A tale of two crickets: global climate and local competition shape the distribution of European *Oecanthus* species (Orthoptera, Gryllidae)

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Abstract

Climate change is reshaping species' distributions around the globe, yet different factors may drive species' responses at different spatial scales from global to local. Environmental conditions and biotic interactions may thus change in relative importance in terms of influencing species' occurrence according to the considered spatial extent, making a multi-scale approach key to understanding species' distributions and future range dynamics. In this study, we tested the relative roles of climate and interspecific competition in shaping the distributions of two cryptic species of Orthopterans at global and regional scales. Namely, we assessed the spatial responses to climate change in two *Oecanthus* tree crickets (*O. pellucens* and *O. dulcisonans*) that show ecological and morphological resemblance, and partial range overlap. We found significant and species-specific associations with bioclimatic variables related to temperature and to precipitation. We also observed divergence in predicted responses between the two species, showing massive range loss for *O. pellucens* and slight expansion for *O. dulcisonans* under future scenarios. This result was also supported by environmental niche analysis, indicating *O. pellucens* as a significantly more specialized taxon in terms of climatic niche. At a regional scale, we present evidence for how interspecific competition may play a strong and asymmetrical role in determining species' presence, with only *O. pellucens* being significantly affected by *O. dulcisonans*, and not vice-versa. Our results shed light on the potential responses of Orthopterans to climate change, and on the spatial-specific respective roles of climate and competition in shaping species' distributions. Moreover, we highlight how, within cryptic species complexes, competition dynamics and niche specialization may represent key elements in determining winners and losers in the race against climate change.

Highlights

- Insect responses to climate change have been poorly investigated, particularly in the case of groups such as Orthopterans.

- Cryptic species may diverge in their responses to climate change, as a result of differing relationships with environmental conditions and the degree of niche specialization.

- By using an integrated approach of species distribution and niche modeling, we assessed the relative roles of bioclimatic variables and competition in shaping current and future distribution of two species of tree cricket (*Oecanthus* spp.) at two spatial scales.

- Environmental variables affecting cryptic species' probability of occurrence differ between taxa and between spatial scales, in this study with evidence also of influence of inter-specific competition at a regional scale.

Keywords: climate change, competition, competitive exclusion, ecological niche modeling, *Oecanthus*, Orthoptera, range shifts, species distribution modeling, tree crickets

Introduction

Large-scale anthropogenic pressures such as land-use and climate change are reshaping biodiversity at unprecedented rates. Climate change, in the form of increasing temperatures, extreme weather events and decreasing or altered rainfall patterns, is affecting biogeographical patterns for an increasingly growing number of species (Ackerly et al. 2010, Donelson et al. 2019, Maxwell et al. 2019, Smeraldo et al. 2021). Despite some evidence of species' adaptation to climate change, as well as extinction events being documented, the most frequent reported responses to climate change by wildlife are distributional, such as range shifts, contractions and/or expansions (Thomas 2010).

Numerous factors determine whether and how species respond to changes in climatic conditions, and such responses may differ even for closely related species, sharing apparently similar ecology and/or morphology (Struck et al. 2018). Correlative techniques to model species distributions are among the most widespread approaches to test hypotheses about species' spatial dynamics and ecological niches, and for assessing responses to climate change and predicting distributional changes in time. A wealth of well-established methodological protocols and relatively simple assumptions (Santini et al. 2021) have also made these techniques very popular and widespread in the ecological literature (Lobo 2016, Silva et al. 2019). Species' responses to climate change may be driven by different factors at variable spatial scales, e.g. global vs local, where different environmental conditions, and biotic interactions, may change their importance in affecting species' occurrence (Seo et al. 2009).

One of the most common results of the application of Species Distribution Models (SDMs) is the description of spatial changes in ranges (shifts, contractions, or expansions). Yet, whether and how these responses lead to novel interactions between species has so far been a rather neglected topic (Blois et al. 2013, Araújo and Rozenfeld 2014, Cardador et al. 2021, Salinas-Ramos et al. 2021). The scarcity of studies integrating biotic interactions when assessing species' responses to climate change is mainly due to the difficulties in finding effective proxies for such interactions. The identification of biotic interactions is particularly difficult at large scales and when considering proxies that may be effectively estimated in a spatially explicit way, and thus mapped in order to be integrated within SDMs (Pellissier et al. 2010, Blois et al. 2013, Wisz et al. 2013). Moreover, while SDMs have been extensively applied for a variety of organisms in the last decades, published studies are heavily taxon-biased towards vertebrates, thus leaving huge gaps in our comprehension of animals' responses to climate change (see Mammola et al. 2021). Arthropods are excellent models to test hypotheses on climate change and on how species' distributions are shaped by different factors across spatial scales (Vanhanen et al. 2007, Høye 2020), as most species are strongly dependant on specific climatic conditions, so that

they may readily respond to environmental alterations (Feldmeier et al. 2018, Mammola et al. 2021). Yet, our current knowledge gap about the detailed array of biotic and abiotic drivers of insect distributions, as well as the scarce availability of presence records for most species, hamper the effective use of SDMs for the study of insects (Lobo 2016). The high spatial resolution at which arthropods, such as insects, mostly use and perceive their environment (e.g., at the microhabitat scale) also makes biotic interactions likely relevant when assessing a species' environmental preferences at local scales, as interspecific interactions such as competition, predation or facilitation may lose importance when upscaled to large geographical extents (Newbold 2010, Warren et al. 2010). Yet, very few studies have applied SDMs to the study of arthropod responses to climate change, and even fewer have integrated biotic interactions within their framework (Hortal et al. 2010, Warren et al. 2010, Taucare-Ríos et al. 2016, Mammola et al. 2021). Even within Arthropods, strong taxonomical biases in research efforts occur, with most studies being conducted on charismatic or aesthetically appreciated taxa such as Lepidoptera and large Arachnids, while other groups are poorly covered, (e.g., ground beetles – Carabidae – and Orthoptera; Høye 2020, Mammola et al. 2021, Koot et al. 2022). Nonetheless, many species within such neglected taxonomic groups are key elements of the ecosystems they are a part of, or are considered as priority species for conservation (Samways and Lockwood 1998), so that understanding their responses to climate change is pivotal to foster ecosystem and species conservation in the future (Penone et al. 2013, Bidau 2014).

In this study, we aim to test species' spatial responses to climate change at a continental scale, while at the same time assessing the potential role of interspecific competition in shaping distributions at a regional scale, focusing on a poorly studied arthropod group. Namely, we used two cryptic species of tree crickets from the genus *Oecanthus* (Orthoptera, Gryllidae) as models. Specifically, we followed an approach integrating species distribution and environmental niche factorial modeling, to make the following hypotheses and associated predictions:

1) *Oecanthus* crickets are potentially responsive to climate change (Löffler et al. 2019, Fumy et al. 2020); for this reason, we predict that both species will shift their potential distribution in time, under the assumption of unlimited dispersal;

2) Cryptic species diverge in their ecological requirements, despite a close morphological resemblance, ecological similarity, and partially overlapping distributions (Vodă et al. 2015); we predict that the two *Oecanthus* species will be influenced by different sets of bioclimatic factors and will differ in their responses to climate change;

3) Specialization on climatic conditions hampers species' responsiveness to climate change

(Walters et al. 2012); we therefore predict that differences in specialization degree between *O. dulcisonans* and *O. pellucens* will match species' responses to climate change, and we expect lower specialization to translate into smaller distributional changes.

4) Eco-behavioural similarities may translate in competitive interactions that shape the two species' distributions at the local scale (Barnagaud et al. 2014); consequently, we predict that regional distributional patterns will include competition as a relevant factor.

Materials and Methods

Study species

Oecanthus crickets are small-sized, nocturnal and semi-arboreal Orthopterans, well distributed in all bioregions across the world with the exception of the poles (Metrani and Balakrishnan 2005), with two species found in Europe (*O. pellucens* and *O. dulcisonans*). The Italian tree cricket *O. pellucens* is very common and widespread across the Palearctic, being found in areas characterised by Mediterranean climate from Southern Europe to Western Asia, and usually associated with natural and semi-natural ecotonal habitats such as edges, forest margins and woody crops (e.g., vineyards). *Oecanthus dulcisonans* was only recently recognized as a distinct cryptic species from *O. pellucens*, based on micro-morphological and bioacoustic features (Cordero et al. 2009); as such, its ecology and distribution are relatively poorly known. This species is present along most coastal areas of the Mediterranean basin, from North Africa to Southern Europe and the Arabian Peninsula, where it mostly occurs in dry habitats with herbaceous natural and semi-natural vegetation, wood margins and scrubland. The ranges of the two species partially overlap, both being present in Southern Italy (and Sardinia), France (including Corsica), Iberian Peninsula, Greece and Crete. Both species show a typical peak of calling activity in summer months (June–September), but can also be found to be active in autumn at lower latitudes (Labadessa and Todisco 2016).

Study area and presence records

We defined our study area *a posteriori*, as the area encompassing all the selected presence records for the two target species. The area comprised the entire Mediterranean basin and surrounding territories, extending north to the UK and southern Scandinavia, east to Kazakhstan, west to the Canary Islands, and south to Yemen (Latitudinal range: 9.0-61.0°N, Longitudinal range: -22.0-62.0°E; Figure 1). We did not include any buffer around records, since these were already well distributed across the study area, which thus captured the environmental variability of both presence and absence areas. Presence records for both species were collected from several sources, including GBIF (Global Biodiversity Information Facility) via the *rgbif* package (Chamberlain et al. 2017), the authors' own data, and published references (see reference list in Table S1 in Supplementary materials). All records were filtered and selected if georeferenced with <5 km accuracy. Moreover, since the recent description of *O. dulcisonans*, we only included records deposited after year 2010, to limit the risk of past misidentification between the two species. Additional records were included from iNaturalist (www.inaturalist.org) only when audio or video recordings were uploaded and inspected, to ensure accurate identification (Cordero et al. 2009). Records were then controlled for duplicates, which were removed before further analyses. The remaining presence records were thinned at 5 km distance by using the *spThin* package (Aiello-Lammens et al. 2015), i.e. multiple records were reduced to a single presence within this distance, in order to limit spatial biases towards the environmental conditions of intensively sampled areas (e.g., central Europe for *O. pellucens*), and maintaining a resolution comparable to that of
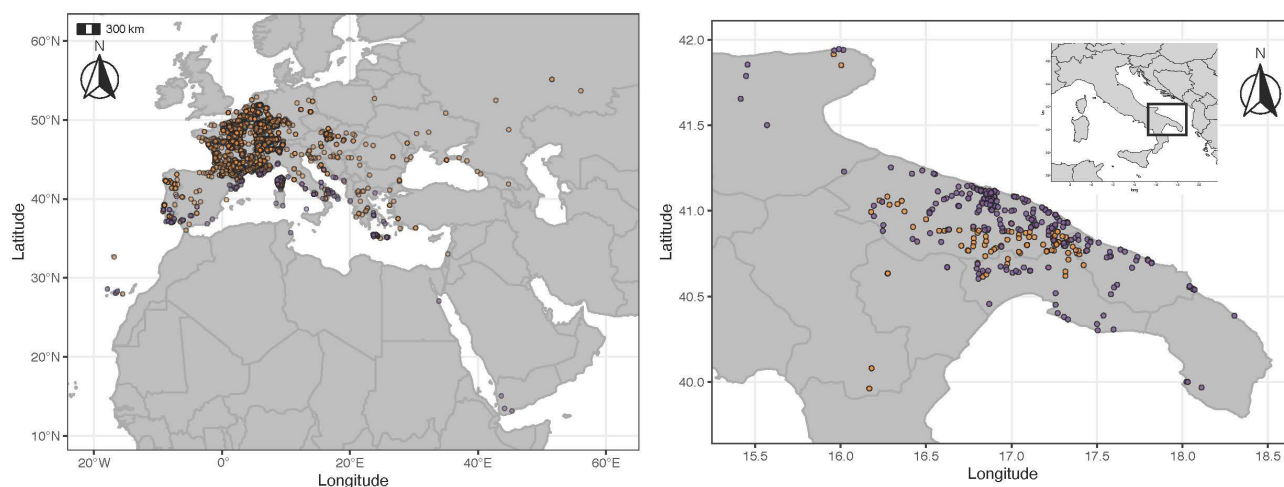
Figure 1. Global (left) and regional (right) distribution of occurrence records (before thinning) of *Oecanthus pellucens* (in orange) and *O. dulcisonans* (in purple). Inset in the right map shows location of the regional focus.

climate data. For regional models and inclusion of biotic interactions as predictor variables, we defined the model area as the territory of the Apulia administrative region and its immediate surroundings (Southern Italy; Figure 1); in this case, we collated detailed presence records derived from systematic acoustic surveys conducted since 2015 (Labadessa and Todisco 2016) that provide a comprehensive picture of the species' actual distributions. This procedure led to the inclusion of 5,578 and 172 records at the global scale for *O. pellucens* and *O. dulcisonans*, respectively, and to 54 and 73 records at the regional scale.

Environmental predictors

We downloaded 19 bioclimatic variables as descriptors of climatic conditions from Worldclim2 (Fick and Hijmans 2017), with a 1 km (30 arc seconds) resolution. Multicollinearity among variables within the study area was controlled by running a Variance Inflation Factor (VIF) analysis, retaining only variables with vif values <5 (Curto and Pinto 2011). We conducted the VIF analysis by using the *vifstep* function built in the sdm R package (Naimi and Araújo 2016). This procedure identifies a measure for each environmental predictor, as assessed in the entire extent of the study area, of how much it can be explained by the others, and removes those with values above the threshold set. After the stepwise VIF procedure, we retained 8 and 6 independent bioclimatic variables at the global and regional scale respectively (Table S1 in Supplementary materials).

To test for the species' spatial responses to climate change, we also modelled future possible distribution of both target species under the RCP 8.5 concentration pathway scenario to year 2070, i.e., under the worst-case scenario considering an average Earth temperature increase of 2.0-3.7°C (Riahi et al. 2011), using the same bioclimatic predictors used to model current species' suitability.

At the regional scale only, we produced a proxy of competition pressure data layer by using the *raster* package for R (Hijmans et al. 2015), which consisted of a raster of Euclidean distances of each species' occurrence to the closest record of the other species within the testing area (Mpakairi et al. 2017), separately for *O. pellucens* and *O. dulcisonans*. Each raster was stacked together with the retained bioclimatic layers selected by the vif procedure, and used as predictor for regional modeling, i.e., distances from records of *O. dulcisonans* were used to predict the presence of *O. pellucens*, and vice-versa. For regional models, we then repeated the same procedure specified for global models at current time, running each species' model twice, once with bioclimatic predictors only (climate-only models) and once including the competition layer between the two species (climate + competition models). We did not include land-cover variables as predictors, since both species are highly mobile, colonise a wide range of habitat types and, more importantly, are able to persist in habitat patches of very limited size, e.g. roadsides (Labadessa and Todisco 2016), i.e. far beyond the resolution of vegetational

maps available at both global and regional scales. We also excluded elevation because of its strong correlation with several bioclimatic variables (e.g., temperatures).

Species distribution modeling

We built SDMs based on a bioclimatic envelope approach (Pearson and Dawson 2004), separately for *O. pellucens* and O. *dulcisonans*, through an ensemble forecasting method as implemented in the *sdm* R package (Naimi and Araújo 2016). Ensemble forecasting is a well-established procedure that reduces uncertainty of predictions by single model algorithms (Watling et al. 2015). We considered three modeling techniques: Generalised Linear Models (GLMs), Random Forests (RFs), and Maximum Entropy Models (Maxent), performing 10 runs for each technique (Tagliari et al. 2021, Bosso et al. 2022). The three algorithms were selected as they are considered among the best performing ones and, taken together, provide robust and reliable predictions (Kaky et al. 2020). For RFs and GLMs, we generated pseudo-absences (background data, n=10,000) by adopting a randomisation approach (Barve et al. 2011), as this has been shown to result in high predictive accuracy (Barbet-Massin et al. 2012). For model training, we randomly selected 70% of occurrence data, using the remaining 30% for model performance testing. We assessed model performance in predicting species' distribution by measuring the area under the receiver operating characteristic curve (AUC) and the True Skill Statistics (TSS), two validation methods widely used in sdms (Araújo and New 2007). AUC is a threshold-independent statistics which assesses model discrimination ability and ranges between 0 (equal to random distribution) and 1 (perfect prediction). TSS is threshold-dependent, and compares the numbers of correct predictions to those attributable to random guessing, ranging from -1 (a performance no better than random) to +1 (total agreement). The combined use of these validation statistics is recommended when assessing the performance of predictive distribution models (Allouche et al. 2006).

Responses of individual species to each environmental predictor were assessed by inspecting the response curves, while each variable's relative importance, quantified as the AUC improvement in model performance due to the inclusion of the target variable, was calculated by the specifically devoted function in the *sdm* package (*getVarImp*). To determine the spatial patterns of suitable areas for each species, both current and future SDMs were reclassified into binary maps (presence/absence), using a logistic threshold maximising sensitivity and specificity to make results more comparable, where values below the threshold (0.5) represented presumed absences, while those above the threshold were considered as potential occurrences. Such an approach is widely used for model binarization (e.g., Algar et al. 2009), and recommended as one of the most accurate ones (Liu et al. 2005). Finally, we exported the binary model outputs to QGIS3.8 (QGIS Development Team, Open

Source Geospatial Foundation Project, http://qgis. osgeo.org), and used the number of occurrence pixels to calculate the percent changes in suitable habitat, separately for each species, and the percent of the potential range overlap between the two, as assessed by current and future models.

Niche analysis

To further investigate potential differences in the species-climatic environment relationships at the regional level, we extracted climate data at occurrence points using the set of variables retained by the VIF analysis, while climatic environment background was extracted by 5,000 random points. Ecological Niche Factor Analysis (ENFA) was then conducted using the *CENFA* package in R (Rinnan and Lawler 2019), using all occurrences present within the focal area for both species, as ENFA does not suffer from spatial autocorrelation of sampling points (Basille et al. 2008). ENFA is a multivariate niche analysis technique that summarises the environmental multidimensional volume along two axes, namely marginality (M) and specialisation (S). The former indicates the position of the species' niche within the available environmental space, with values of M>1 indicating a significant deviance from the background points, i.e. the species' expressed environmental optimum is significantly different from average background conditions. Specialisation instead is a measure of niche breadth relative to the environmental background, with values of S>1 indicating narrower niche breadth, i.e. specialisation to a specific subset of conditions.

Results

Species distribution modeling – global model

Our models achieved robust levels of predictive performances for the two species at global scale, both for the current timeframe and for future projections, as evaluated by AUC (>0.95) and TSS (>0.70). *Oecanthus pellucens* shows a current potential distribution covering most of continental Europe, including the UK and the Atlantic coasts of the Iberian Peninsula, and the east to the south-eastern coasts of the Black Sea. The suitable range of *Oecanthus dulcisonans* is instead currently restricted to the coasts of the western Mediterranean basin, including larger islands, Crete and eastern Greece, as well as the Atlantic coasts of the Iberian Peninsula (Figure 2). The analysis of single-variable importance in predicting the species' probability of occurrence at a global scale (Table 1) highlighted seasonal variations in temperature (Bio04) and precipitation (Bio15) as the main drivers for the distribution of *O. pellucens*, which showed a negative response to increasing values of both these factors (Figure S1 in Supplementary materials). For *O. dulcisonans*, the main drivers of potential distribution were instead mean diurnal temperature range (Bio02), and mean temperature of the driest quarter (Bio09), followed by precipitation seasonality (Bio15) and annual mean temperature (Bio01). This species responded with a steep drop in probability of occurrence at increasing values of mean diurnal temperature ranges, and an increase in response to the mean temperature of warmest
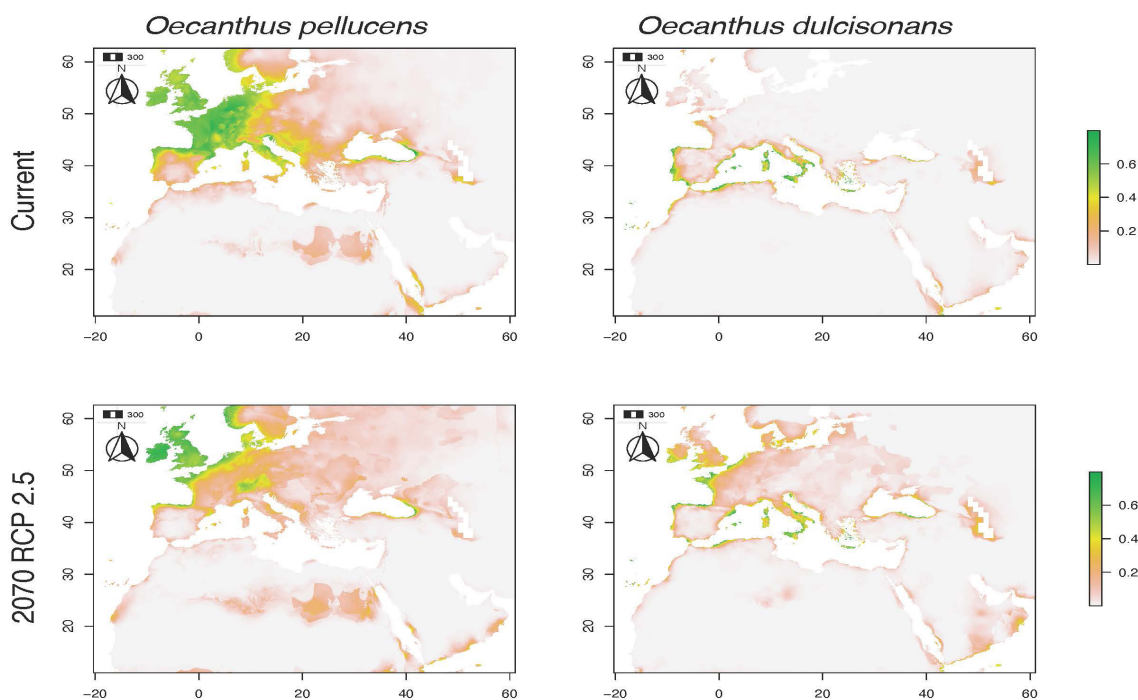
Figure 2. Present (upper row) and future (lower row) predicted suitable ranges for *Oecanthus pellucens* (left) and *O. dulcisonans* (right) according to species distribution models.

Table 1. Variable relative importance of species distribution models at global and regional scales for *Oecanthus pellucens* and *O. dulcisonans*; reported numbers of occurrences result from spatial-autocorrelation correction. Variable importance is calculated as the relative AUC improvement in model prediction.

Species	Scale	N occurrences	Predictor	Relative importance (%)
Oecanthus pellucens	Global	5,578	Bio1	3.6
			Bio2	6.2
			Bio4	17.0
			Bio8	1.8
			Bio9	3.6
			Bio13	1.2
			Bio15	31.0
			Bio19	3.8
	Regional	54	Bio3	14.2
			Bio4	26.9
			Bio8	6.9
			Bio14	30.0
			Bio18	7.3
			Bio19	4.8
			Competition	31.3
Oecanthus dulcisonans	Global	172	Bio1	12.8
			Bio2	27.2
			Bio4	9.6
			Bio8	0.9
			Bio9	20.8
			Bio13	3.4
			Bio15	16.3
			Bio19	0.5
	Regional	73	Bio3	36.2
			Bio4	6.7
			Bio8	18.0
			Bio14	36.5
			Bio18	3.5
			Bio19	13.6
			Competition	1.3

quarter (Figure S2 in Supplementary materials). Future projections to 2070 under a worst-case scenario predicted strongly diverging responses by the two species. *O. pellucens* showed a dramatic decrease in the extent of climatically suitable areas (-66.7%), which will likely be restricted to the UK and northern coasts of central Europe, as well as to the alpine region and the coasts of the Black Sea. Conversely, *O. dulcisonans* showed a less marked change in the distribution of potential suitable range, mainly expanding northwards to the coasts of western and central Europe and the UK, showing an overall increase in the extent of suitable areas (+35.6%) (Figure 2). Similarly, the overlap between suitable ranges of the two species showed a significant variation, with an increase of 150% between current and future scenarios.

Species distribution modeling − regional model

Regional models also showed good performance in predicting both species' probability of occurrence, yet those including biotic interactions (climate + competition models) performed better than climate-only ones, which showed an evident drop in AUC values (from 0.98 to 0.90 in *O. pellucens*, and from 0.94 to 0.89 in *O. dulcisonans*) and as such are not shown. The most important variables explaining the distribution of the two tree crickets within the region (Table 1) were the distance from the closest competitor record, precipitation of driest month, and temperature seasonality for *O. pellucens*, and precipitation of the driest month and isothermality for *O. dulcisonans*. *O. pellucens* strongly increased its probability of occurrence at increasing distances from

the closest record of *O. dulcisonans*, instead showing a negative effect of increasing seasonality. Conversely, *O. dulcisonans* increased its probability of occurrence at higher values of isothermality. Both species showed a steep increase in suitability at summer precipitation values >25mm (see figures S1-S2 in Supplementary materials).

ENFA

The habitat of *O. pellucens* was significantly different from the mean environmental climatic conditions available in the study area (M=1.31), with the species showing a high degree of climatic specialisation (S=3.166). The first three significant ENFA factors explained 86.2% of the total variance in niche structure, with the first specialisation component (Spec1) explaining 50.5% of this total. Precipitation of the driest month and isothermality featured the highest coefficients along the marginality axis, while temperature seasonality had the highest on the first specialisation axis. The *Oecanthus dulcisonans* niche also occupied a non-random position within the available climatic environment (M=1.33), a metric mostly driven by isothermality, and showed a relatively lower specialisation degree (S=2.228) than *O. pellucens*. For *O. dulcisonans*, the first three ENFA factors explained 81.52% of niche variance, with the highest coefficients along the first specialisation axes being associated with precipitation of the warmest

quarter and mean temperature of the wettest quarter (Figure 3).

Discussion

We provided a first assessment of the bioclimatic niches of *Oecanthus pellucens* and *O. dulcisonans*, evaluating their potential distributions under current and future climatic scenarios. At the same time, we tested whether and how bioclimatic variables changed in importance at different spatial scales, also highlighting the potential role of interspecific competition in shaping the local distributions of these species (see also: Wisz et al. 2013, Araújo and Rozenfeld 2014, Mpakairi et al. 2017).

Our results support our first hypothesis by showing that both species will potentially respond to climate change with conspicuous distributional shifts and range contraction or expansion, since their potential distributions are driven by specific bioclimatic conditions (Hortal et al. 2010). *Oecanthus pellucens* proved to be strongly associated with stable climates with predictable rainfall and temperature patterns, as found in many sub-Mediterranean and continental areas across Europe. Conversely, *O. dulcisonans* is more likely to occur on coastal areas with a warmer climate, a preference reflected by its currently known distribution, which mostly spans along temperate dry areas (Peel et al. 2007). As a response to these

Oecanthus pellucens   *Oecanthus dulcisonans*
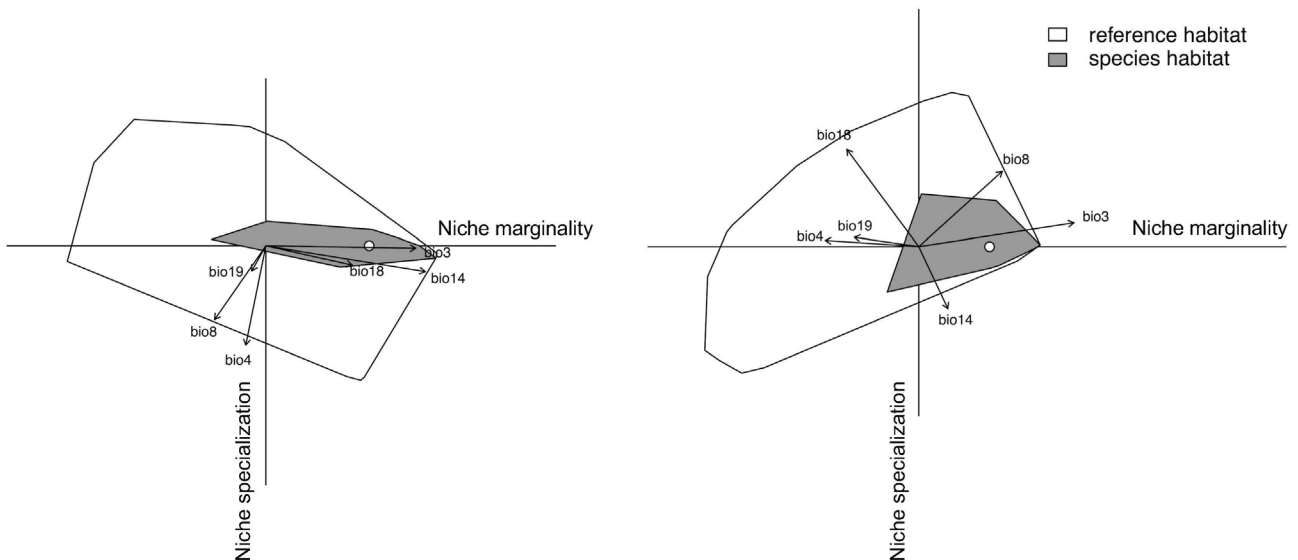
Figure 3. Ecological Niche Factor Analysis (ENFA) of suitable climatic habitat for *Oecanthus pellucens* (left) and *O. dulcisonans* (right). The X-axis corresponds to the marginality axis in the multivariate space; Y-axis corresponds to the first specialisation axis in the multivariate space. Arrow length indicates the magnitude with which each variable accounts for the variance on each of the two axes. The white and grey minimum convex polygons correspond to the multivariate space enclosing all of the available points (reference habitat) and used points (species habitats), respectively. The white circle indicates niche position (median marginality) relative to the average background environment (the plot origin). Environmental variables: Bio03 = Isothermality; Bio04 = Temperature seasonality; Bio08 = Mean temperature of the wettest quarter; Bio14 = Precipitation of driest month; Bio18 = Precipitation of warmest quarter; Bio19 = Precipitation of coldest quarter.

differences in their favoured bioclimatic conditions, the two species are predicted to diverge in their responses to climate change, thus confirming our second hypothesis that even closely resembling species sharing similar habitats may react differently to climate change (Struck et al. 2018). Specifically, the association to stable/oceanic climates (i.e., temperate areas without extremely dry periods; Peel et al. 2007) will potentially induce a dramatic range contraction and northward shift in *O. pellucens*, with a predicted decrease of over 65%, and a slight range northward expansion in *O. dulcisonans*. Range shifts also translate into a significant shift in the location of overlapping suitable areas between the two species (as also found for two *Meta* spiders by Mammola and Isaia 2017, and for New World's vertebrates by Krosby et al. 2015).

Climate can affect species' ranges at large scales, yet habitat characteristics and biotic interactions are well known to increase in their importance at local scales (Thuiller et al. 2004, Araújo and Luoto 2007, Pellissier et al. 2010), as well documented when modeling insect distributions (Hortal et al. 2010, Warren et al. 2010). As a consequence, modeling and predicting species' distributions at different spatial scales is highly effective to provide a clearer picture of distributional drivers, including both biotic and abiotic factors (Cabeza et al. 2010, Raffini et al. 2020, Warren et al. 2010, König et al. 2021), as we did for the two European *Oecanthus* crickets. Our models took into account a worst-case climatic scenario of high-intensity future gas emissions, meaning that the predicted responses may represent extreme cases. However, large scale distributional changes among insects, including our study species, have been possibly ascribed to climate change (Poniatowski et al. 2020). To be specific, *O. pellucens* was recently recorded as expanding into North-western Germany and the UK (Burton 2001, Poniatowski et al. 2020), where our models and previously published ones both predicted further expansion of its suitable climatic habitat (Feldmeier et al. 2018).

Despite their range overlap at a global scale, the two *Oecanthus* species are rarely found in syntopy, which is only reported in southern Italy, Spain, France and Greece (see Labadessa and Todisco 2016). This observation confirms our regional models, where a proxy for interspecific competition ranked high among the variables influencing the local presence of *O. pellucens* only. In fact, the latter was more likely to occur at the regional scale in areas farther from *O. dulcisonans*, whose presence in turn was not apparently affected by the congeneric species. This asymmetric biotic interaction suggests the occurrence of interspecific competition and possible displacement (as in Mpakairi et al. 2017) and points at *O. pellucens* as the 'loser' species in terms of competitive dominance (Carrete et al. 2010). Whether and how this competition actually occurs and on which resources, e.g. food, shelter, acoustic space or others (Roca and Proulx 2016), is yet to be clarified with more field-based approaches. However, due to the similarities in their behavioural features, competitive exclusion

between the two *Oecanthus* is likely dependent on acoustic interference, as already demonstrated among sympatric orthopterans (Greenfield 1988). *Oecanthus pellucens* is also known to negatively respond to anthropogenic acoustic interference (Orci et al. 2016), and may thus be also sensitive to interspecific competition for acoustic space (van der Mescht et al. 2021).

Potential sensitivity to competition is also supported by our niche analysis, indicating *O. pellucens* as a more specialised taxon than its congeneric competitor, which shows a greater climatic niche plasticity and may prove more efficient in persisting in suboptimal areas, thus possibly gaining a competitive advantage (Lancaster et al. 2017). In fact, *O. pellucens* is considered a specialised orthopteran (Feldmeier et al. 2018) in terms of environmental preferences. A higher degree of specialisation upon specific climatic conditions in *O. pellucens* actually translated into more dramatic changes of the species' potential distribution under future climate change scenarios, and in the negative effect of *O. dulcisonans* on its occurrence at regional scales. Our predictions on the distributions of the two *Oecanthus* in Europe also forecast that the overlapping areas between the two ranges will increase in the future. This scenario could possibly exacerbate competitive dynamics at local scales (Alaniz et al. 2018, Siepielski et al. 2018, Legault et al. 2020), with potentially negative effects on the conservation of the less dominant *O. pellucens* (Cabeza et al. 2010).

Conclusions

The case of *Oecanthus* crickets exemplifies how the coupling of global and regional modeling may provide more complete insights into how insect distributions relate to climate at different spatial scales. This case study also highlights a potential framework for assessing potential competitive dynamics, by relying on detailed and systematic presence records. Understanding scale dependencies in species' distributions and including biotic interactions is also key to increase our understanding of insects' biogeographical patterns and to providing better predictions that may inform conservation policy in the Anthropocene (Goulson 2019, Montgomery et al. 2020).

Acknowledgements

Author Contributions

RL conceived the idea and collected original data, RL and LA curated final dataset compilation, LA

performed analyses, both authors wrote and revised the manuscript.

Data Accessibility Statement

No novel script or code was created for this work; all original data are available from RL, upon reasonable request.

Supplemental Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
Table S1. Bioclimatic variables retained for species distribution modeling (sdm) of Oecanthus pellucens and O. dulcisonans, at global and regional scales.
Figure S1. Response curves of Oecanthus pellucens to the three most relevant variables, as assessed by ensemble sdms at global and regional scales.
Figure S2. Response curves of Oecanthus dulcisonans to the three most relevant variables, as assessed by ensemble sdms at global and regional scales.

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