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

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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 prioritisation measures in the future decades, claiming for further attention on mountainous entomofauna in a warming world.

Key words. Climate change, ensemble modelling, flea beetles, habitat suitability models, host plants, *Neocrepidodera*.

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 (Thuiller *et al*., 2005; 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).

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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 & Bеždek, 2014). Some genera spread over several zoogeographical regions, while others are strictly endemic to narrow areas. Nonetheless, even when characterised 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 specialisation 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 specialisation 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 geographical 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 (EM) 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 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 characterising 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 *Neocrepidodera 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 *Neocrepidodera 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 whether 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

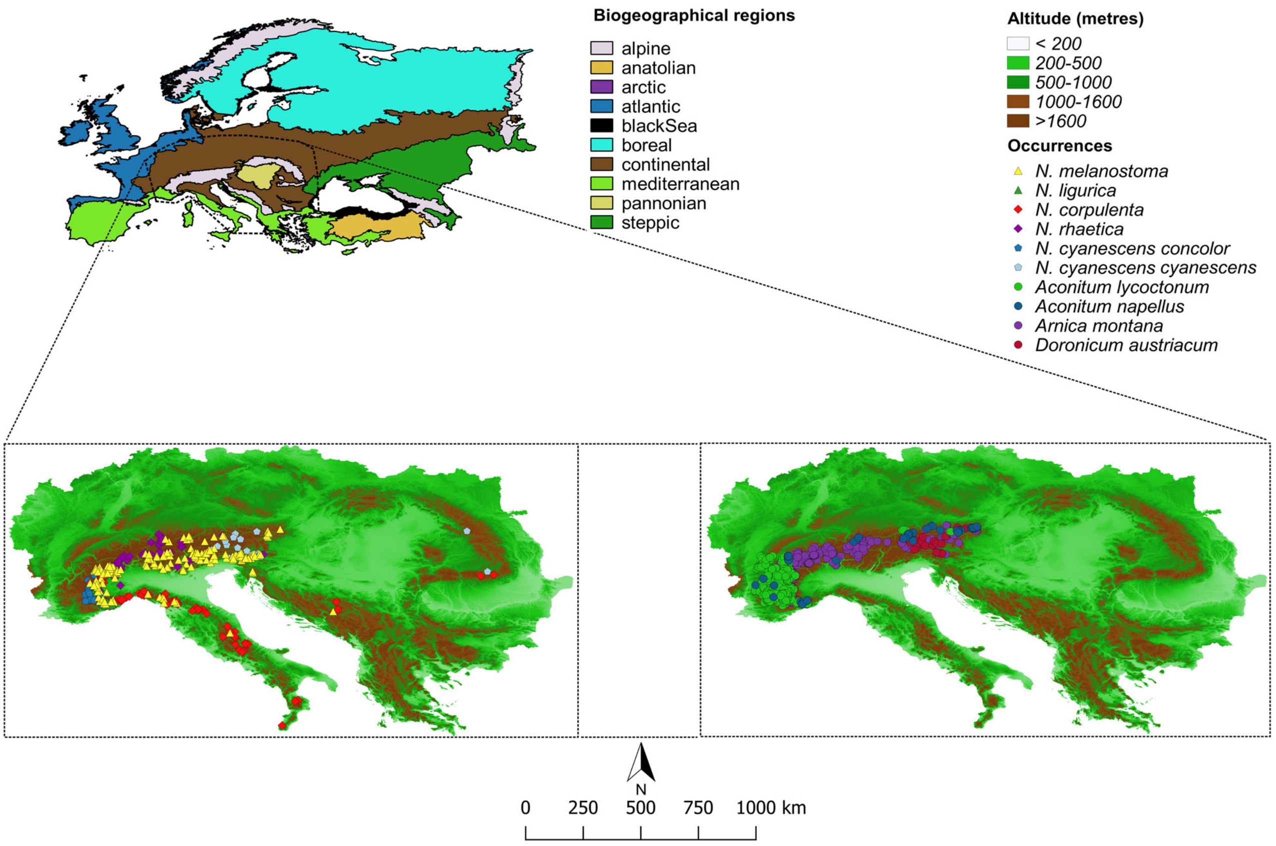

Fig. 1. European biogeographical regions, as defined by the European Environmental Agency (EEA), with a zoom on the study area, showing the altitudinal zonation and the occurrences for the six target *Neocrepidodera* taxa and the candidate host plants. [Color figure can be viewed at wileyonlinelibrary.com]

(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 characterised.

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 the literature search and from the Global Biodiversity Information Facility (GBIF) database. In the latter case, occurrence records were scrutinised 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 Conservatoire Botanique National Alpin (CBNA), 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 data sets of *Neocrepidodera* and those of the candidate host plants shared the same reference system. Figure 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 the 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 environmental 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 data sets were instead used to obtain a representation of the geographical range of each *Neocrepidodera* taxon through α-hull-based polygons, drawn by means of the R package 'alphahull' (Pateiro-López & Rodríguez-Casal, 2010), which are less affected by biases in range estimates than the classic minimum convex polygons (Burgman & Fox, 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 s 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, 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.

The 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 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 generalised linear model (GLM), generalised additive model (GAM) and generalised boosted regression models (GBMs). For each algorithm, two-way interactions among predictors were allowed. With respect to the other relevant parameterisation 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 fivefold 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, 10 000 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 10 000 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 oversimplified 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 data set 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 data set for HSMs building comprised 90% of the available thinned occurrences and the 10 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 10 000 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 binarisation 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 data sets 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 ≥0.7 and AUC ≥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 randomisation 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 three permutation runs were first averaged and then scaled to percent contributions (Bucklin *et al*., 2015).

The wmean EM for each of the six 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 the 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 binarised predictions (i.e. suitable vs unsuitable areas), we chose as binarisation 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 binarisation criterium when dealing with presence-background HSMs (Liu *et al*., 2013). The obtained thresholds are listed in the Supporting Information Text S1.

The binarised 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: (i) areas predicted to be suitable for both the considered flea beetle and the corresponding host plant under the current scenario, and (ii) 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 the study by 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 randomisation 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

Table 1. Predictors selected to build the HSMs for the target *Neocrepidodera* taxa and the candidate host plants.

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

HS = habitat suitability.

performed on the presence-pseudoabsence data sets 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 the Supporting Information Table S3, whereas Table 2 summarises the percent importance scores obtained for the relevant predictors within the EMs built for the host plants and the *Neocrepidodera*.

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, 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*

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*.

Candidate Host Plants EMs

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 EMs

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

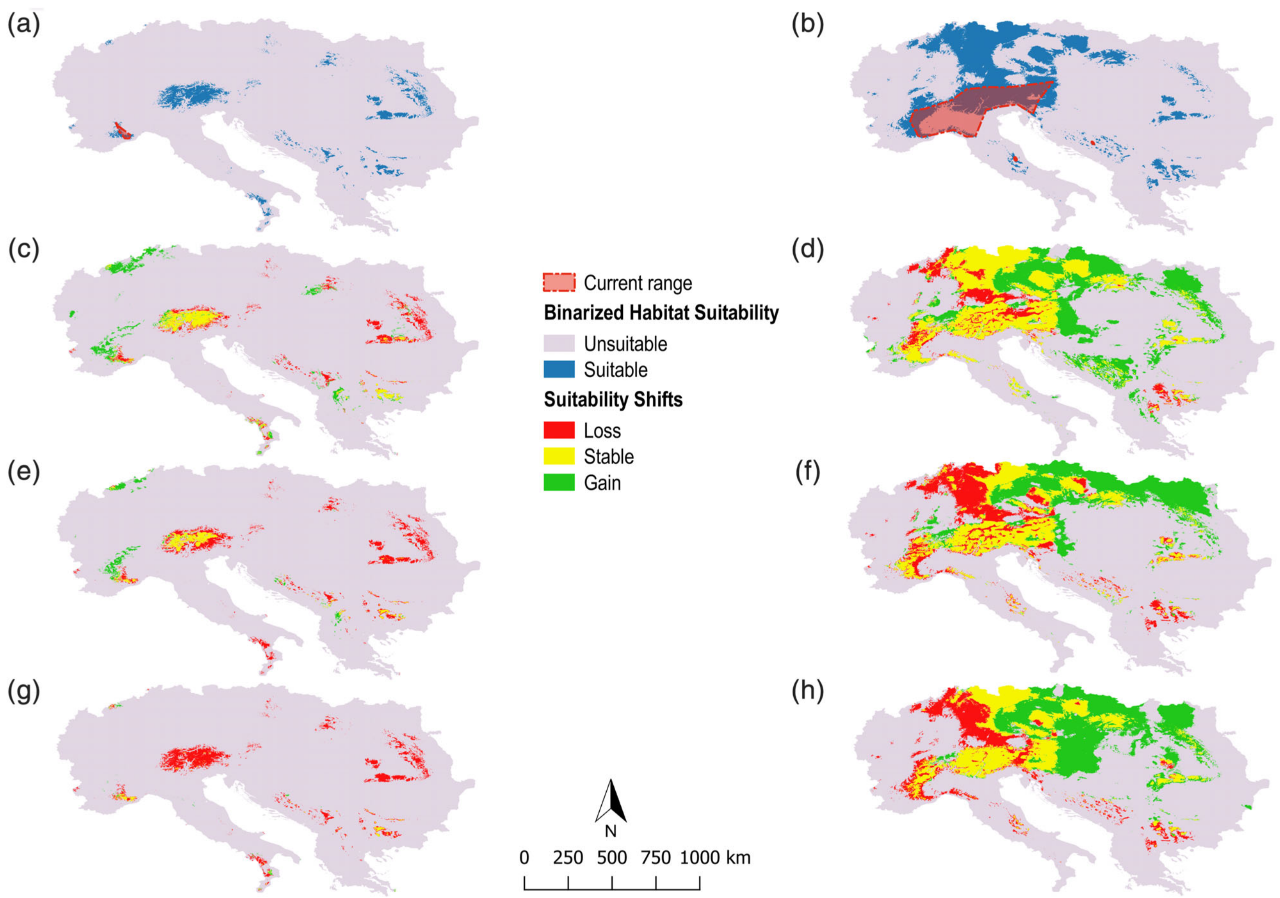

Fig. 2. Suitable areas under the current scenario, obtained from the predictions of the weighted mean EM, and α-hull-based current range (hatched polygons) for (a) *N. ligurica* and (b) *N. melanostoma*; predicted shifts in HS by 2070 under RCPs 2.6, 4.5 and 8.5 for (c), (e), and (g) *N. ligurica*, and (d), (f) and (h) *N. melanostoma*, respectively. [Color figure can be viewed at wileyonlinelibrary.com]

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 the Supporting Information Figs. S5 and S6 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 and S4). 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*) (Supporting Information 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* (Supporting Information Fig. S6).

Continuous maps resulting from the cv EMs built for the current scenario were reported in the 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, and 4a).

The binarised 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 the 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).

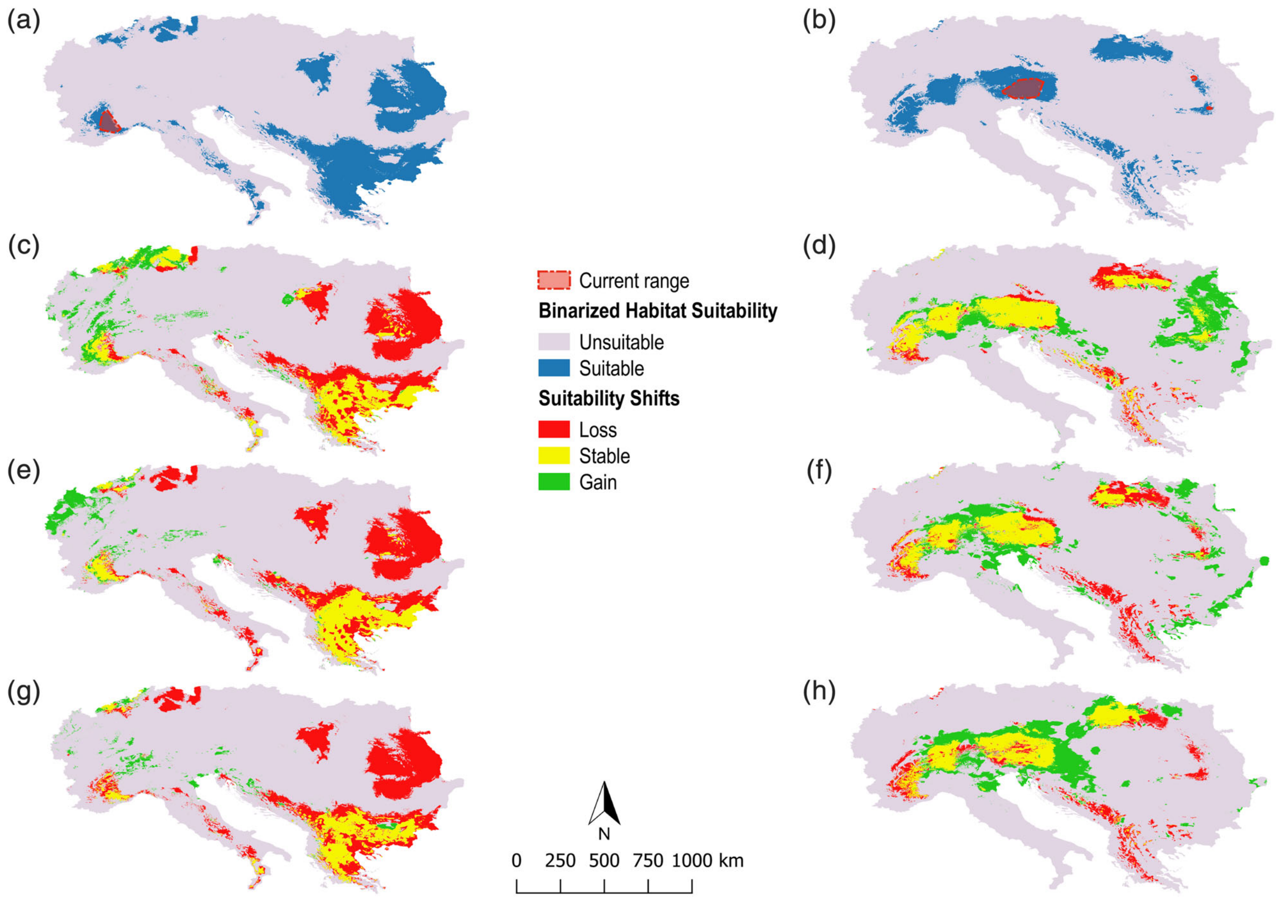

Fig. 3. Suitable areas under the current scenario, obtained from the predictions of the weighted mean EM, and α-hull-based current range (hatched polygons) for (a) *N. cyanescens concolor* and (b) *N. cyanescens cyanescens*; predicted shifts in HS by 2070 under RCPs 2.6, 4.5 and 8.5 for (c), (e) and (g) *N. cyanescens concolor*, and (d), (f) and (h) *N. cyanescens cyanescens*, respectively. [Color figure can be viewed at wileyonlinelibrary.com]

However, when tested for niche divergence through the niche similarity test, the niches of the two species resulted not more different from 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 (Fig. 3a, b). The niches of the two subspecies are clearly differentiated along the first principal component, to which high contribution was given by BIO6 (Fig. 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 contribution given by suitability for *Aconitum lycoctonum* to this axis (Fig. 5b1). Even though the niche equivalency test rejected the hypothesis of the niches of the two *N. cyanescens* subspecies being equivalent ($P < 0.001$), the niche similarity test did not permit to infer a significant divergence once the differences in background conditions were considered ($P = 0.598$).

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

Neocrepidodera ligurica, *N. cyanescens concolor*, *N. corpulenta* and *N. rhaetica* were predicted to lose by 2070, the great majority of currently suitable areas, especially under RCP8.5 (Figs. 2g, 3g, and 4g, h). *Neocrepidodera cyanescens cyanescens*, instead, was predicted to maintain under all the RCPs the major part of suitable areas corresponding to the core of its current range (Fig. 3d, f, h); moreover, it was predicted to gain broad suitable areas in Central and Eastern Alps under all the RCPs and in the Carpathians under RCP2.6 (Fig. 3d). Finally, *N. melanostoma* was predicted to maintain stable areas in Eastern Alps and potentially gain broad suitable areas even under the more pronounced warming scenarios (Fig. 2d, f, h).

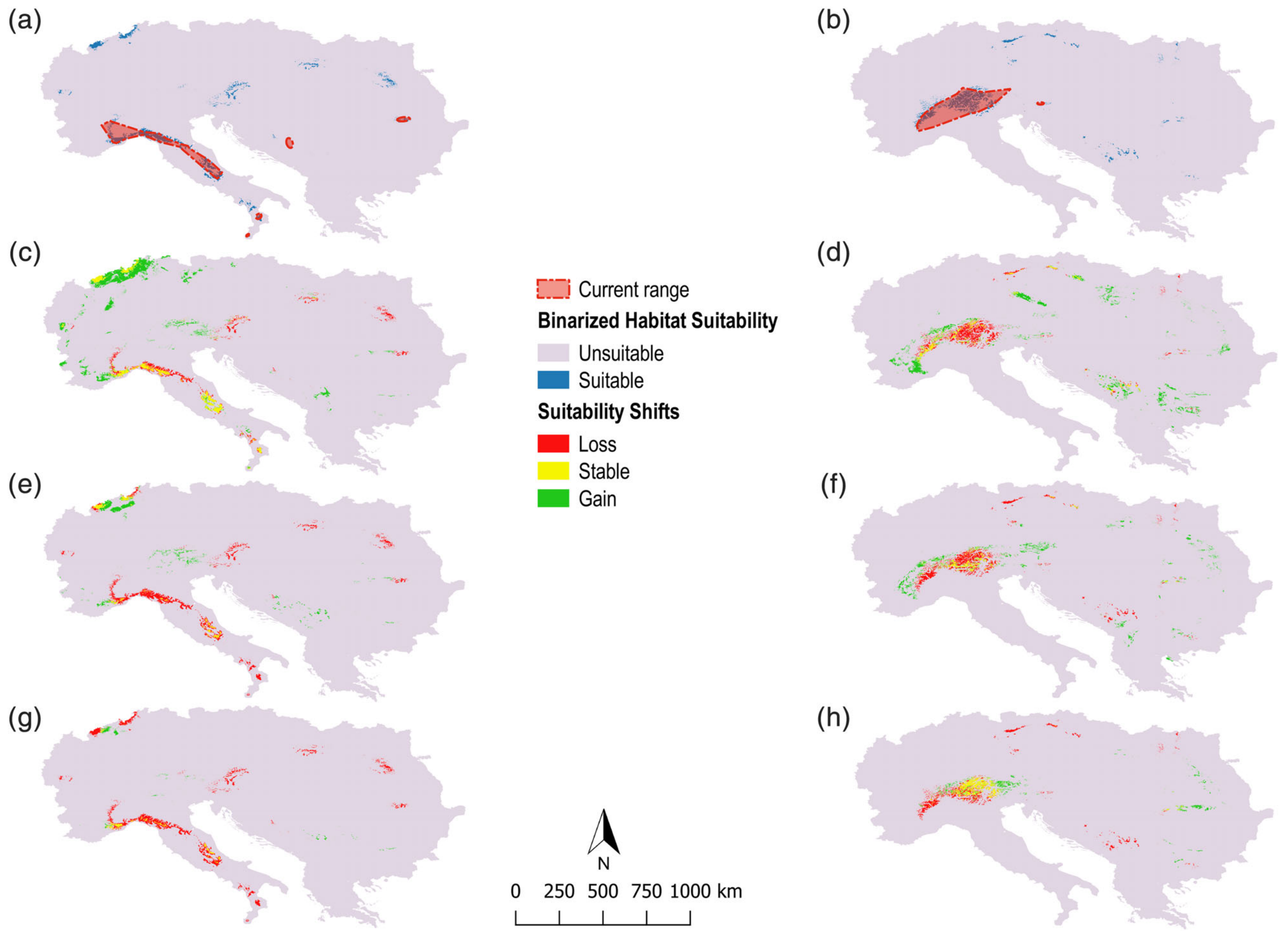

Fig. 4. Suitable areas under the current scenario, obtained from the predictions of the weighted mean EM, and α-hull-based current range (hatched polygons) for (a) *N. corpulenta* and (b) *N. rhaetica*; predicted shifts in HS by 2070 under RCPs 2.6, 4.5 and 8.5 for (c), (e) and (g) *N. corpulenta*, and (d), (f) and (h) *N. rhaetica*, respectively. [Color figure can be viewed at wileyonlinelibrary.com]

Anyway, most of this predicted gain corresponds to areas located far away from the current range of the species, while large portions of the currently occupied territories were predicted to become unsuitable under RCP4.5 and RCP8.5 (Fig. 2f, h).

The variation in the extent of overlapping suitable area between each of the two *N. cyanescens* subspecies and the candidate *Aconitum* hosts from the current scenario to 2050 and 2070 under the three RCPs was reported, respectively, in Fig. 6a,c. Differently, Fig. 6b,d shows the 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 and 2070. The same information for *N. corpulenta* and *N. rhaetica* with respect to *Doronicum austriacum* and *Arnica montana* was summarised in Fig. 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 (Fig. 6a, c), 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 (Fig. 6b,d), respectivley.

Considering *N. cyanescens cyanescens*, both the extent of overlapping suitable areas with the two *Aconitum* species (Fig. 6a,c) and the percentage of suitable area for the flea beetle hosting suitable conditions also for the host plants (Fig. 6b,d) 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 (Fig. 7a, c). 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, c).

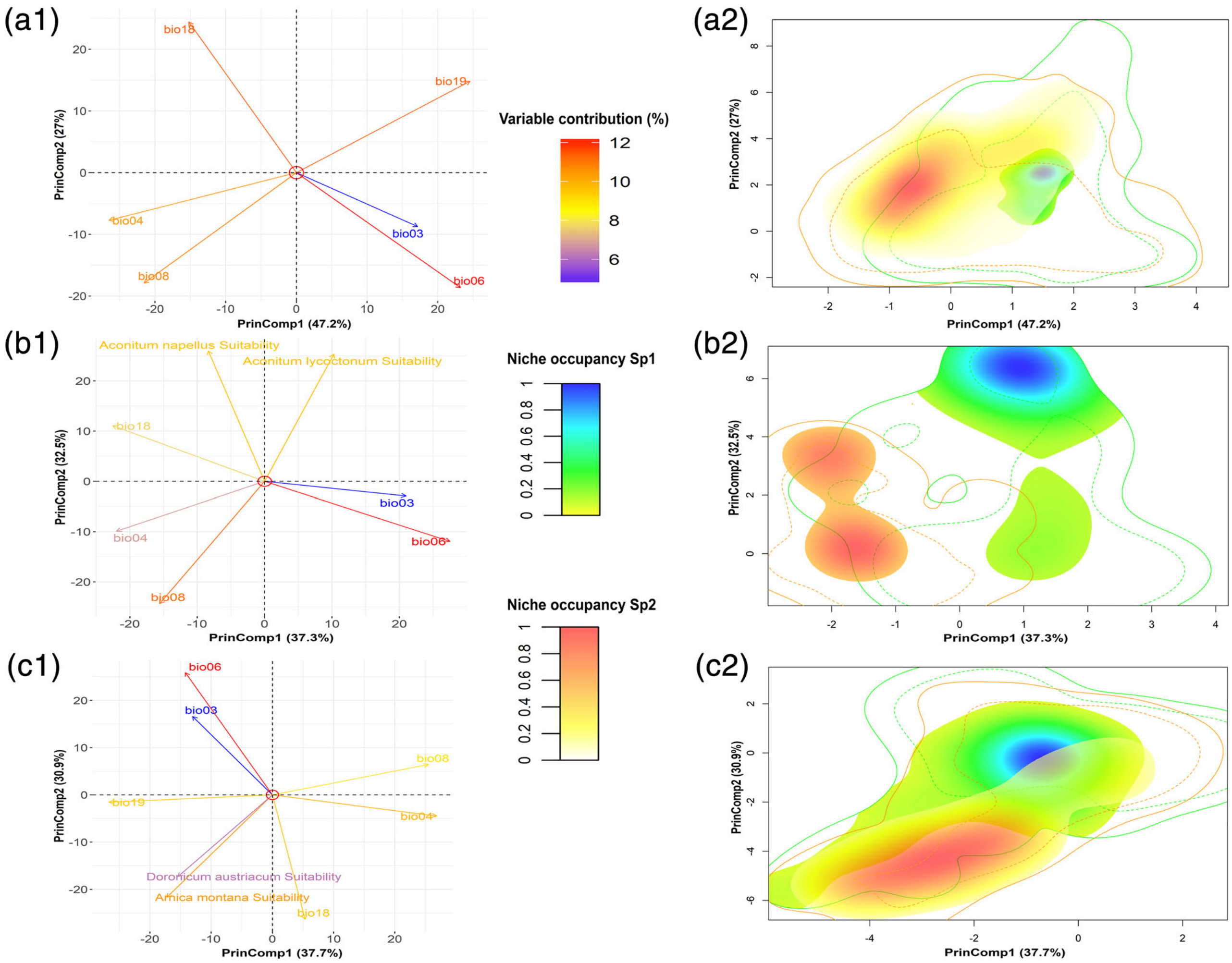

Fig. 5. Contributions of the input predictors along the first two principal components ('PCA-env', Broennimann *et al.*, 2012) for: (a1) *N. ligurica* and *N. melanostoma*; (b1) *N. cyanescens concolor* and *N. cyanescens cyanescens*; (c1) *N. corpulenta* and *N. rhaetica*. Density of occurrence in the 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. [Color figure can be viewed at wileyonlinelibrary.com]

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 Supporting Information 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

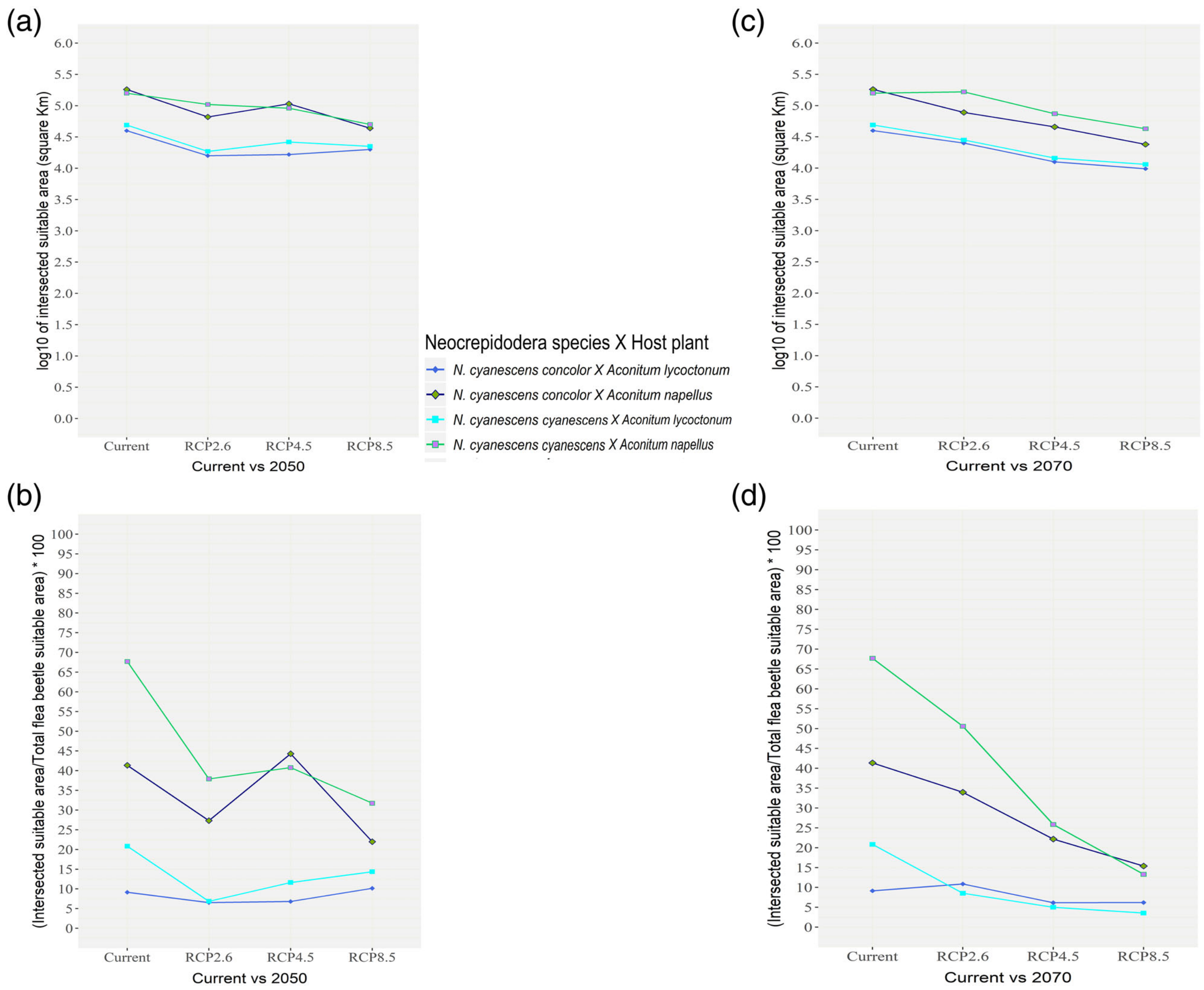

Fig. 6. Variation in the extent of overlapping suitable area between the two *N. cyanescens* subspecies and the corresponding candidate host plants (*Aconitum lycoctonum* and *A. napellus*) from the current scenario to 2050 (a) and 2070 (c) under the three RCPs; variation in the percent extent of overlapping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

currently occupied ones, and thus the former would be difficulty colonised; moreover, most of them are predicted to be lost even under moderate warming (Figs. 2 and Supporting Information 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.

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

The density of occurrence in environmental space modelled for *N. corpulenta* and *N. rhaetica* highlighted the existence of a certain range of environmental conditions suitable to both species, even though the respective maximum density zones are

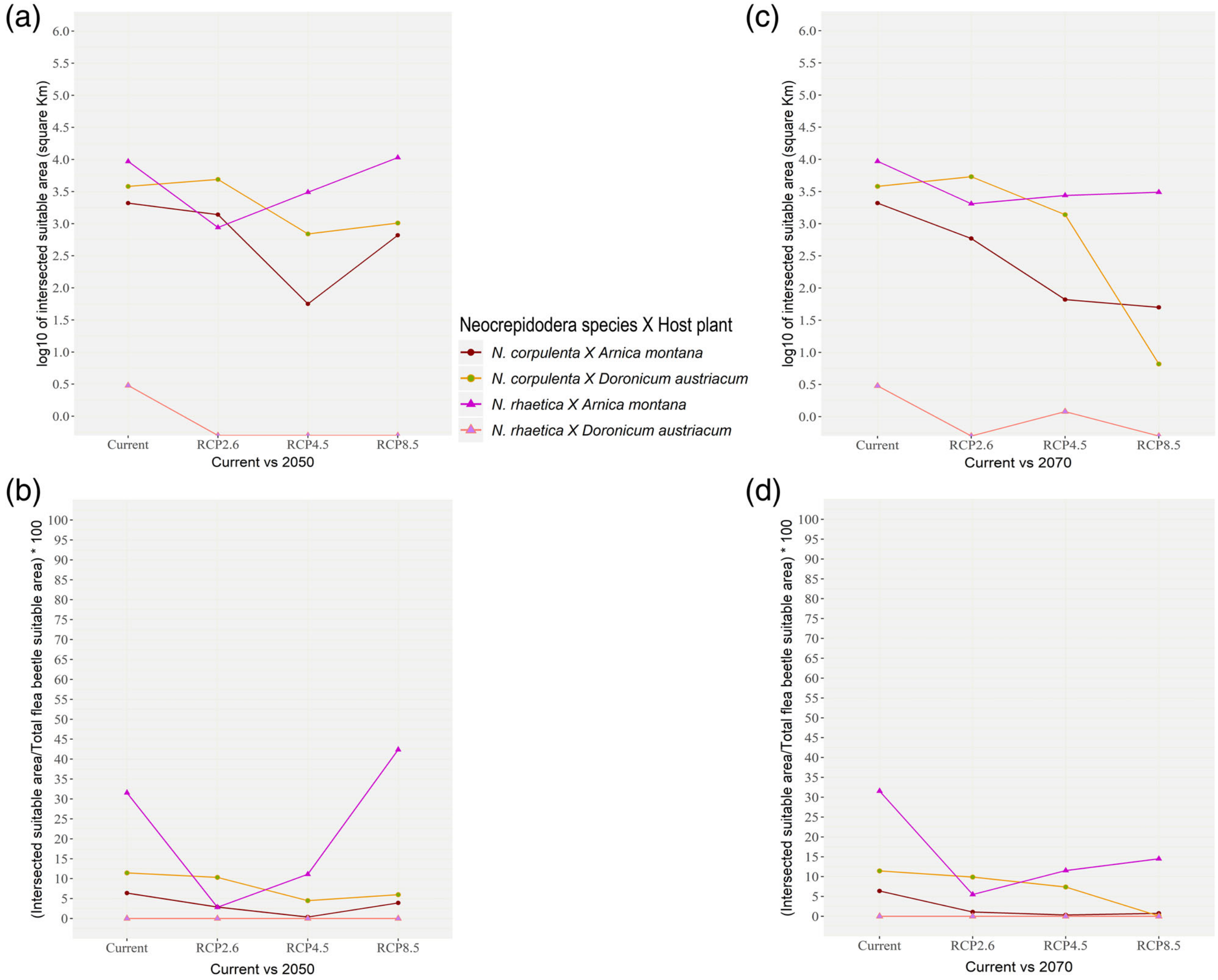

Fig. 7. Variation in the extent of overlapping suitable area between *N. corpulenta*, *N. rhaetica* and the corresponding candidate host plants (*Arnica montana* and *Doronicum austriacum*) from the current scenario to 2050 (a) and 2070 (c) under the three RCPs; variation in the percent extent of overlapping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

clearly separated (Fig. 5c2). This is coherent with the existence of a parapatric area in Western Alps where the two species currently co-occur (Iannella *et al*., 2017; Reino *et al*., 2017). With respect to the predicted suitability shifts, both species may face direct threats to the persistence of their populations in the next future: indeed, the patches of stable or gained suitable areas predicted for the two species mainly under RCP 2.6 and RCP4.5, many of which unlikely to be colonised due to their distance from the currently occupied areas, would difficultly counterbalance the overwhelming loss of suitable territories across most of the species' range (Figs. 4 and Supporting Information Fig. S10).

The contribution of host plant suitability resulted to be preponderant only within the Em obtained for *N. cyanescens concolor* (Table 2). Nonetheless, the three-dimensional response surfaces representing the combined contribution of host suitability and influential bioclimatic variables (Supporting Information Figs. S5 and S6) 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 and 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 with 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 prioritisation 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). *Neocrepidodera 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 colonise regions with suitable conditions and reach the equilibrium with the environment (Guisan *et al*., 2017).

In conclusion, even though detailed prioritisation 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.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Coordinates and sources of the occurrence records for both the target *Neocrepidodera* taxa and the candidate host plants are listed in the attached .xls file.

Text S1. TSS-max thresholds: *N. ligurica* = 0.29; *N. melanostoma* = 0.49; *N. cyanescens concolor* = 0.20; *N. cyanescens cyanescens* = 0.22; *N. corpulenta* = 0.68; *N. rhaetica* = 0.39; *Aconitum lycoctonum* = 0.59; *Aconitum napellus* = 0.21; *Arnica montana* = 0.67; *Doronicum austriacum* = 0.64.

Table S2. Pairwise Pearson's *r* correlation coefficient for each possible pair of input bioclimatic variables, across the full study area extent. The pairs showing $r \geq 0.7$ have the corresponding value highlighted in light red, while those showing $r \leq -0.7$ have the value highlighted in yellow; variables excluded from modelling to avoid multicollinearity are highlighted in red.

Table S3. Spatially-thinned presence points of the target *Neocrepidodera* taxa and the candidate host plants. For each taxon, the number of presence points within the different countries is also reported.

Figure S1. Partial response curves of the three bioclimatic predictors with the highest percent importance scores within the Ensemble Models obtained for: a) *Aconitum lycoctonum*; b) *Aconitum napellus*; c) *Arnica montana*; d) *Doronicum austriacum*.

Figure S2. Partial response curves of the four bioclimatic predictors with the highest percent importance scores within the Ensemble Models obtained for a) *N. ligurica* and b) *N. melanostoma*.

Figure S3. Partial response curves of the two bioclimatic predictors with the highest percent importance scores within the obtained Ensemble Models, along with the response curves of the predictors representing habitat suitability for *Aconitum lycoctonum* and *Aconitum napellus*, for a) *N. cyanescens concolor* and b) *N. cyanescens cyanescens*.

Figure S4. Partial response curves of the two bioclimatic predictors with the highest percent importance scores within the obtained Ensemble Models, along with the response curves of the predictors representing habitat suitability for *Arnica montana* and *Doronicum austriacum*, for a) *N. corpulenta* and b) *N. rhaetica*.

Figure S5. Three-dimensional response surfaces representing: the combined effect of *Aconitum lycoctonum* suitability and BIO6, and *Aconitum napellus* suitability and BIO6, on predicted suitability for *N. cyanescens concolor*; the combined effect of *Aconitum lycoctonum* suitability and BIO18, and *Aconitum napellus* suitability and BIO18, on predicted suitability for *N. cyanescens cyanescens*.

Figure S6. Three-dimensional response surfaces representing: the combined effect of *Arnica montana* suitability and

BIO8, and *Doronicum austriacum* suitability and BIO8, on predicted suitability for *N. corpulenta*; the combined effect of *Arnica montana* suitability and BIO6, and *Doronicum austriacum* suitability and BIO6, on predicted suitability for *N. rhaetica*.

Figure S7. Maps representing the Coefficient of Variation obtained, for the current-climate scenario, from the Ensemble Models built for the six target *Neocrepidodera* taxa; occurrence points of each taxon are shown on the corresponding map as green circles.

Figure S8. Predicted shifts in habitat suitability by 2050, under the three considered RCP scenarios, for *N. ligurica* and *N. melanostoma*.

Figure S9. Predicted shifts in habitat suitability by 2050, under the three considered RCP scenarios, for *N. cyanescens concolor* and *N. cyanescens cyanescens*.

Figure S10. Predicted shifts in habitat suitability by 2050, under the three considered RCP scenarios, for *N. corpulenta* and *N. rhaetica*.

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