The role of climate and biotic factors in shaping current distributions and potential future shifts of European Neocrepidodera (Coleoptera, Chrysomelidae)

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Insect Conservation and Diversity

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Journal:	*Insect Conservation and Diversity*
Manuscript ID	ICDIV-19-0099.R1
Manuscript Type:	Original Article
Date Submitted by the Author:	n/a
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Keywords:	Habitat Suitability Models, Flea Beetles, Neocrepidodera, Climate Change, Ensemble Modelling, Host Plants

The role of climate and biotic factors in shaping current distributions and potential future shifts of European *Neocrepidodera* (Coleoptera, Chrysomelidae)

Running title: Drivers of *Neocrepidodera* distributions

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ABSTRACT

1. The Western Paleartic species of *Neocrepidodera* Heikertinger (Coleoptera: Chrysomelidae: Galerucinae: Alticini) mostly occur in medium and high elevation ecosystems particularly sensitive to climate change.
2. Here, using ensemble projections from state-of-the-art habitat suitability modelling techniques, we investigated how climate change and associated changes in host availability may affect the persistence of three pairs of closely related *Neocrepidodera* taxa.
3. Modelled niches and suitability patterns reflected the current distributions of the targeted taxa. *Neocrepidodera ligurica* occupies a small portion of the broader environmental niche of *N. melanostoma*, and its narrow geographical range makes this species particularly vulnerable to potential loss of suitable habitats in Western Alps. *Neocrepidodera cyanescens cyanescens* and *N. cyanescens concolor* were found to occupy separate niches, but the non-significance of the niche similarity test suggested their divergence being probably due to allopatric processes. *Neocrepidodera corpulenta* and *N. rhaetica* showed partially overlapping niches, coherently with their co-occurrence in Western Alps. Most of the targeted taxa were predicted to potentially lose large portions of currently suitable areas in the forthcoming decades.

4. Notwithstanding the candidate host plants did not emerge as most important predictors, except *Aconitum lycoctonum* for *N. cyanescens concolor*, a clear reduction of potential insect-plant co-occurrence areas resulted for most future scenarios.
5. Climate was confirmed to noticeably affect the distribution of the targeted taxa, among which *N. ligurica*, *N. cyanescens concolor*, *N. corpulenta* and *N. rhaetica* may need specific prioritization measures in the future decades, claiming for further attention on mountainous entomofauna in a warming world.

Keywords: Habitat Suitability Models, Flea Beetles, *Neocrepidodera*, Climate Change, Ensemble Modelling, Host Plants

INTRODUCTION

The potential effects of ongoing and future human-related climate change on biodiversity at both global and regional scales represent one of the most studied and debated issues of our epoch. More and more evidence has been found that relates global warming to detrimental changes in both the abiotic and biotic characteristics of a wide range of habitats, threatening a large number of animal and plant species (Bellard *et al.*, 2012; Dullinger *et al.*, 2012; Zhang *et al.*, 2017; Archis *et al.*, 2018; Iannella *et al.*, 2018). The species prevalently inhabiting mountainous regions severely suffer from climate change, due to the associated rapid and dramatic modifications in the high-altitudes ecosystems (Inouye, 2008; Forrest *et al.*, 2012; Li *et al.*, 2016; Urbani *et al.*, 2017; Rogora *et al.*, 2018). In this context, Habitat Suitability Models (HSMs) (Guisan *et al.*, 2017) represent a powerful investigation tool, whose huge increase of implementations in the last two decades has marked a noticeable break-through in conservation biogeography (Franklin, 2013). Indeed, the use of HSMs to investigate the factors which shape the potential distribution of species showing puzzling biogeographical patterns can provide useful insights (Acevedo *et al.*, 2012; Iannella *et al.*, 2017; Reino *et al.*, 2017), especially in a climate change context.

The Alticini tribe comprises small-to-medium-sized phytophagous Coleoptera from the Chrysomelidae family, subfamily Galerucinae, named 'flea beetles' because of the presence of a metafemoral extensor tendon that enables them to jump. They are probably the largest and most diversified tribe of Chrysomelidae, comprising about 550 genera and over 8000 species worldwide (Nadein & Beždek 2014). Some genera spread over several zoogeographical regions, while others are strictly endemic to narrow areas. Nonetheless, even when characterized by limited distributions, genera or species-groups can differentiate in a high number of species (Biondi & D'Alessandro 2008, D'Alessandro *et al*., 2014, 2016). Host plants for the Alticini tribe are known from almost all the vascular plant families, generally with high levels of specialization and close relation with the vegetation types (Jolivet & Verma 2002; Biondi *et al*., 2015; D'Alessandro *et al*., 2018). The large number of species, the diversification of distribution ranges, the differentiation capability, the close relation with the vegetation types and the high levels of trophic specialization, make flea beetles sensitive to various environmental changes. Thus, flea beetles represent a good model for the investigation of evolutionary and biogeographical hypotheses and processes at different geographic scales (D'Alessandro *et al*., 2014, 2018; Urbani *et al*., 2015, 2017).

The flea beetle genus *Neocrepidodera* Heikertinger (Coleoptera: Chrysomelidae: Galerucinae: Alticini) is widespread, with about 100 species in the Palaearctic, Nearctic and Oriental regions. The Palaearctic taxa were revised by Biondi (1989, 1993), Konstantinov (1991), Konstantinov and Vandenberg (1996), Baselga and Novoa (2005), Baselga (2006) and Döberl (2010). This genus occurs in Europe with 30 species, according to the Pan-European Species Directories Infrastructure (PESI, 2018). The Western Palaearctic species are generally associated with medium and high elevations, and they show a high rate of endemism and vicariance deemed to be mainly linked with the Quaternary paleoclimatic events (Biondi 1989, 1993).

Notwithstanding the noticeable peculiarities characterising the biogeography and ecology of these phytophagous beetles, no previous study implementing HSMs has been carried out on any *Neocrepidodera* species to investigate the relative distributional drivers.

Here, we used Ensemble Forecasting techniques (Araujo & New, 2007), which permit the combination of multiple HSMs into a single Ensemble Model through different averaging criteria, to assess the potential future responses of three pairs of *Neocrepidodera* taxa to different climate change scenarios. Specifically, three Representative Concentration Pathways (RCPs), depicting increasing radiative forcing due to human-induced greenhouse gas (GHG) emissions, were considered for model projections.

Recent studies have highlighted the usefulness of including within the HSMs some predictors representing biotic interactions (Hof *et al.*, 2012; Gherghel *et al.*, 2018; Paiva-Silva *et al.*, 2018) and/or the response of the resources used by animal species to the same abiotic variables used to model the species' potential distribution (Thuiller *et al.*, 2018). Thus, for two selected pairs of closely related *Neocrepidodera* taxa, we implemented a nested modelling framework in which the predictions from Ensemble Models (EMs) built for the candidate host plants were included as predictors in the EMs built for the hosted flea beetles.

Moreover, we investigated, through measurements of niche overlap and statistical testing of niche divergence (Warren *et al.*, 2008; Broennimann *et al.*, 2012), whether the current distribution patterns characterizing the three pairs of *Neocrepidodera* taxa analysed could be linked to actual differences in their environmental and/or resource requirements. Results from such niche analysis could be helpful to clarify both the factors shaping the biogeography of the selected *Neocrepidodera* taxa and the potential differences in their response to climate change resulting from the performed Ensemble Forecasts.

MATERIALS AND METHODS

Study area and target taxa

The study area encompasses three major mountainous massifs, which host almost all the occurrence records of the targeted taxa (Fig. 1): the Apennines, which run north-south across most of peninsular Italy; the Alps, whose arc covers Southern France, Northern Italy, Switzerland, Austria, Southern Germany and extends southeast in the Balkans; the Carpathians, going through Poland, Slovakia, Czech Republic, Austria, Hungary, Ukraine, Romania and Serbia.

We focused the analyses on three pairs of *Neocrepidodera* species and subspecies:

1) *N. ligurica* J. Daniel, 1904 versus *N. melanostoma* Redtenbacher, 1849, with the latter occurring in the Central and Northern Apennines, throughout the Alpine arc and in some localities of the Dynaric Alps, and the former occupying a narrow portion of the *N. melanostoma* distribution in the Ligurian, Maritime and Cottian Alps;
2) *N. cyanescens cyanescens* Duftschmid, 1825 versus *N. cyanescens concolor* K. Daniel, 1900, the first spread across the Eastern Alps and present in some localities in the Carpathians and in Transylvania, and the latter distributed in the Ligurian and Maritime Alps;
3) *N. corpulenta* Kutschera, 1860 versus *N. rhaetica* Kutschera, 1860; the former species is spread all along the Apennines chain, and present in some localities in the Balkans, in the Carpathians, in Transylvania and in the Western Alps, where it shares a parapatric zone with *N. rhaetica*, which replaces *N. corpulenta* in the rest of the Alpine arc.

We analysed the above-mentioned *Neocrepidodera* taxa by pairs to assess if differential responses to climatic and/or biotic factors could be linked to niche divergence phenomena between the closely related taxa forming each pair. This way, the environmental drivers contributing to their current disjunct (the two *N. cyanescens* subspecies), parapatric (*N. corpulenta* - *N. rhaetica*) or nested (*N.*

ligurica – N. melanostoma) distributions, as well as the potential shifts in response to climate change, could be better characterized.

Occurrence records (GPS resolution or exact locality) for the target taxa were retrieved from Maurizio Biondi's and other entomological collections, from the checklist of the Italian fauna (Biondi, 2006), from literature search and from the GBIF (Global Biodiversity Information Facility) database. In the latter case, occurrence records were scrutinized through both expert-based evaluation and literature search about the localities reported to host *Neocrepidodera*, to check their coherence with the known autoecology and biogeographical history of the considered taxa.

Considering available evidence about preferred host plants of some *Neocrepidodera* species (Biondi, 1993), we selected two species of Ranunculaceae, namely *Aconitum lycoctonum* L., 1753 emend. Koelle and *A. napellus* L., 1753 emend. Skalický, as candidate host plants for *N. cyanescens cyanescens* and *N. cyanescens concolor*, while for *N. corpulenta* and *N. rhaetica* we chose as candidate hosts two species of Asteraceae, namely *Arnica montana* L., 1753 and *Doronicum austriacum* Jacq., 1774. No plants were included as biotic predictors within the HSMs built for *N. ligurica* and *N. melanostoma* because less evidence about preferred hosts of these species is available so far.

Occurrence data for the selected plant species were gathered from the database of the CBNA (Conservatoire Botanique National Alpin), containing georeferenced records (ETRS89 reference system) from both France and other European countries; we considered only records with a minimum resolution of 1 km temporally ranging from the middle 1960s to 2013. Since the presence points of the *Neocrepidodera* taxa were recorded using the WGS84 geographic coordinate system, we projected them to the ETRS89 reference system in ArcMap 10.0 (ESRI 2011) before model building; thus, the occurrence datasets of *Neocrepidodera* and those of the candidate host plants shared the same reference system. Fig. 1 shows the distribution of presence points retrieved for the

Neocrepidodera taxa and for the host plants, while coordinates and sources of these occurrence records are listed in Supporting Information Table S1.

The available occurrences for each *Neocrepidodera* and plant taxon were spatially thinned through the "spThin" R package (Aiello-Lammens *et al.*, 2015). For each taxon, three thinning iterations were performed setting 'thin.par' = 2 km to rarefy occurrences falling within neighbouring cells of the raster maps representing the considered predictors (see 'Environmental variables'). Then, the thinned dataframe with the highest number of remaining occurrences was selected for model building to preserve as information as possible about enviromental conditions at occurrence locations (Anderson & Raza, 2010), given the limited amount of data available for some *Neocrepidodera* taxa (e.g. *N. cyanescens concolor* and *N. ligurica*).

The full occurrence datasets were instead used to obtain a representation of the geographic range of each *Neocrepidodera* taxon through α-hull-based polygons, drawn by means of the R package "alphahull" (Beatriz Pateiro-López & Alberto Rodríguez-Casal, 2010), which are less affected by biases in range estimates than the classic minimum convex polygons (Burgman & Cox, 2003).

Environmental variables

Current

Nineteen downscaled bioclimatic variables from Worldclim version 1.4 (Hijmans *et al.*, 2005; Dullinger *et al.*, 2012) were chosen as climate-related candidate predictors and downloaded as raster files at 30 seconds resolution (i.e. approximately 1 km^2). The downloaded rasters were projected from the original WGS84 reference system to ETRS89-LAEA (Lambert Azimuthal Equal Area) by means of the 'projectRaster' function from the "raster" R package (Hijmans *et al.*, 2015), to match the metric reference system of the occurrence data (ETRS89) and preserve cell extent across the full latitudinal range of the study area.

Presence of multicollinearity within the set of candidate predictors, which may lead to distortions in the estimation of model parameters and variable importance (Dormann, 2007; Crase *et al.*, 2012; Dormann *et al.*, 2013), was first checked by calculating the Pearson *r* coefficient for each pair of variables across the study area. For the pairs with Pearson $| r | > 0.7$, we kept the variable presumed to be more relevant to the species' ecology (Dormann *et al.*, 2013; Brandt *et al.*, 2017). Since hidden multicollinearity issues could still affect the data after having discarded the variables showing high pairwise correlations across the study area, further refinement on the candidate predictors was accomplished performing Variance Inflation Factor (VIF) analyses (Guisan *et al.*, 2006, 2017) on the set of presence-pseudoabsence points used to build the HSMs (see 'Model building').

Future

Two time horizons (2050 and 2070) and three Representative Concentration Pathways (RCPs; RCP2.6, RCP4.5 and RCP8.5) (Meinshausen *et al.*, 2011), based on the Rossby Centre Regional Climate Model RCA4 (Strandberg *et al.*, 2014), were considered to investigate potential future distributional shifts of the target *Neocrepidodera* taxa in response to increasing GHGs concentration trajectories. As for the layers representing current climate, the WGS84-based rasters for the future scenarios were projected to ETRS89-LAEA through the 'projectRaster' function.

Model building

Model building was performed in R (R Core Team, 2018) through the package "biomod2" (Thuiller *et al.*, 2016). The algorithms selected to build the HSMs were Generalized Linear Model (GLM), Generalized Additive Model (GAM) and Generalized Boosted Regression Models (GBM). For each algorithm, two-way interactions among predictors were allowed. With respect to the other relevant parameterization arguments, the default 'BIOMOD_ModelingOptions' settings were maintained for GLM ('quadratic' formula type, binomial error distribution with logit link function, and stepwise AIC as model selection criterium) and for GAM ('s_smoother' cubic-spline smoother and binomial error distribution with logit link function). For GBM, we set 5-fold cross-validation with 5000 fitted trees

for each iteration, while other relevant parameters were maintained to the default values ('shrinkage' = 0.001, 'bag.fraction' = 0.5).

For both the target *Neocrepidodera* taxa and the selected host plants, pseudoabsences (hereafter, PAs) were generated by means of a geographical exclusion strategy. First, a buffer ranging from 2 km to 200 km around the thinned occurrences was generated for each taxon through the 'gBuffer' and gDifference' functions of the "rgdal" R package (Bivand *et al.*, 2014). Then, 10000 PAs were drawn at random within the obtained buffer polygon, after having clipped this latter to the boundaries of the study area to avoid the generation of PAs within raster cells with no values for the predictors (i.e. at sea). The clipping was performed through the 'Extract by Mask' function in ArcMap 10.0. Finally, 10 sets of 1000 PAs each were generated for HSMs calibration, randomly sampling without replacement from the previously drawn 10000 PAs.

The choice of a geographically-buffered PAs sampling, as well as the number of PAs sets and the sample size of these latter, was based on Barbet-Massin *et al.* (2012), who demonstrated that this approach is well suited to the algorithms we selected and that it ameliorates HSMs' accuracy when few occurrence records are available.

The chosen buffer distances were intended to avoid both the selection of PAs within the same cell of a presence point, or from the immediately contiguous cells, and the selection of PAs too far from presence localities. Indeed, PAs selected in a restricted region around occurrence localities would have increased the probability of obtaining low performing HSMs (VanDerWal *et al.*, 2009); on the other hand, the generation of PAs within a noticeably broad area would have increased the probability of PAs falling in regions with bioclimatic conditions pronouncedly different than those of presence localities, potentially leading to over-simplified and artificially accurate HSMs (Chefaoui & Lobo, 2008; VanDerWal *et al.*, 2009).

The PAs sets generated for each taxon and the respective thinned occurrences were then joined in a single dataset and converted to biomod2-suited format by means of the 'BIOMOD_FormatingData'

function ('PA.strategy' set to 'user.defined'). Particularly, for each *Neocrepidodera* taxon and each host plant, the dataset for HSMs building comprised 90% of the available thinned occurrences and the ten sets of 1000 PAs previously generated. The remaining thinned occurrences were instead joined with 100 additional PAs randomly drawn within the buffer polygon, excluding the 10000 PAs already generated for model building, to build an independent evaluation dataset with which the continuous habitat suitability (hereafter, HS) predictions from the Ensemble Model (hereafter, EM) could be later compared to select a binarization threshold.

Values of the bioclimatic variables retained after the preliminary check of pairwise correlations, as well as suitability values from the wmean EMs (see 'Model evaluation and Ensemble Forecast') obtained for the candidate host plants, were extracted at occurrences and PAs points through the 'extract' function of the "raster" R package. Then, a VIF analysis was performed on these predictors through the 'vif.step' function of the "usdm" R package (Naimi, 2015), and the ones exceeding the recommended threshold of VIF = 10 (Guisan *et al.*, 2017) were discarded from the modelling framework.

Model evaluation and Ensemble Forecast

Three iterations of a random split-sample cross-validation approach (Thuiller *et al.*, 2016; Guisan *et al.*, 2017) were performed on the datasets generated for HSMs building, each time using 80% of the data for model calibration and the remaining 20% as test data. Thus, 90 HSMs (i.e. 3 algorithms * 3 split-sample runs * 10 PAs sets) were finally built for each target taxon. Then, the HSMs whose predictions on the test data reached a chosen threshold value for both the True Skill Statistic (TSS) (Allouche *et al.*, 2006) and the Area Under the Curve (AUC) of the Receiver Operating Characteristic Curve (ROC) (Fielding & Bell, 1997; Phillips *et al.*, 2006) were retained for the EM building process: the selected thresholds were TSS $\geq$ 0.7 and AUC $\geq$ 0.8. In the ensemble modelling step, we used the 'weighted mean of probabilities' (wmean) and the 'coefficient of variation of probabilities' (cv) algorithms implemented in the 'BIOMOD_EnsembleModeling' function. The wmean algorithm

represents a form of weighted averaging in which the more an HSM attains high discrimination scores on test data the higher its predictions are weighted in the EM (Marmion *et al.*, 2009); here, the contribution of the single HSMs to the wmean EM was weighted based on their TSS scores. The cv EM, instead, provides information about the degree of uncertainty in the EM building process. Indeed, it returns the coefficient of variation of HS values over the component HSMs (Thuiller *et al.*, 2016), so that the higher the cv value at a certain pixel, the higher the variability in the HS values predicted for that pixel by the different HSMs.

The algorithm-independent randomization procedure of the BIOMOD modelling framework (Thuiller *et al.*, 2009) was used to calculate the contribution of the single predictors within the obtained wmean EMs, setting the number of permutations to 3. Contribution scores from the 3 permutation runs were first averaged and then scaled to percent contributions (Bucklin *et al.*, 2015).

The wmean EM for each of the 6 future scenarios (2 time horizons * 3 RCPs) was computed by means of the 'BIOMOD_EnsembleForecasting' function, projecting to that scenario the HSMs selected for ensemble modelling and then weighting their predictions based on the weights they achieved in the wmean EM built under current conditions. Successively, we used the 'BIOMOD_RangeSize' function to investigate potential shifts in suitable areas for the target *Neocrepidodera* taxa and the corresponding candidate host plants with respect to the current conditions (i.e. suitable areas lost, remaining stable or gained). Since this function needs binarized predictions (i.e. suitable vs unsuitable areas), we chose as binarization approach the maximisation of the TSS (max-TSS), computed by means of the 'Find.Optim.Stat' function comparing the wmean EM continuous predictions with the previously set-aside evaluation data. This is reported to be an appropriate binarization criterium when dealing with presence-background HSMs (Liu *et al.*, 2013). The obtained thresholds are listed in Supporting Information Text S1.

The binarized raster maps for the current scenario and those representing the predicted HS shifts within the future scenarios were converted to shapefiles in ArcMap 10.0. Then, the 'Intersect'

function of ArcMap 10.0 was used to extract, for each *Neocrepidodera* - host plant pair, the overlap polygons representing: 1) areas predicted to be suitable for both the considered flea beetle and the corresponding host plant under the current scenario, and 2) the different combinations of the Stable and Gain categories, representing areas predicted to be suitable in the projection scenario for both the flea beetle and the candidate host. The extent of these overlap polygons was then computed to quantify the effect of future warming conditions on the potential co-occurrence of the target *Neocrepidodera* taxa and the respective candidate hosts.

Niche analysis

In order to understand how the relative positions of the considered *Neocrepidodera* taxa in the environmental space could relate to their current distribution patterns, we implemented the 'PCA-env' approach described in Broennimann *et al.* (2012). The set of input predictors used to build the HSMs was thus reduced to two uncorrelated principal components, based on which kernel-smoothed densities of occupancy of the taxa in the environmental space were built. Moreover, for each pair of *Neocrepidodera* taxa, biplots were produced through the "factoextra" R package (Kassambara & Mundt, 2017) to show the contribution of the input predictors along the two principal component axes.

The Schoener's *D* metric (Schoener, 1970; Warren *et al.*, 2008) was calculated, through the 'ecospat.niche.overlap' function of the "ecospat" R package (Di Cola *et al.*, 2017), to assess the degree of niche overlap within each pair of *Neocrepidodera* taxa. The obtained niche overlap values were statistically tested first for the niche equivalency hypothesis (Warren *et al.*, 2008; Broennimann *et al.*, 2012) through the 'ecospat.niche.equivalency.test' function, and then for the more conservative niche similarity hypothesis (Warren *et al.*, 2008; Broennimann *et al.*, 2012) by means of the 'ecospat.niche.similarity.test' function. For both tests, the observed niche overlap is compared to the 95th percentile of the null distribution built through the specific randomization procedure (1000

pseudo-replicates for both tests): if the observed *D* falls outside this interval, the null hypothesis can be rejected.

RESULTS

Nine bioclimatic variables were retained as candidate predictors after the check for multicollinearity across the entire study area (see Supporting Information Table S2): BIO2 (Mean diurnal temperature range), BIO3 (Isothermality), BIO4 (Temperature seasonality), BIO5 (Maximum temperature of warmest month), BIO6 (Minimum temperature of coldest month), BIO8 (Mean temperature of wettest quarter), BIO17 (Precipitation of driest quarter), BIO18 (Precipitation of warmest quarter) and BIO19 (Precipitation of coldest quarter). The VIF analyses successively performed on the presence-pseudoabsence datasets led to the final sets of uncorrelated predictors listed in Table 1.

The number of residual occurrences after the spatial thinning for the target *Neocrepidodera* taxa and the candidate hosts, along with the countries hosting these presence records, are reported in Supporting Information Table S3, while Table 2 summarizes the percent importance scores obtained for the relevant predictors within the Ensemble Models (EMs) built for the host plants and the *Neocrepidodera*.

290 **Table 1.** Predictors selected to build the HSMs for the target *Neocrepidodera* taxa and the candidate host plants. HS = Habitat Suitability

Host plants	**Predictors**
Aconitum lycocotnum *Aconitum napellus* *Arnica montana* *Doronicum austriacum*	BIO3; BIO4; BIO6; BIO8; BIO18; BIO19
Neocrepidodera	**Predictors**
N. ligurica *N. melanostoma*	BIO3; BIO4; BIO6; BIO8; BIO18; BIO19
N. cyanescens concolor *N. cyanescens cyanescens*	BIO3; BIO4; BIO6; BIO8; BIO18; *Aconitum lycoctonum* HS; *Aconitum napellus* HS
N. corpulenta *N. rhaetica*	BIO3; BIO4; BIO6; BIO8; BIO18; BIO19; *Arnica montana* HS; *Doronicum austriacum* HS

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Table 2. Averaged percent importance scores of: the three most contributing bioclimatic predictors for *Aconitum lycoctonum, Aconitum napellus*, *Arnica montana* and *Doronicum austriacum*; the four most contributing bioclimatic predictors for each target *Neocrepidodera* taxon, along with host plant Habitat Suitability (HS) for *N. cyanescens concolor*, *N. cyanescens cyanescens*, *N. corpulenta* and *N. rhaetica*.

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Candidate Host Plants Ensemble Models					
Taxon	**Predictor**	**Percent Contribution**	**Taxon**	**Predictor**	**Percent Contribution**
Aconitum lycoctonum	BIO6	33.6	*Aconitum napellus*	BIO6	46.0
	BIO18	27.0		BIO8	37.1
	BIO8	18.5		BIO4	11.6
Arnica montana	BIO6	37.5	*Doronicum austriacum*	BIO6	39.0
	BIO4	21.6		BIO8	19.1
	BIO8	18.4		BIO4	16.0
***Neocrepidodera* Ensemble Models**					
Taxon	**Predictor**	**Percent Contribution**	**Taxon**	**Predictor**	**Percent Contribution**
N. ligurica	BIO4	22.6	*N. melanostoma*	BIO6	34.4
	BIO6	21.0		BIO18	21.2
	BIO3	18.6		BIO4	18.7
	BIO19	16.5		BIO3	10.6
N. cyanescens concolor	*Aconitum lycoctonum* HS	28.7	*N. cyanescens cyanescens*	BIO18	43.3
	BIO6	18.9		BIO6	21.9
	BIO3	16.2		BIO2	9.3
	BIO18	14.0		BIO8	8.5
	BIO8	9.1		*Aconitum napellus* HS	8.1
	Aconitum napellus HS	4.5		*Aconitum lycoctonum* HS	2.1
N. corpulenta	BIO8	18.9	*N. rhaetica*	BIO6	19.9
	BIO3	18.0		BIO8	19.5
	BIO4	15.5		BIO3	14.2
	BIO19	13.8		BIO4	10.5
	Arnica montana HS	8.4		*Arnica montana* HS	9.0
	Doronicum austriacum HS	3.4		*Doronicum austriacum* HS	8.9

Apart from *Aconitum lycoctonum*, for which precipitation of the warmest quarter (BIO18) obtained the second highest importance score, temperature-linked variables, particularly minimum temperature of the coldest month (BIO6), clearly resulted as the most important predictors for all the candidate host plants (Table 2). From the corresponding partial response curves, Habitat Suitability (HS) for the host plants appears to decrease, once the remaining predictors have been set to their mean value, as temperature, or its seasonality (BIO4), increases (Supporting Information Fig. S1). Temperature-linked variables resulted as predominant predictors also for *N. ligurica* and *N. melanostoma*, with the first species showing comparable importance scores for BIO4 and BIO6 (Table 2), and the latter being instead more markedly dependent upon BIO6. Different partial responses to BIO6 emerged for the two species, with the response curve obtained for *N. ligurica* being monotonically decreasing and the one obtained for *N. melanostoma* being more bell-shaped-like (Supporting Information Fig. S2). Considering the two pairs of *Neocrepidodera* taxa for which suitability for the respective candidate hosts was included among the predictors, only from the EM built from *N. cyanescens concolor* an host plant, namely *Aconitum lycoctonum*, resulted as the most important predictor (Table 2). Nonetheless, the three-dimensional response surfaces represented in Supporting Information Figs. S5-6 show that, at the least for one of the candidate host plants, the combined effect of host suitability and of the most important bioclimatic predictor, once all the remaining predictors have been set to their mean value, produced higher predicted HS values than the single predictors individually did (cf. Supporting Information Figs. S3-4). Indeed, for both the *N. cyanescens* subspecies, higher suitability values for *Aconitum lycoctonum* synergistically increase suitability for the flea beetles in combination with BIO6 (*N. cyanescens concolor*) and, even though less clearly, with BIO18 (*N. cyanescens cyanescens*) (Fig. S5). This pattern did not emerge considering the combined effect of HS for *Aconitum napellus* and the same bioclimatic predictors. With respect to the pair *N. corpulenta – N. rhaetica*, a positive effect on flea beetle suitability emerged from the combination of *Arnica montana* suitability and BIO6 for *N. rhaetica* and, to a lesser extent,

from the combination of *Doronicum austriacum* suitability and mean temperature of the wettest quarter (BIO8) for *N. corpulenta* (Fig. S6).

Continuous maps resulting from the cv EMs built for the current scenario were reported in Supporting Information Fig. S7. The coefficient of variation among the predictions of the component HSMs is less than 0.4 across most of the study area for *N. melanostoma*, *N. cyanescens cyanescens* and *N. rhaetica*, while wider areas with cv > 0.4 emerged for *N. ligurica*, *N. cyanescens concolor* and *N. corpulenta*, primarily outside their currently occupied range (see Figs. 2a, 3a, 4a)

The binarized HS under the current scenario for the three considered *Neocrepidodera* pairs and the respective predicted HS shifts under the different 2070 RCP scenarios are shown in Figs. 2-4, while predicted HS shifts for 2050 under the different RCPs were reported in Supporting Information Figs. S8-10.

The core of *N. ligurica* density of occurrence in the bioclimatic space corresponds to a peripherical portion of the wider density of occurrence of *N. melanostoma* (Fig. 5a2), resulting in markedly broader suitable areas for this latter species also in geographical space (Figs. 2a-b). The niches of *N. ligurica* and *N. melanostoma*, whose overlap value was $D = 0.054$, appeared not to be equivalent ($P < 0.001$ in the niche equivalency test). However, when tested for niche divergence through the niche similarity test, the niches of the two species resulted not more different than expected by chance ($P = 0.652$), based on differences in the bioclimatic conditions characterising the respective ranges.

Neocrepidodera cyanescens concolor and *N. cyanescens cyanescens* showed null niche overlap ($D = 0$) reflected by strong divergences in their occupancy of the environmental space (Fig. 5b2), which is coherent with the mostly different areas predicted as suitable for them under the current scenario (Figs. 3a-b). The niches of the two subspecies are clearly differentiated along the first principal component, to which high contribution was given by BIO6 (Figs. 5b1-2). Moreover, the centre of the occurrence density for *N. cyanescens concolor* is more shifted towards positive values of the second principal component than the one for *N. cyanescens cyanescens* is, which could be due to the

345 contribution given by suitability for *Aconitum lycoctonum* to this axis (Fig. 5b1). Even though the
346 niche equivalency test rejected the hypothesis of the niches of the two *N. cyanescens* subspecies being
347 equivalent ($P < 0.001$), the niche similarity test did not permit to infer a significant divergence once
348 the differences in background conditions were considered ($P = 0.598$).

349 The niche overlap value for *N. corpulenta* and *N. rhaetica* was $D = 0.201$, reflected by their densities
350 of occurrence showing noticeable overlap but clearly separated centres (Fig. 5c2). As for the two
351 previous pairs of *Neocrepidodera*, according to the niche equivalency test the modelled niches of *N.*
352 *corpulenta* and *N. rhaetica* are not equivalent ($P < 0.001$). Anyway, the result of the niche similarity
353 test ($P = 0.562$) did not permit to reject the null hypothesis of the niches being less different than
354 expected based on the environmental conditions in the respective ranges.

355 *Neocrepidodera ligurica*, *N. cyanescens concolor*, *N. corpulenta* and *N. rhaetica* were predicted to
356 lose by 2070 the great majority of currently suitable areas, especially under RCP8.5 (Figs. 2g, 3g, 4g,
357 4h). *N. cyanescens cyanescens*, instead, was predicted to maintain under all the RCPs the major part
358 of suitable areas corresponding to the core of its current range (Figs. 3d, 3f, 3h); moreover, it was
359 predicted to gain broad suitable areas in Central and Eastern Alps under all the RCPs and in the
360 Carpathians under RCP2.6 (Fig. 3d). Finally, *N. melanostoma* was predicted to maintain stable areas
361 in Eastern Alps and potentially gain broad suitable areas even under the more pronounced warming
362 scenarios (Figs. 2d, 2f, 2h). Anyway, most of this predicted gain corresponds to areas located far
363 away from the current range of the species, while large portions of the currently occupied territories
364 were predicted to become unsuitable under RCP4.5 and RCP8.5 (Figs. 2f, 2h)

365 The variation in the extent of overlapping suitable area between each of the two *N. cyanescens*
366 subspecies and the candidate *Aconitum* hosts from the current scenario to 2050 and 2070 under the
367 three RCPs was reported, respectively, in Fig. 6a and Fig. 6c. Differently, Fig. 6b and Fig. 6d show
368 the variation in the percent extent of overlapping suitable area with respect to the overall suitable area
369 for the flea beetle under the different RCPs in 2050 and 2070. The same information for *N. corpulenta*

and *N. rhaetica* with respect to *Doronicum austriacum* and *Arnica montana* was summarized in Figs. 7a-d.

The overlap of suitable areas for *N. cyanescens concolor* and the two *Aconitum* species was predicted to decrease both in 2050 and 2070 (Figs. 6a, 6c), with a clear negative trend along the RCP gradient in 2070. The percentage of suitable area for *N. cyanescens concolor* hosting suitable conditions also for *A. lycoctonum* was predicted to remain close to its current value (~ 10%) under all the three RCPs, both in 2050 and 2070, while a marked decrease in the percent extent of overlapping suitable areas for *N. cyanescens concolor* and *A. napellus* was predicted both in 2050 (except under RCP4.5) and in 2070 (Figs. 6b, 6d).

Considering *N. cyanescens cyanescens*, both the extent of overlapping suitable areas with the two *Aconitum* species (Figs. 6a, 6c) and the percentage of suitable area for the flea beetle hosting suitable conditions also for the host plants (Fig. 6b, 6d) were predicted to decrease with respect to current conditions both in 2050 and in 2070, with clearly decreasing trends along the RCP gradient emerging from projections to 2070.

The extent of overlapping suitable areas for the pairs *N. corpulenta – A. montana* and *N. corpulenta – D. austriacum* was predicted to greatly decrease with respect to current conditions under RCP4.5 and RCP8.5, especially in 2070 (Figs. 7a, 7c). Under RCP 8.5, in 2070 the percentage of suitable area for *N. corpulenta* predicted to be suitable also for the candidate host fell to 0 both for *A. montana* and for *D. austriacum* (Fig. 7d). The extent of overlapping suitable areas for *N. rhaetica* and *D. austriacum* was almost null under the current scenario as well as in 2050 and 2070 under the different RCPs (Fig. 7a, 7c). Finally, considering the pair *N. rhaetica – A. montana*, a decrease in both the net extent and the relative percentage of overlapping suitable area with respect to the current conditions emerged for all the future scenarios, except in 2050 under RCP8.5 because of the stable and gained areas predicted under this scenario for *N. rhaetica* in Central and Eastern Alps (see Fig. S10), regions which are suitable to *A. montana* as well (results not shown).

DISCUSSION

Given the tight bound of the considered *Neocrepidodera* taxa with the mountainous and alpine ecosystems (Biondi, 1993), the identification of the variables shaping and constraining their environmental niches represents an important first step to shed light on the potential future distributional shifts of these flea beetles in response to the ongoing and future climate change (Bibi *et al.*, 2018; Lamprecht *et al.*, 2018; Rogora *et al.*, 2018).

The current distributional patterns of the *Neocrepidodera* taxa within each pair are reflected in the environmental niches depicted through both the Ensemble Modelling approach and the PCA-env procedure.

Neocrepidodera ligurica occurs in a peripheric portion, in Western Alps, of the broader geographic range of *N. melanostoma*, and the density of occurrence of the former species in the environmental space indeed falls at the borders of that of *N. melanostoma* (Fig. 5a2). The narrow climatic niche of *N. ligurica*, associated with its restricted current geographic range (Fig. 2a), could represent a major threat to the future conservation of this species in the face of climate change (Murray *et al.*, 2010; Brown & Yoder, 2015; Brunetti *et al.*, 2019). Indeed, most of the areas predicted to be suitable outside the species range under the current scenario are very distant from the currently occupied ones, and thus the former would be difficulty colonized; moreover, most of them are predicted to be lost even under moderate warming (Figs. 2, S8). Differently, *N. melanostoma* seems to be threatened by climate change only to some extent: in fact, notwithstanding the populations occurring in Western Alps may suffer from the loss of suitable areas in the next decades, especially considering RCP4.5 and RCP8.5, the obtained Ensemble Forecasts to 2070 predicted the gain of broad suitable areas in the northeastern portion of the study area under all the considered RCPs.

417 The two *N. cyanescens* subspecies were found to occupy clearly differentiated environmental niches
418 (Figs. 5b1-2). Nonetheless, the negative result of the niche similarity test indicates that such
419 differentiation is due to the differences in the environmental conditions the two subspecies experience
420 in their respective ranges, suggesting that their divergence might have been prompted by allopatric
421 processes rather than directly by niche divergence (Pyron, 2009; McCormack *et al.*, 2010; Alvarado-
422 Serrano, 2014). *Neocrepidodera cyanescens concolor* resulted to be potentially threatened by climate
423 change as dramatically as *N. ligurica*, with major loss of currently suitable areas under RCP4.5 and
424 RCP8.5 (Figs. 3, S9). Differently, *N. cyanescens cyanescens* will likely maintain wide suitable areas
425 within the core of its current range and it is also predicted to gain some peripherical territories under
426 all the considered scenarios, which bodes well for the conservation of its current populations, at least
427 in Eastern Alps.

428 The density of occurrence in environmental space modelled for *N. corpulenta* and *N. rhaetica*
429 highlighted the existence of a certain range of environmental conditions suitable to both species, even
430 though the respective maximum density zones are clearly separated (Fig. 5c2). This is coherent with
431 the existence of a parapatric area in Western Alps where the two species currently co-occur (Iannella
432 *et al.*, 2017; Reino *et al.*, 2017). With respect to the predicted suitability shifts, both species may face
433 direct threats to the persistence of their populations in the next future: indeed, the patches of stable or
434 gained suitable areas predicted for the two species mainly under RCP 2.6 and RCP4.5, many of which
435 unlikely to be colonized due to their distance from the currently occupied areas, would difficultly
436 counterbalance the overwhelming loss of suitable territories across most of the species' range (Figs.
437 4, S10).

438 The contribution of host plant suitability resulted to be preponderant only within the Ensemble Model
439 obtained for *N. cyanescens concolor* (Table 2). Nonetheless, the three-dimensional response surfaces
440 representing the combined contribution of host suitability and influential bioclimatic variables (Figs.
441 S5-6) suggested that areas with suitable climatic conditions for the flea beetle and higher potentiality

of insect-plant co-occurrence may require particular attention for the conservation of some *Neocrepidodera* taxa. This is particularly true considering *A. lycocotum* with respect to the two *N. cyanescens* subspecies and *A. montana* with respect to *N. rhaetica*.

It is important to notice the predicted future decrease in the extent of potential co-occurrence areas for almost all the considered insect–plant pairs, especially under the more pronounced warming scenarios (Figs. 6-7). This could represent a double jeopardy for those flea beetles predicted to experience a noticeable contraction of their potential distribution in response to warming climate, as *N. cyanescens concolor, N. corpulenta* and *N. rhaetica*. Indeed, even though *A. montana* and *D. austriacum* did not unequivocally emerge as important predictors of *N. corpulenta* and *N. rhaetica* suitability, the reduction of potential co-occurrence under almost all the considered future scenarios (Fig. 7) could represent a trend of contraction in response to warming climate common to other high-altitude Asteraceae species not considered here (Dullinger *et al.*, 2012) and possibly associated to these two flea beetles in a stronger manner than *D. austriacum* and *A. montana*.

Thus, the inclusion of variables related to biotic interactions within the HSMs confirmed to be, even though not completely resolutive in our study, a useful and informative praxis when applying these models to conservation biogeography (Van der Putten *et al.*, 2010; Hof *et al.*, 2012; Franklin, 2013; Gherghel *et al.*, 2018; Thuiller *et al.*, 2018).

From a conservation perspective, it should be pointed out that some of the targeted *Neocrepidodera* taxa will probably require thoughtful prioritization measures in the next future. The restricted current distribution of *N. ligurica* and *N. cyanescens concolor*, the narrow bioclimatic niche of the former, the strong reduction of potential co-occurrence with *A. lycoctonum* predicted for the latter and the dependence of both taxa on temperature-related variables (see Table 1), all represent important alarm bells for the persistence of their current populations. In fact, restricted ranges and sensitivity to changes in temperature regimes already emerged as strong risk factors from previous studies on other orophilous endemic insects (Urbani *et al.*, 2017; Brunetti *et al.*, 2019). *N. rhaetica* and *N. corpulenta*

should be given appropriate consideration as well: indeed, notwithstanding they are more widely distributed than the above-cited taxa, the remaining suitable areas predicted under future warming conditions resulted to be far less extended and more fragmented than under current climate.

However, it should also be mentioned that the representation of the environmental niche emerging from the implemented modelling framework may not properly represent the full fundamental niche of the considered taxa. In fact, the lack of absence and/or abundance data does not permit to have a complete quantification of a species niche (Brotons *et al.*, 2004; Howard *et al.*, 2014); moreover, "proximal" factors other than potential host availability, like dispersal capabilities and population dynamics, could have hampered the target taxa to colonize regions with suitable conditions and reach the equilibrium with the environment (Guisan *et al.*, 2017).

In conclusion, even though detailed prioritization indications could not be provided based only on HSMs forecasting (Sofaer *et al.*, 2018; Peterson *et al.*, 2018), our results highlighted the need to deepen the knowledge about the threats that *Neocrepidodera* and other phytophagous insects will face in the future decades. It is of the utmost importance to keep on investigating the potential effects of climate change on both fauna and flora of mountainous ecosystems, encouraging the integration, when possible, of modelling, experimental and field-based research.

ACKNOWLEDGEMENTS

We are grateful to the Editor and the two anonymous Reviewers for their insightful comments, which permitted us to improve the clearness of this manuscript.

Figures captions

Figure 1. European biogeographical regions, as defined by the European Environmental Agency (EEA), with a zoom on the study area, showing the altitudinal zonation and the occurrences for the six target *Neocrepidodera* taxa and the candidate host plants.

Figure 2. Suitable areas under the current scenario, obtained from the predictions of the weighted mean Ensemble Model, and α-hull-based current range (hatched polygons) for (a) *N. ligurica* and (b) *N. melanostoma*; predicted shifts in habitat suitability by 2070 under RCPs 2.6, 4.5 and 8.5 for (c), (e) and (g) *N. ligurica*, and (d), (f) and (h) *N. melanostoma*, respectively.

Figure 3. Suitable areas under the current scenario, obtained from the predictions of the weighted mean Ensemble Model, and α-hull-based current range (hatched polygons) for (a) *N. cyanescens concolor* and (b) *N. cyanescens cyanescens*; predicted shifts in habitat suitability by 2070 under RCPs 2.6, 4.5 and 8.5 for (c), (e) and (g) *N. cyanescens concolor*, and (d), (f) and (h) *N. cyanescens cyanescens*, respectively.

Figure 4. Suitable areas under the current scenario, obtained from the predictions of the weighted mean Ensemble Model, and α-hull-based current range (hatched polygons) for (a) *N. corpulenta* and (b) *N. rhaetica*; predicted shifts in habitat suitability by 2070 under RCPs 2.6, 4.5 and 8.5 for (c), (e) and (g) *N. corpulenta*, and (d), (f) and (h) *N. rhaetica*, respectively.

Figure 5. Contributions of the input predictors along the first two principal components ('PCA-env', Broennimann *et al.*, 2012) for: (a1) *N. ligurica* and *N. melanostoma*; (b1) *N. cyanescens concolor* and *N. cyanescens cyanescens*; (c1) *N. corpulenta* and *N. rhaetica*. Density of occurrence in the environmental space defined by the principal components for: (a2) *N. ligurica* (Sp1) and *N. melanostoma* (Sp2); (b2) *N. cyanescens concolor* (Sp1) and *N. cyanescens cyanescens* (Sp2); (c2) *N. corpulenta* (Sp1) and *N. rhaetica* (Sp2). Within the density plots, solid contour lines represent the full environmental background and dashed contour lines represent 50% of the background environment.

508 **Figure 6.** Variation in the extent of overlapping suitable area between the two *N. cyanescens*
509 subspecies and the corresponding candidate host plants (*Aconitum lycoctonum* and *A. napellus*) from
510 the current scenario to 2050 (a) and 2070 (c) under the three RCPs; variation in the percent extent of
511 overlapping suitable area with respect to the overall suitable area for the flea beetle under the different
512 RCPs in 2050 (b) and 2070 (d).

513 **Figure 7.** Variation in the extent of overlapping suitable area between *N. corpulenta, N. rhaetica* and
514 the corresponding candidate host plants (*Arnica montana* and *Doronicum austriacum*) from the
515 current scenario to 2050 (a) and 2070 (c) under the three RCPs; variation in the percent extent of
516 overlapping suitable area with respect to the overall suitable area for the flea beetle under the different
517 RCPs in 2050 (b) and 2070 (d).

518

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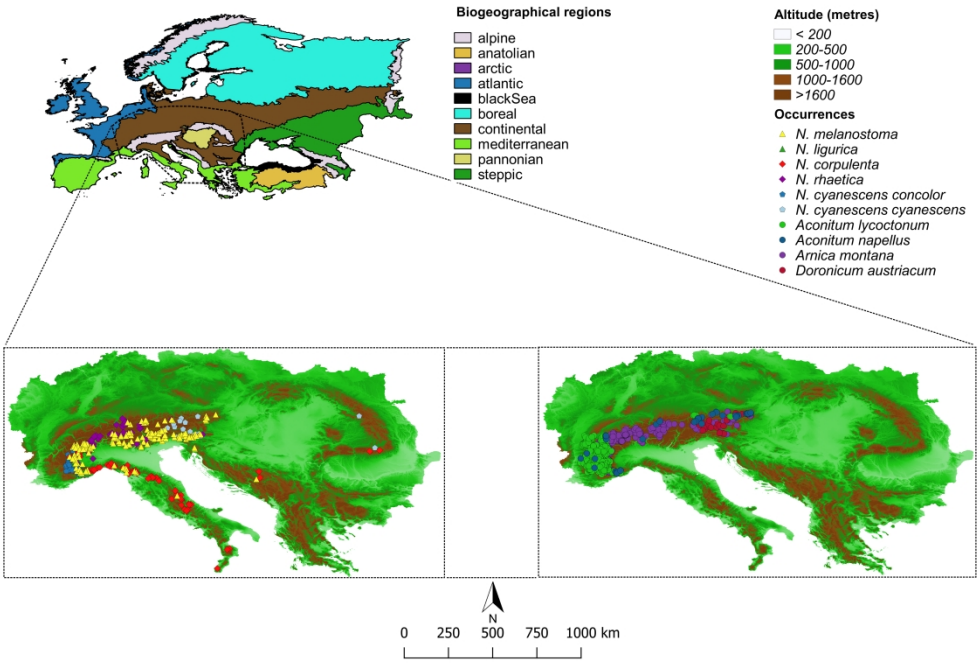

Figure 1. European biogeographical regions, as defined by the European Environmental Agency (EEA), with a zoom on the study area, showing the altitudinal zonation and the occurrences for the six target *Neocrepidodera* taxa and the candidate host plants.

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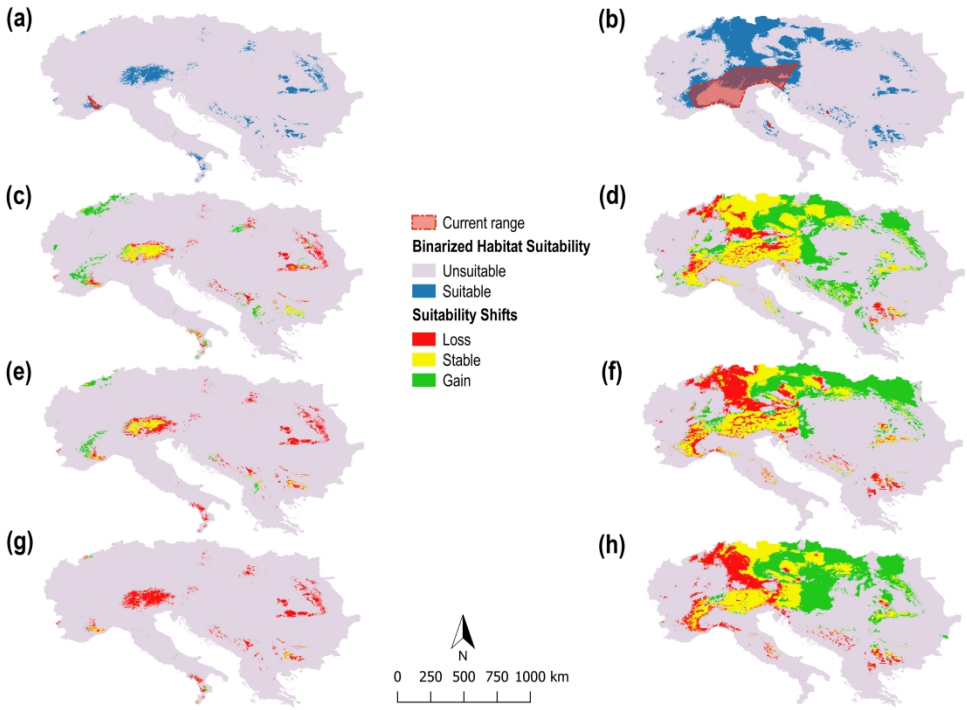

Figure 2. Suitable areas under the current scenario, obtained from the predictions of the weighted mean Ensemble Model, and α-hull-based current range (hatched polygons) for (a) *N. ligurica* and (b) *N. melanostoma*; predicted shifts in habitat suitability by 2070 under RCPs 2.6, 4.5 and 8.5 for (c), (e) and (g) *N. ligurica*, and (d), (f) and (h) *N. melanostoma*, respectively.

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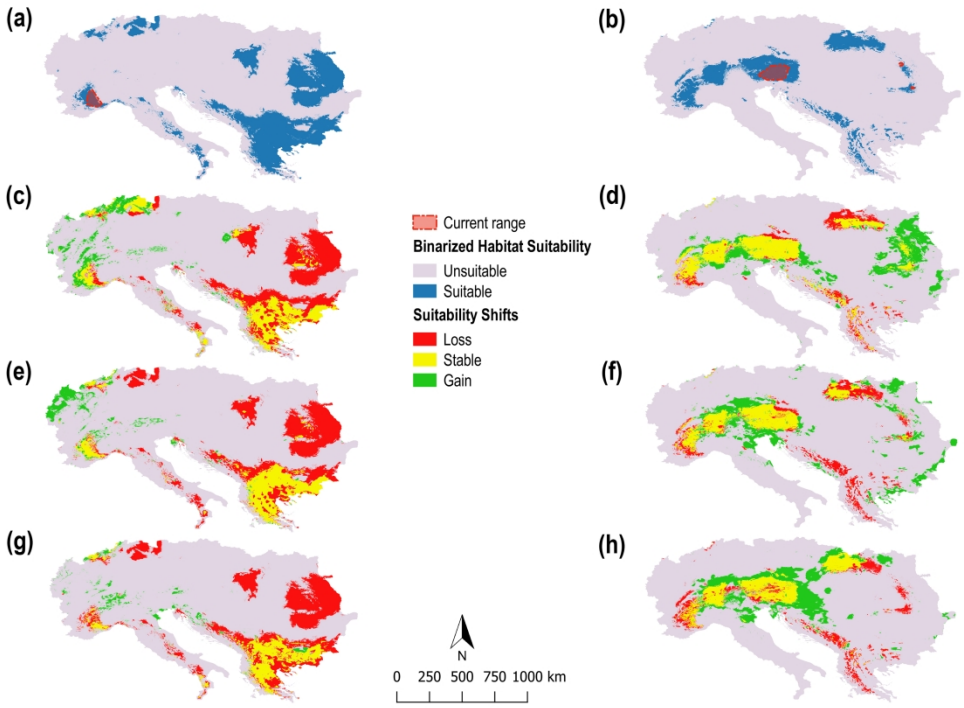

Figure 3. Suitable areas under the current scenario, obtained from the predictions of the weighted mean Ensemble Model, and α-hull-based current range (hatched polygons) for (a) *N. cyanescens concolor* and (b) *N. cyanescens cyanescens*; predicted shifts in habitat suitability by 2070 under RCPs 2.6, 4.5 and 8.5 for (c), (e) and (g) *N. cyanescens concolor*, and (d), (f) and (h) *N. cyanescens cyanescens*, respectively.

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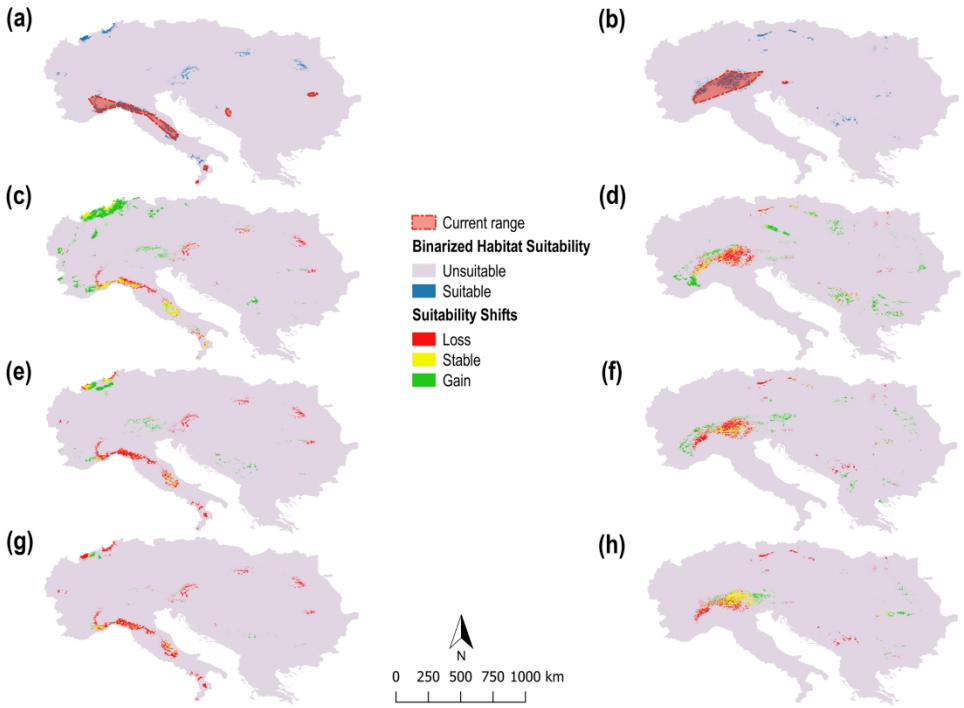

Figure 4. Suitable areas under the current scenario, obtained from the predictions of the weighted mean Ensemble Model, and α-hull-based current range (hatched polygons) for (a) *N. corpulenta* and (b) *N. rhaetica*; predicted shifts in habitat suitability by 2070 under RCPs 2.6, 4.5 and 8.5 for (c), (e) and (g) *N. corpulenta*, and (d), (f) and (h) *N. rhaetica*, respectively.

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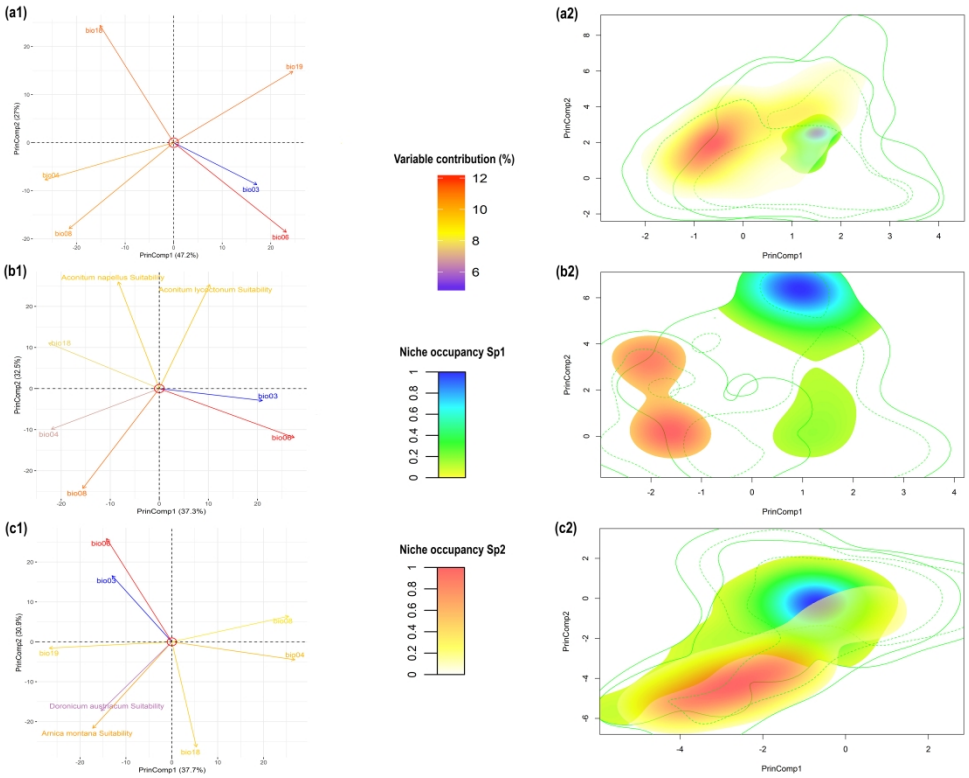

Figure 5. Contributions of the input predictors along the first two principal components ('PCA-env', Broennimann et al., 2012) for: (a1) *N. ligurica* and *N. melanostoma*; (b1) *N. cyanescens concolor* and *N. cyanescens cyanescens*; (c1) *N. corpulenta* and *N. rhaetica*. Density of occurrence in the environmental space defined by the principal components for: (a2) *N. ligurica* (Sp1) and *N. melanostoma* (Sp2); (b2) *N. cyanescens concolor* (Sp1) and *N. cyanescens cyanescens* (Sp2); (c2) *N. corpulenta* (Sp1) and *N. rhaetica* (Sp2). Within the density plots, solid contour lines represent the full environmental background and dashed contour lines represent 50% of the background environment.

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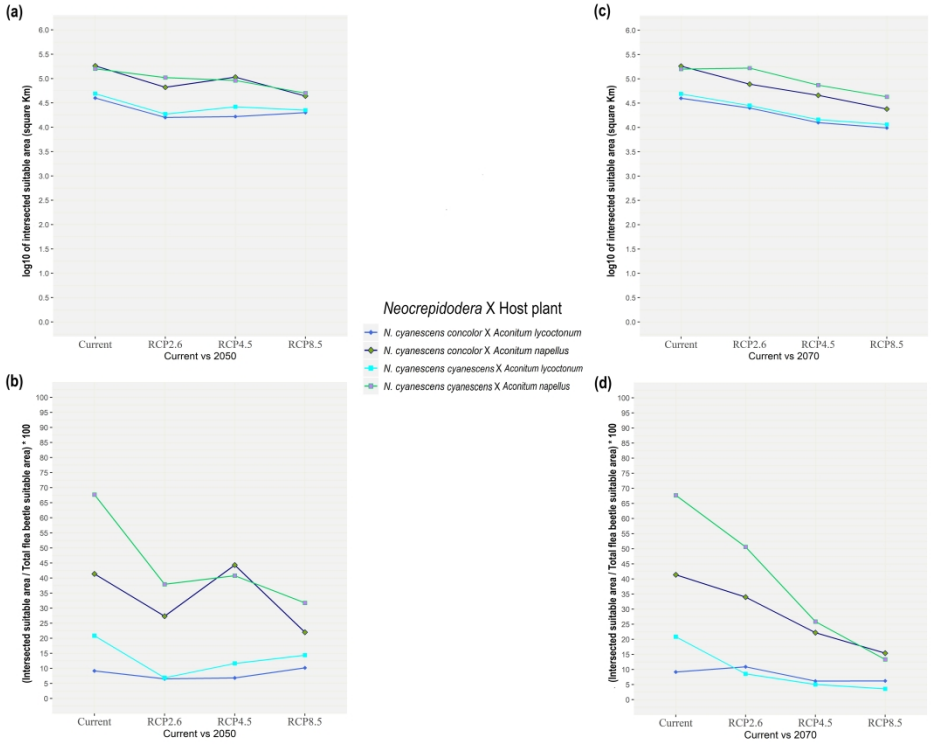

Figure 6. Variation in the extent of overlapping suitable area between the two *N. cyanescens* subspecies and the corresponding candidate host plants (*Aconitum lycoctonum* and *A. napellus*) from the current scenario to 2050 (a) and 2070 (c) under the three RCPs; variation in the percent extent of overlapping suitable area with respect to the overall suitable area for the flea beetle under the different RCPs in 2050 (b) and 2070 (d).

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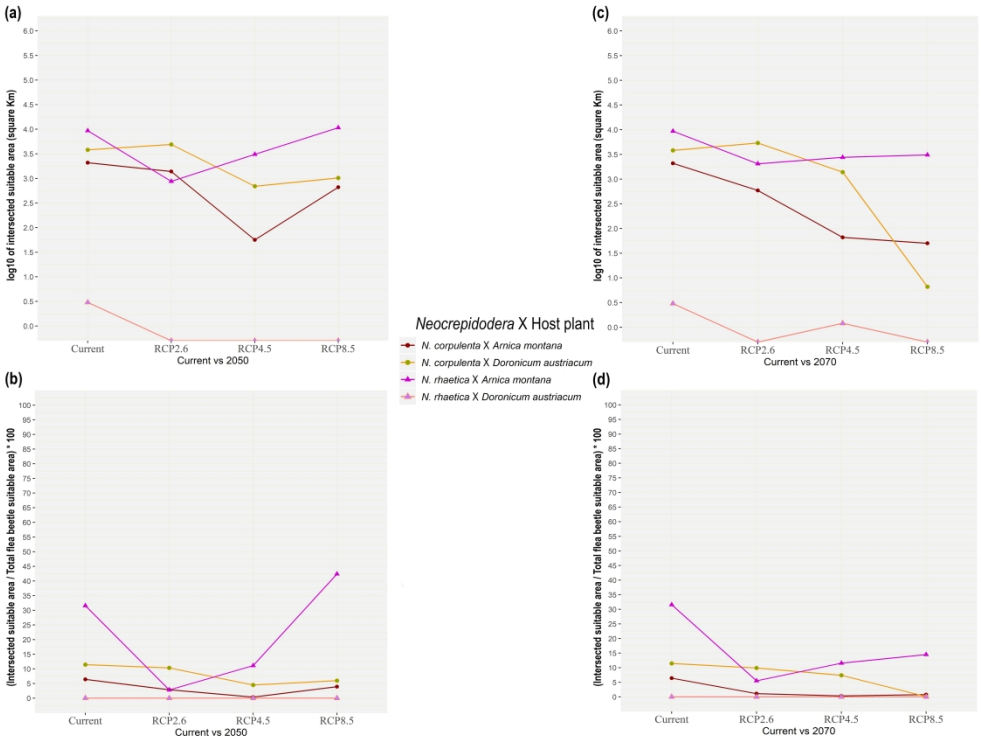

Figure 7. Variation in the extent of overlapping suitable area between *N. corpulenta*, *N. rhaetica* and the corresponding candidate host plants (*Arnica montana* and *Doronicum austriacum*) from the current scenario to 2050 (a) and 2070 (c) under the three RCPs; variation in the percent extent of overlapping suitable area with respect to the overall suitable area for the flea beetle under the different RCPs in 2050 (b) and 2070 (d).

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