable" pixels in the future (Kruskal-Wallis tests with p-values < 0.01; Figure 5.E). Mammals and reptiles also presented a significant reduction in the proportion of pixels categorized as "RF potential suitability" range (Kruskal-Wallis tests with p-values < 0.01; Figure 5.F), whereas no changes were detected for the other groups (Kruskal-Wallis tests with p-values > 0.05). Similar results were obtained with GBIF data (see Appendix 4).

Discussion

The first aim of this study was to assess whether the available estimate of the fundamental thermal niche limits (FL) of species among six groups of animals (marine actinopterygians, freshwater actinopterygians, amphibians, malacostracans, mammals and reptiles) are expectedly larger than the realised thermal niche limits (RL). Secondly, we wanted to see if and how these differences could impact the distribution of animals in the future. For the upper bound, our results indicate that FL is, as expected, higher than RL for marine actinopterygians and reptiles but lower than RL for mammals and freshwater actinopterygians. For the lower thermal bound, freshwater actinopterygians, amphibians, mammals and reptiles have a lower LR than FL, contrary to our expectations. Regarding species distribution, as we expected, the "suitable" range of all groups, according to both FL and RL, will decrease for the upper bound, but the "potentially suitable" range will increase for all groups studied. For the lower bound, we did not expect any change in "suitable" and "potentially suitable" ranges. Mammals and reptiles, however, show an increase in the "suitable" range according to FL, and a decrease in the "potentially suitable" range.

For the upper bound, we found divergent results between the different groups studied. Some had FL higher than RL, while others showed the opposite. Depending on the taxonomical group studied, type of environmental data used to calculate RL, the metrics to determine FL and/or the lack of observed species occurrence data might have biased the results. For reptiles and marine actinopterygians we were able to use rasters that approximate very closely the temperatures experienced by the species in these groups. The results for these two groups follow the theory. Their LF is higher than their LR. However, for freshwater actinopterygians

13

and amphibians, we were forced to use a terrestrial temperature raster. Morrill et al (2005), have shown that terrestrial temperatures can reasonably be used as a proxy for freshwater temperatures, but they tend to overestimate the actual water temperature during the summer (also see Kirk & Rahel, 2021). It is therefore likely that we have overestimated RL for these two groups. Specific freshwater temperature rasters would be needed for freshwater animals. Finally, for mammals, it is probably the approach used to estimate the FL that is responsible for this result. Bennett et al (2018) cautioned that thermal neutral zone limits, used as physiological limits for mammals, are not limits that compromise the survival of individuals. These limits indicate thresholds beyond which individuals must actively thermoregulate, and therefore are not really estimating the FL. In addition, many studies seem to not expose individuals to temperatures sufficiently extreme to generate a metabolic response (McKechnie et al., 2017; Wolf et al., 2017). Different measures and experiments would therefore be needed to estimate the correct physiological thermal limits of mammals. For malacostracans, too few species were included in the study to have meaningful results.

For the lower bound, the same remarks apply. Mammals have a higher LF than other groups, supporting the fact that their physiological thermal tolerances are underestimated. The RL of amphibians and freshwater actinopterygians is probably lower than the temperatures they truly experience, as terrestrial temperatures decrease more than water temperatures in winter. Furthermore, these groups of species have behavioural adaptations to overwinter in water (Sullivan, 1986; Boutilier et al., 1997). These species can therefore spend cold periods in water with a temperature above their LF, while air temperatures (outside water) are below their LF. Marin actinopterygians may also migrate to avoid cold temperatures (Quinn et al., 1997; Hurst, 2007; Jansen & Gislason, 2011), yet our method does not consider changes in geographical distribution during the year. This is probably why FL is not statistically lower than RL for this group. Similarly, reptiles can migrate over short distances to find overwintering habitat (Southwood & Avens, 2010) where temperatures may remain above their LF.

Long-distance migration is used by many marine and flying animals (Alerstam et al., 2003). Among mammals, some bat species (58 species of *Chiroptera* order in our study) migrate and congregate in hibernacula, to spend the winter (Rodrigues & Palmeirim, 2008). This could explain (in addition to the overestimation of FL at lower bound) how these mammals can have FL higher than RL, for the lower bound. Migration could also explain why FL is higher than RL at the lower bound, in marine actinopterygians (35 species in our study). While the presence of a migration barrier prevents freshwater actinopterygians from migrating long distances, the absence of a migration barrier in the ocean favours the seasonal migration of marine actinopterygians (Hurst, 2007). This could partially explain (in addition to differences in the rasters used) the divergence in results between the two groups of actinopterygians, at the lower bound. Freshwater actinopterygians probably use other adaptive mechanisms to survive during cold periods in areas that FL considers "unsuitable".

Freshwater actinopterygians have different strategies for overwintering depending on whether they are adapted to warm or cold waters. Coldwater species feed throughout the winter, whereas warmwater species store lipids and endure starvation during the winter

(Sullivan, 1986). In addition, freshwater actinopterygians will try to find an ideal place in the river to overwinter. That is, a place that is safe from flooding, ice and well oxygenated, where energy requirements are reduced (Cunjak, 2011). In these areas, the water is probably kept above the FL of freshwater actinopterygians, as it does not freeze. Some overwintering amphibians have an opposite strategy. They can suspend their metabolism to stay under the ice, where oxygen availability is reduced (Boutilier et al., 1997) but where the water temperature is maintained above FL. Other terrestrial amphibian species avoid negative temperatures but are able to endure periods of freezing for several days by storing cryoprotective molecules. This allows them to survive periods of freezing temperatures (Storey & Storey, 1986).

Future changes in suitability within the current geographical range of species are broadly the same for all groups, for the upper bound. "FL suitability" and "RL suitability" decrease, while "RF potential suitability" increases. For the latter, however, a distinction must be made between species with FL higher than RL and species with FL lower than RL. In the first case, the "RF potential suitability" is a part of the geographical range that will be "potentially suitable" in the future. In the second case, it is a part of the geographical range where mechanisms (such as facilitation, microhabitats, behavioural or physiological adaptations) will be necessary for the survival of the species (Scheffers et al., 2014; Soberón & Arroyo-Peña, 2017). The latter case is therefore more a "potentially adaptive" range. Groups with many species with FL higher than RL (i.e. marine actinopetrygians and reptiles) have a "RF potential suitability" that increases more than that of other groups. These species (which are not exposed to FL upper bound) could therefore persist over a large part of their geographic range, described as unsuitable according to RL. For species that have RL higher than FL at the upper bound, the increase of "RF potential suitability" indicates that the proportion of the range where adaptive mechanisms are required will increase in the future. This is not good news, as the conditions in these environments are stressful for the individuals. Mortality in these habitats could therefore increase, making these species even more vulnerable to climate change. For the lower bound, the "RF potential suitability" of mammals and reptiles will decrease in the future. As many species in these two groups have a lower LR than FL for the lower bound (in contrast to the theory), the decrease in this part of the range is good news, as it means that the species will be less exposed to stressful conditions. Sink populations may also be responsible for the presence of species in the "RF potential suitability" range (Soberón & Arroyo-Peña, 2017). The fact that this range is decreasing could mean that some sink populations could succeed in establishing themselves in these environments in a sustainable manner. For the other groups, where "RF potential suitability" will not change significantly, the geographical range of the species is likely to be less impacted by climate change during the cold months.

The fundamental niche should be measured on many environmental variables (such as water availability) that affect the limits of the niche. By considering the interactions between the different environmental variables, our study could predict the "suitable" and "potentially suitable" range with more accuracy. Moreover, it should not only consider the survival, but also the reproductive capacity of species as it also drives species distribution (Kearney &

15

Porter, 2009). Our study does not consider these aspects of the fundamental niche, because the data are not available. It would therefore be necessary to take them into account, as soon as the data are available, to improve the predictions of the "suitable" and "potentially suitable" ranges. Studies measuring the survival thermal limits as well as reproductive capacity, without biotic interactions, in function of other environmental variations (e.g. water availability gradient), should therefore be conducted, to more accurately approximate the limits of the fundamental niche. It would also be interesting to use rasters that better approximate the actual temperatures experienced by the species, to measure the limits of the realized niche. For example, for hibernating species, the use of maximum and minimum temperature rasters over the activity period would probably be more relevant as the duration of hibernation is correlated with the temperature of the environment (Geiser & Kenagy, 1988; Nussear et al., 2007). For species that migrate long distances, a maximum temperature raster over the "pre-migration" range and a minimum temperature raster over the "post-migration" range should probably be applied, because environmental temperature can be a (Rodrigues & Palmeirim, 2008; Szesciorka et al., 2020) driver of migration.

To conclude, our study showed that the realised niche is not always more restrictive than the fundamental niche as expected by the theory, due to behaviour, migration and other physiological adaptations. In addition, it demonstrated that the use of physiological data, in addition to field data, provides additional interpretations concerning the necessary adaptations to the limit of the realized niche, for SDM. Currently, SDM use the limits of the realized niche to predict the distribution of species. With the addition of physiological thermal limits, they could predict, for a species known to have a seasonal migration, the areas where the species cannot survive in winter, because the temperature is lower than the fundamental thermal limit. For overwintering species, the use of fundamental limits could be used to indicate in which areas the species is most likely to overwinter. More generally, with knowledge of the behaviour of the species to be studied, the combination of the thermal limits of the fundamental niche and the realised niche could indicate areas of the species' geographic range where a specific adaptive mechanism is likely to be required. We therefore recommend the consideration of physiological thermal limits, in addition to occurrence data, in SDM studies that predict changes in geographic range over the year, or that would like to highlight the use of a specific adaptive mechanism in a part of the geographic range.

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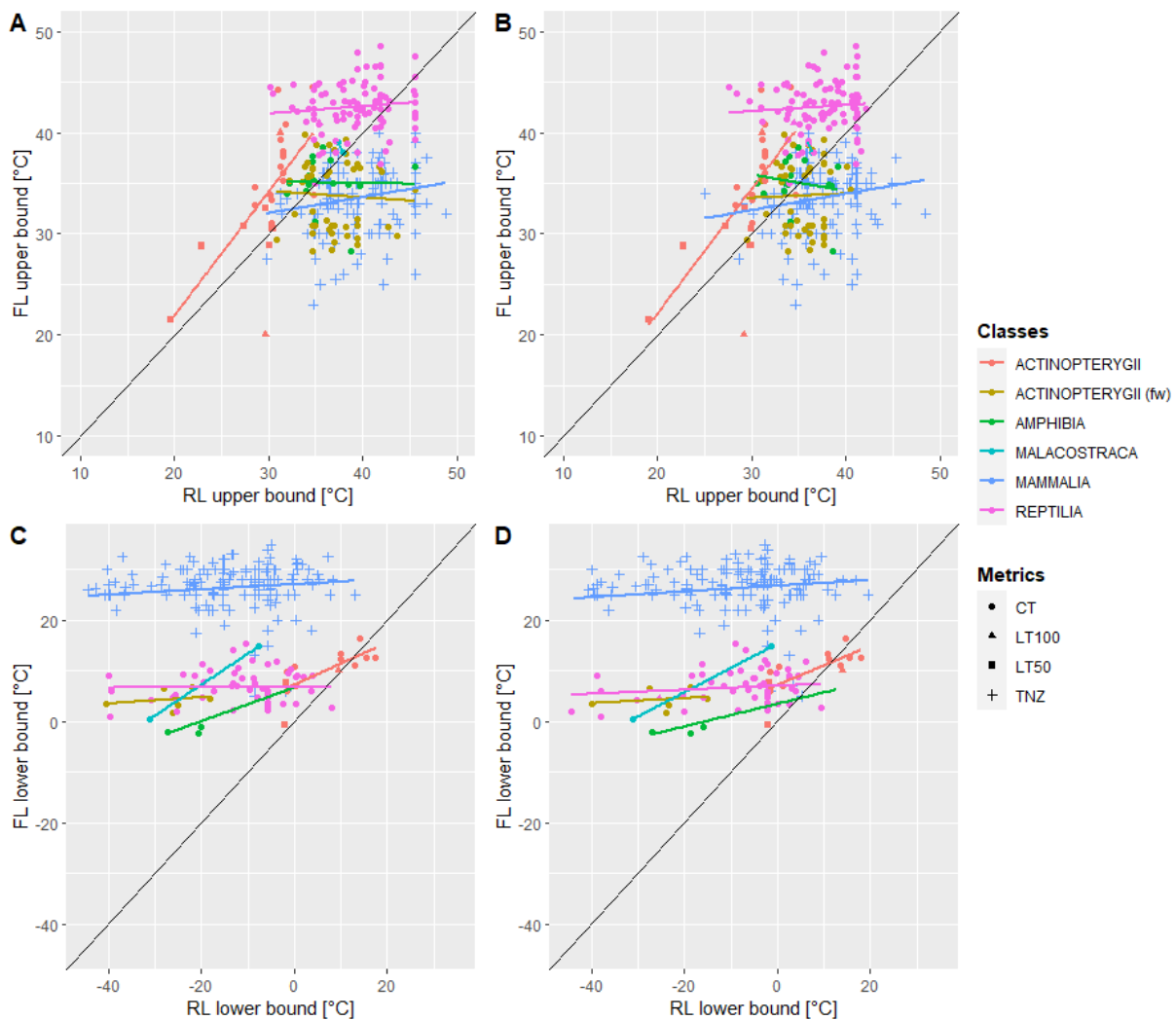
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Supplementary materials

R script for the study is available on GitHub: https://github.com/punky1866/Master-Thesis.git

Appendices

Appendix 1. Comparison of species' FL and RL for both upper and lower bounds between high and low resolutions. Comparison at 2.5' (terrestrial and freshwater species) or 5' (marine species) resolution, for upper bound (A) and lower bound (C). Comparison at 1° resolution, for upper bound (B) and lower bound (D). CT: Critical Threshold; LT100: Lethal Temperature for 100% of individuals; LT50: Lethal Temperature for 50% of individuals; TNZ: Thermal Neutral Zone. RL was estimated from IUCN polygons.
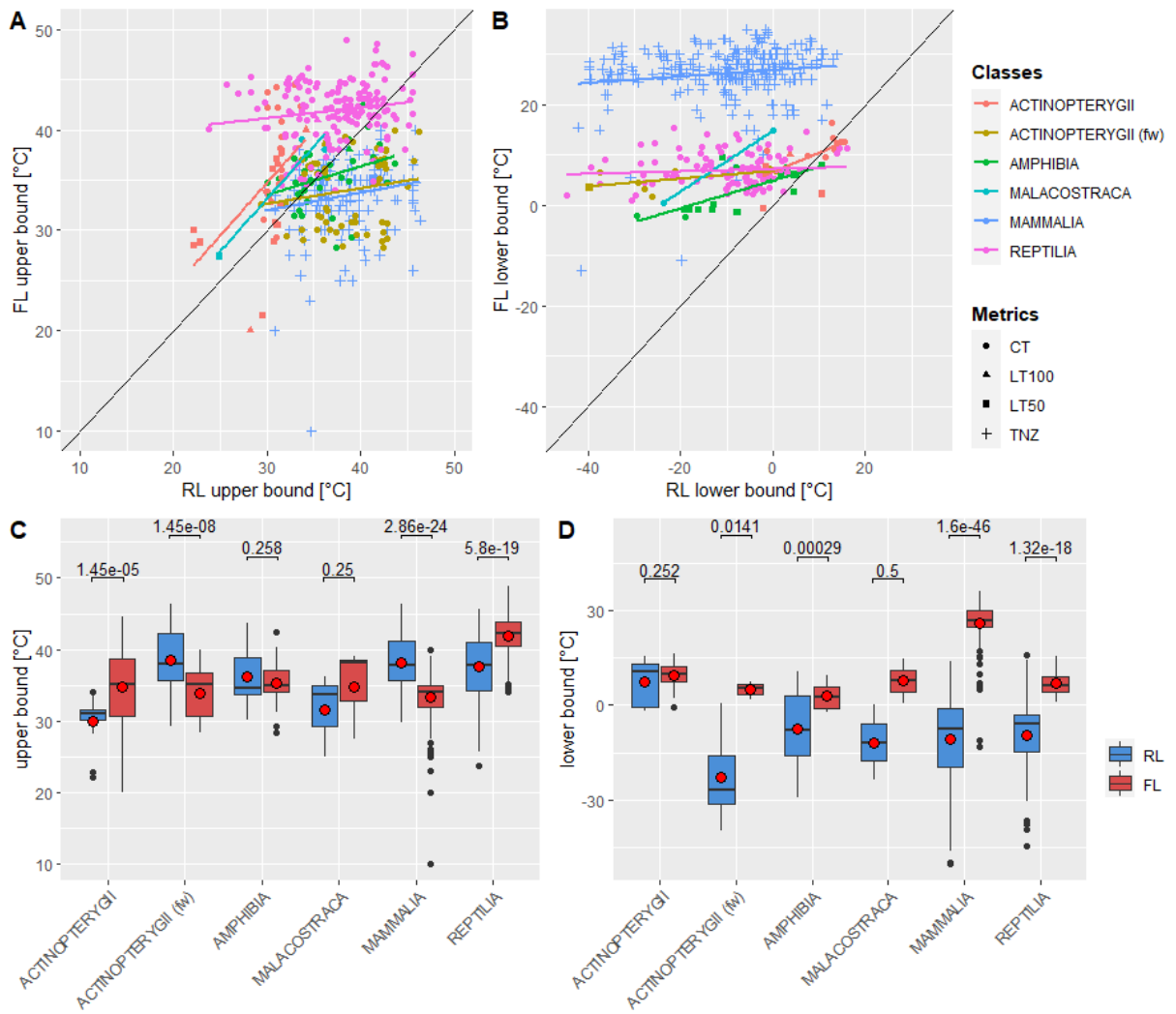
Appendix 2. Comparison of species' FL and RL for both upper and lower bounds. Comparison for upper limits (A)(C) and for lower limits (B)(D). CT: Critical Threshold; LT100: Lethal Temperature for 100% of individuals; LT50: Lethal Temperature for 50% of individuals; TNZ: Thermal Neutral Zone. RL was estimated from GBIF occurrence data.
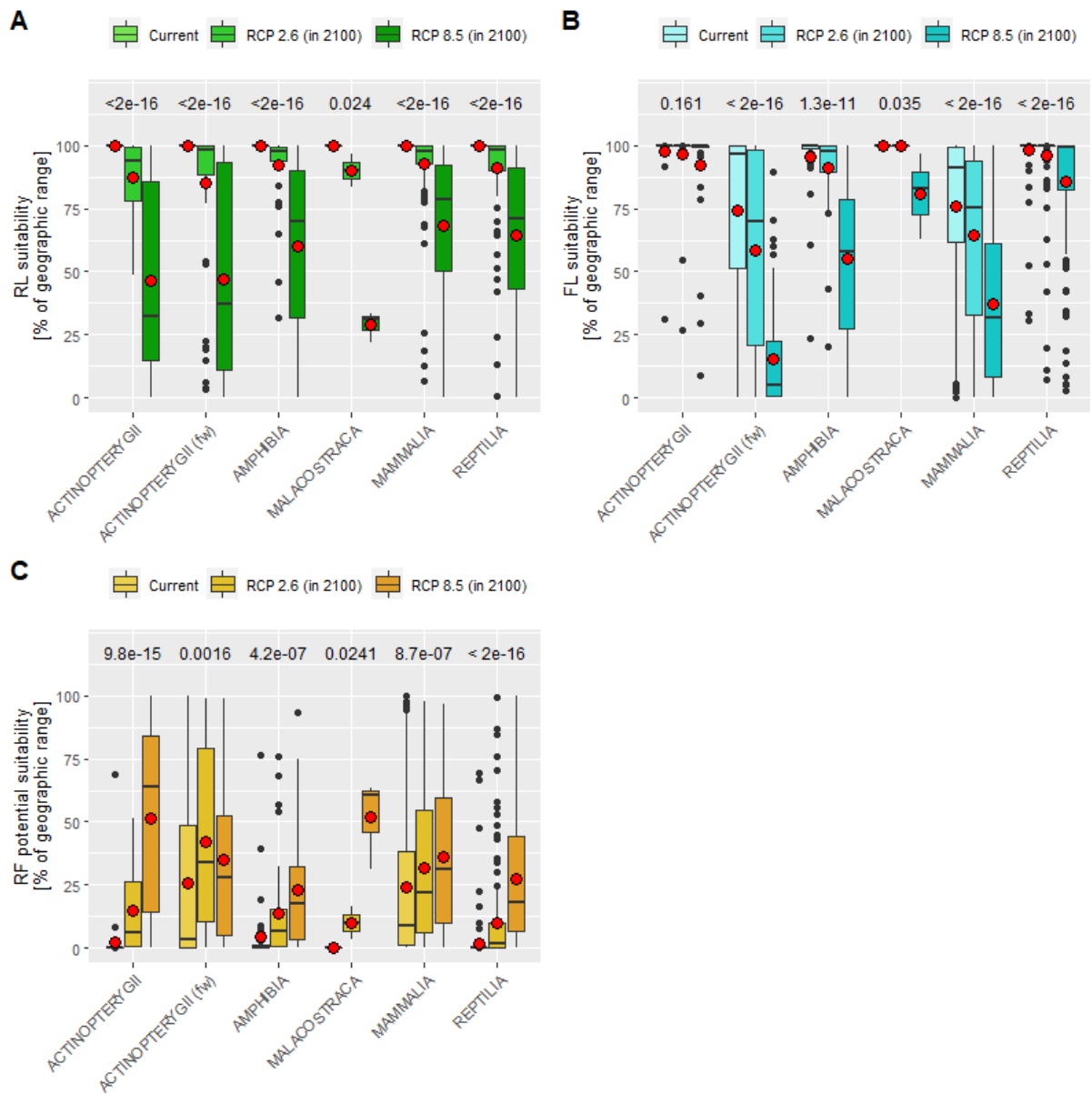
Appendix 3. Changes in "suitable" and "potentially suitable" geographic ranges considering the upper bound. Proportion of cells included within RL (A), within FL (B) and included within the highest limit (FL or RL, depending on the species) but excluded from the other limit (C) across all species for each taxonomic group under the three projections (current, RCP 2.6, RCP 8.5). RL suitability was estimated on the base of GBIF occurrence data. Kruskal-Wallis test p-values are indicated at the top of each sub-figure.
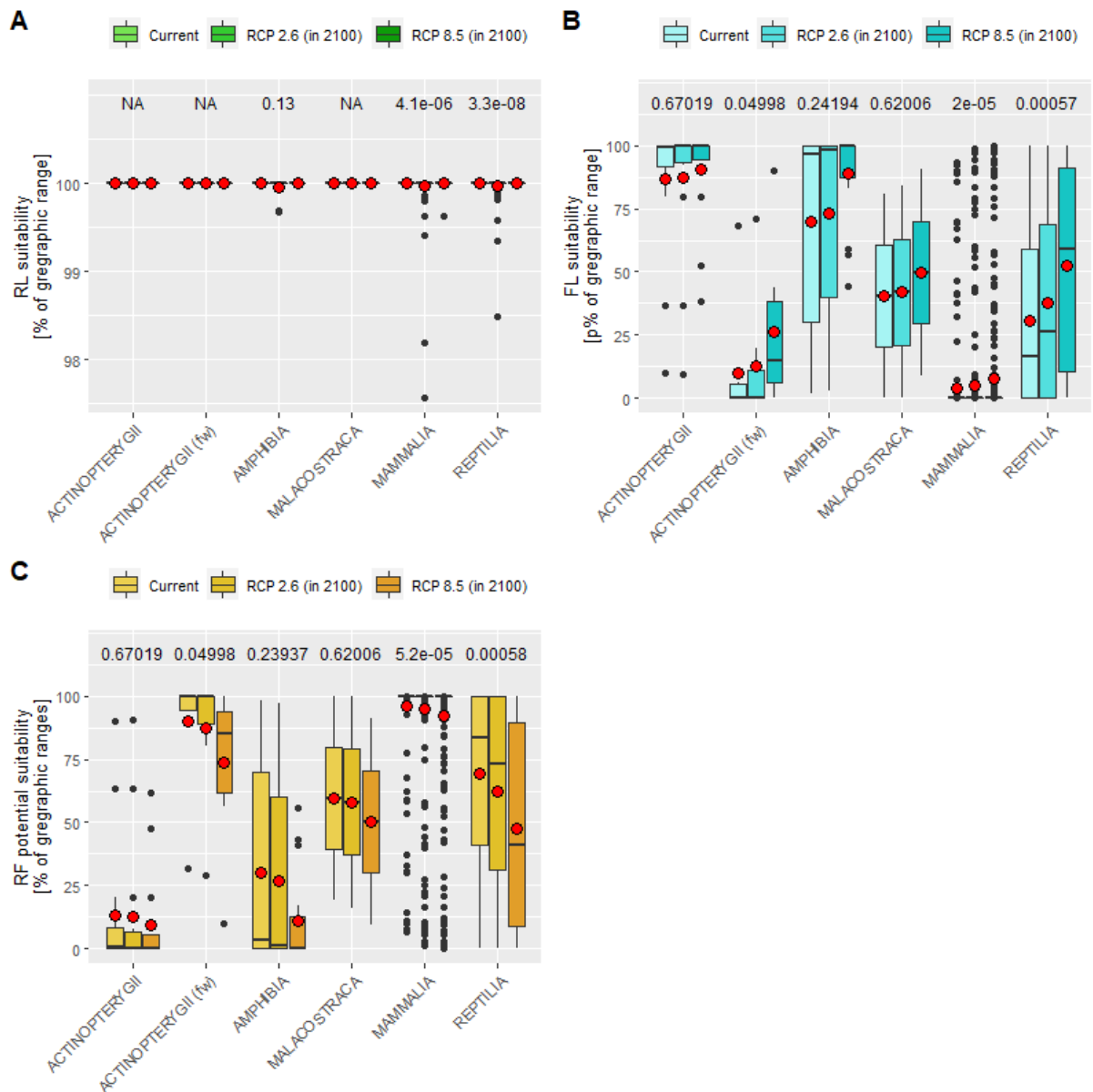
Appendix 4. Changes in "suitable" and "potentially suitable" geographic ranges considering the lower bound. Proportion of cells included within RL (A), within FL (B) and included within the lowest limit (FL or RL, depending on the species) but excluded from the other limit (C) across all species for each taxonomic group under the three projections (current, RCP 2.6, RCP 8.5). RL suitability was estimated on the base of GBIF occurrence data. Kruskal-Wallis test p-values are indicated at the top of each sub-figure. NA: no variation between the 3 projections.