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ORIGINAL ARTICLE

Deciphering range dynamics: effects of niche stability areas and post-glacial colonization on alpine species distribution

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ABSTRACT

Aim Niche stability areas (NSAs) are portions of the species range where climate conditions remain suitable through time. They represent the core of species ranges. Their distribution and extent, coupled with dispersal and colonization, shape the realized range of species. In this study, we quantified the roles of survival within NSAs and post-glacial dispersal in determining the current distribution of two groups of alpine butterflies (two taxa in the *Erebia tyndarus* species complex; three taxa in the *Parnassius apollo–P. phoebus* species complex).

Location Holarctic.

Methods NSAs were identified for each taxon by combining current and past potential distributions models, estimated using different modelling techniques and general circulation models. We then (1) assessed the distributional bias towards NSAs by comparing actual occurrence records with randomized occupancies of the current potential range and (2) quantified post-glacial dispersal by examining the distribution of distances from each occurrence record to the nearest NSA.

Results In almost all taxa, realized distributions are biased towards NSAs. However, while *Erebia*'s present range is strongly dominated by NSAs, some populations of *Parnassius* are found very far from NSAs, suggesting more effective colonization of the available geographical space.

Main conclusions Our study highlights the relative roles of survival within NSAs and post-glacial dispersal in shaping the ranges of different alpine butterflies during the Holocene. Results suggest that *Erebia* was unable to disperse far from NSAs, thus experiencing increasing range fragmentation. *Parnassius* populations, on the other hand, coupled local survival with northward dispersal. As NSAs allowed the long-term survival of the species, acting as sources for recolonization, and tend to preserve most of each species' genetic diversity, identifying NSAs and understanding their importance in determining the current distribution of species represents a pivotal task for the conservation of biological diversity.

Keywords

alpine species, butterflies, climate change, *Erebia*, hindcasting, interglacial refugia, niche stability areas, *Parnassius*, species distribution modelling, species–climate equilibrium

INTRODUCTION

During the Pleistocene, repeated climatic oscillations have strongly influenced both the spatial distribution and the demography of great part of terrestrial organisms in the Holarctic region (Hofreiter & Stewart, 2009). Populations of some species survived environmental changes *in situ* (tolerance), whereas others tracked their habitat, experiencing short- or long-distance movements resulting in colonization of novel areas. These range dynamics have been locally

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associated with demographic processes (i.e. stasis, colonizations or local extinctions) and more or less severe bottleneck events, with only few species facing global extinctions during the Pleistocene–Holocene transition (Dawson *et al.*, 2011). The interplay between the local responses of populations and species to climate changes throughout time shaped both the range and genetic structure of individual species, resulting in the biogeographical and phylogeographical patterns we can observe today (Hewitt, 1996, 1999, 2000; Stewart *et al.*, 2010). Understanding the responses of individual species to Pleistocene climate variability therefore represents a key step to understand the main determinants of species distribution and, consequently the adaptive potential to current and future climate changes.

After Haffer (1969), the study of species persistence to climate fluctuations focused on the concept of refugium. Refugia are usually defined as areas where viable populations may survive adverse climatic conditions, and hence preserve the genetic diversity of the species (Petit *et al.*, 2003; Médail & Diadema, 2009). Subsequently, following climate ameliorations, refugial populations expanded, colonizing (or re-colonizing) the newly available areas (Stewart *et al.*, 2010 and references therein). According to Bennet & Provan (2008), almost all the attention has been devoted to the concept of glacial refugium, whereas the study of interglacial refugia (refugia for cold-adapted species during the warmer interglacial periods) has been relatively neglected. Following the post-glacial climate warming, cold-adapted species experienced different levels of extinction in the southern part of their ranges, associated with upward and poleward shifts. For these species, the net balance of the post-glacial range dynamics often resulted in restricted, disjunct, arctic and/or alpine distributions (Bennet & Provan, 2008; Stewart *et al.*, 2010).

The study of climatic stability has gained interest over the past few years (Dynesius & Jansson, 2000; Svenning & Skov, 2004; Graham *et al.*, 2006; Carnaval & Moritz, 2008; VanDerWal *et al.*, 2009; Sandel *et al.*, 2011; Pellissier *et al.*, 2014). In this context, for a given species, niche stability areas (NSAs) can be defined as those areas in which climatic conditions remained constantly favourable through time, allowing long-term species survival and evolution (Dynesius & Jansson, 2000; Jansson, 2003). Under this definition, these areas represent a generalization of the 'refugial' model, in being agnostic with regard to 'adverse' and 'favourable' conditions, thus allowing straightforward comparison across species with different climatic niches. NSAs host the core of the species distribution, acting as refugia during adverse climatic conditions and, depending on the species' dispersal abilities, as source areas for recolonization following climate amelioration (Hewitt, 1996; Taberlet *et al.*, 1998; Carnaval & Moritz, 2008). Consequently, a quantitative analysis of spatial mismatches between NSAs and the current species range (in terms of both realized and potential distribution) provides a measure of the importance of migrational lags in shaping the distribution of the species (Svenning & Skov, 2007a). Figure 1 schematically illustrates the effects on the alpine species' realized range of two different responses to climate changes, namely local survival in NSAs and northward colonization. If both of these responses occur, the species succeeds in maintaining the species–climate equilibrium (Fig. 1, scenario A): some species, however, may be unable to migrate. In this static view of the species range, each subsequent climate fluctuation will shrink the initial distribution: some populations will undergo extinction due to temporal unsuitability of occupied areas, but no colonization event will replace the lost portion, counterbalancing the negative effects of climate fluctuations. As a result, the species range will be increasingly confined to the higher elevations within the southern part of the initial range (Fig. 1, scenario B). Striking examples of the different degrees of success in maintaining the species–climate equilibrium can be found comparing realized and potential species distributions of European trees (Svenning & Skov, 2004).

Depending on the availability of temporally high-resolution climate surfaces (e.g. millennial-scale climate layers), hindcasting species climatic niches represents an excellent tool to address different research questions such as range dynamics, species extinction, speciation mechanisms, ecological niche conservatism, past species distribution, location of Pleistocene refugia and historical migration pathways (Nogués-Bravo, 2009 and references therein). Correlative species distribution models (SDM) are numerical tools that combine distribution data (species occurrence or abundance in a given set of locations) with information on the environmental characteristics of those locations to understand and predict the species' distribution across a landscape (Elith & Leathwick, 2009). However, some potential limitations and/or assumptions related to the estimation of the species past distribution using SDM have to be acknowledged. First, if the climatic niche is estimated using the current realized distribution, it frequently represents a smaller subset (the realized niche) of the species fundamental niche (*sensu* Soberón & Nakamura, 2009). However, the current realized distribution of a species can be the result of various intrinsic (i.e. climatic tolerance, dispersal ability) and extrinsic (i.e. climate, biotic interactions, source/sink dynamics) range-limiting factors that should be accounted for (Svenning *et al.*, 2011 and references therein). Second, we should assume that climatic niche is nearly stable over the time-scales of interest (Nogués-Bravo, 2009). Finally, we have to acknowledge the uncertainties related to palaeoclimatic reconstructions: a recent comparison of eight different palaeoclimatic simulations, for example, demonstrated an intermodel variation in growing degree days or annual precipitation at the Last Glacial Maximum (LGM) comparable to the LGM-present average anomaly (Gavin *et al.*, 2014). Hence, hindcasting SDM represents a powerful tool to investigate the dynamics of the potential range based on the current realized niche, but the estimates of the past species' distribution have to be interpreted cautiously.

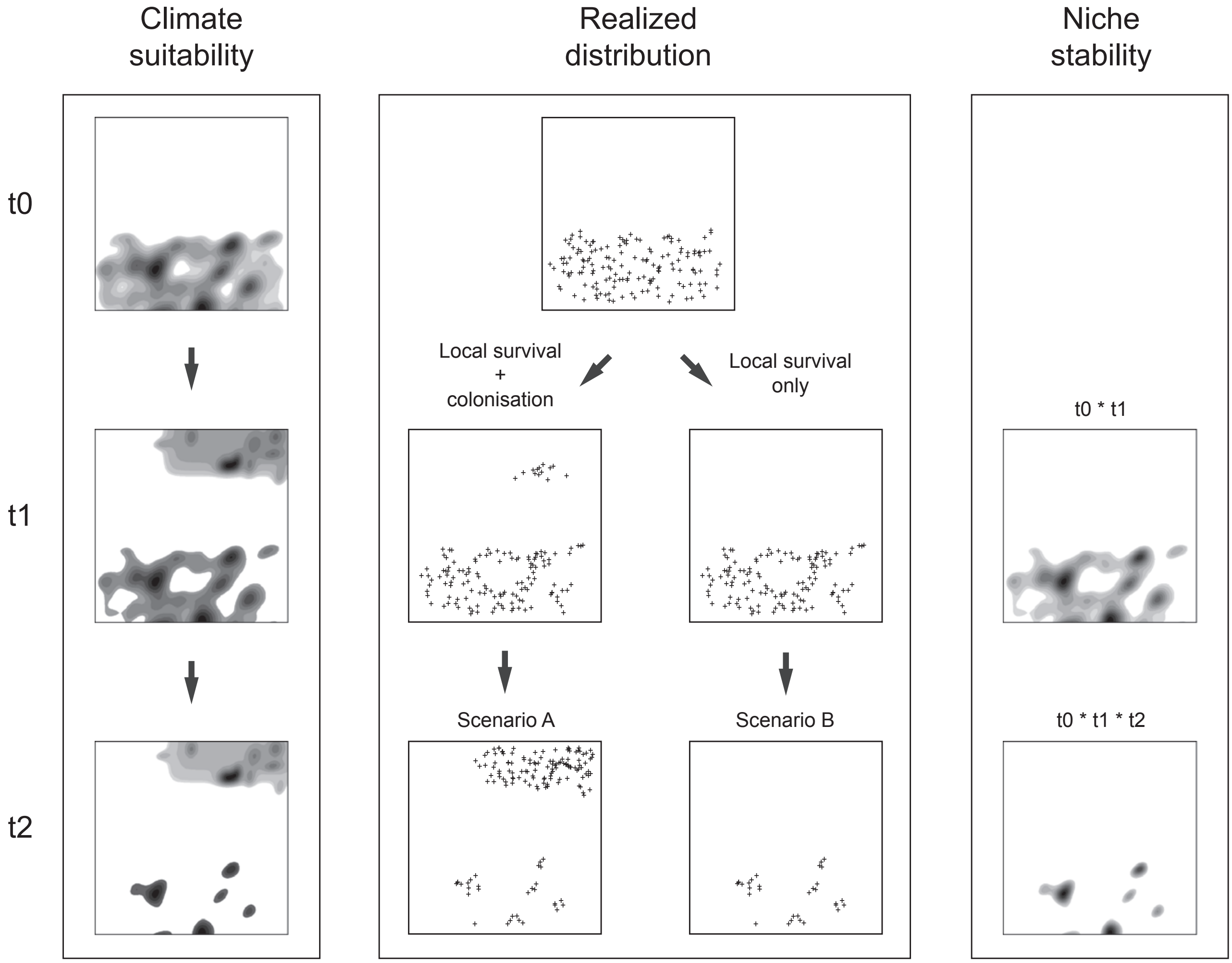

Figure 1 Schematic representation of post-glacial range dynamics due to different species responses to climate change. The *Climate suitability box* represents potential range evolution through time ($t0 \rightarrow t2$). Climate warming involves a progressive fragmentation of the potential range at lower latitudes coupled with the emergence of wide suitable areas at higher latitudes. The *Niche stability box* shows the distribution of niche stability areas (NSAs) defined as those grid cells for which climate remained constantly suitable for the species through time ($t0 * t1$ and $t0 * t1 * t2$). In the *Realized distribution box* we hypothesized two different mechanisms shaping species ranges: *in situ* survival and colonization. Given the species distribution in t0, two different behaviours were highlighted: (i) *in situ* survival coupled with colonization (on the left) and (ii) *in situ* survival only (on the right). If survival is coupled with colonization, the effects of range fragmentation are counterbalanced by colonization events maintaining the species–climate equilibrium (scenario A). In contrast, when survival is the only mechanism working, climate change involves an increase in insularization at lower latitudes, resulting in a series of small isolated populations only within the NSAs (scenario B).

In this study we quantified the importance of dispersal/colonization, as well as of the distribution and extent of NSAs in shaping the current distribution of two groups of closely related alpine butterfly species: the *Erebia tyndarus* species complex (Lepidoptera: Nymphalidae) and the *Parnassius apollo* (Linnaeus, 1758)–*P. phoebus* species complex (Lepidoptera: Papilionidae). The species of both groups share a roughly similar ecology (e.g. all species are strictly alpine in the southern portion of their range) and the two groups have a largely overlapping Holarctic distribution (Fig. 2). The main question we addressed here was: what are the relative roles of dispersal and NSAs during post-glacial range dynamics of different alpine species? We used SDMs and randomizations of species distribution to derive expectations from a null hypothesis of species–climate equilibrium. According to this hypothesis, ideally efficient dispersal allows the species to colonize every area with a suitable climate, so that climatic suitability entirely predicts species presence, with no bias towards NSAs (Fig. 1, scenario A). We then measured deviations from these null expectations to estimate how much the current realized distribution of each taxon is influenced by the geographical distribution of NSAs combined with taxon-specific dispersal limitations. Our rationale is that dispersal inefficiency limits the ability of species to

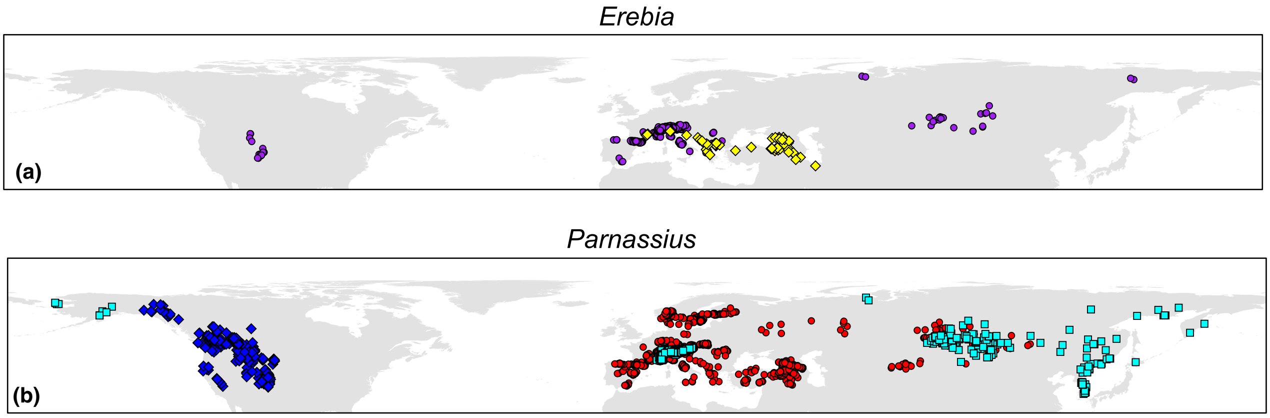

Figure 2 Occurrences of (a) *Erebia* and (b) *Parnassius* used to calibrate models. Symbols identify the different operational units. (a) *Erebia tyndarus* species complex: circles = Euro-Siberian (*Erebia* ES) clade and diamonds = Ponto-Mediterranean (*Erebia* PM) clade (*sensu* Albre *et al.*, 2008). (b) *Parnassius apollo*–*P. phoebus* species complex: circles = *P. apollo*; squares = Palaearctic + Alaskan populations (*P. phoebus* PA) and diamonds = Nearctic populations of the *P. phoebus* species complex (Todisco *et al.*, 2012). Map projection: Behrmann Cylindrical Equal Area.

colonize newly suitable areas, resulting in species–climate disequilibria, with a systematic bias of realized species ranges towards NSAs (Fig. 1, scenario B).

MATERIAL AND METHODS

Distributional data

Records on the presence of the *Erebia* and *Parnassius* species groups were mainly obtained from the Global Biodiversity Information Facility database (GBIF; accessed on 21 December 2012). Given the inter-country differences in data collection and sharing within GBIF, however, spatial bias heavily affects this database (Beck *et al.*, 2014). To reduce the negative effects of spatially biased sampling on modelling predictive performance (Veloz, 2009), we improved the original data set by collecting occurrence data from as many sources as possible: distributional atlases, other databases (e.g. Checklist and Distribution of the Italian Fauna – CKmap v5.3.8), research articles and entomological collections. All records were manually georeferenced based on consultation with different geographical gazetteers (Unites States: US Board on Geographic Names, available at http://geonames.usgs.gov/; Italy: National Geoportal, available at http://www.pcn.minambiente.it/GN/; all other countries: US National Geospatial-Intelligence Agency GEOnet Names Server, available at http://earth-info.nga.mil/gns/html/index.html). We excluded from the data set all records explicitly collected prior to 1950 and/or with no precise information about collection locality. We georeferenced a total of 4793 occurrence records: 1050 for the *Erebia* group and 3743 for the *Parnassius* group (2542 for *P. apollo* and 1201 for the *P. phoebus* species complex). Once we removed within-cell duplicated records we had a total of 668 records for the *Erebia* group and 2358 for the *Parnassius* group (*P. apollo* = 1533; *P. phoebus* = 825; Fig. 2).

Study area, current climate and climate projections

The *Erebia* and *Parnassius* species groups share a mainly overlapping Holarctic distribution, and for both groups the study area includes all land north of 30°N and between 180°W and 180°E. Current climate data (19 climatic variables with 30 arc-second resolution) were obtained from the Worldclim database (Hijmans *et al.*, 2005) and resampled to 10 × 10 km, Behrmann Cylindrical Equal-Area Projection. Simulations of past climate at 6 ka BP and 21 ka BP, based on two general circulation models (GCMs; CCSM and MIROC 3.2), were downloaded from the Palaeoclimatic Modelling Intercomparison Project website (https://pmip2.lsce.ipsl.fr/, accessed on November 2012). Here, we considered 6 and 21 ka BP climates as proxies for the Holocene climate optimum (HCO) and LGM conditions respectively. The GCM data were statistically downscaled using the delta method (Ramirez-Villegas & Jarvis, 2010) to 10 × 10 km. Additionally, following Maiorano *et al.* (2013) we calculate a second set of anomalies to account for the post-industrial climate variation. We used the climate means for 1901–1920 as approximation of the pre-industrial conditions and those for 1983–2002 for the current climate from the CRU TS 2.1 (Mitchell & Jones, 2005).

Identifying population groups

Taxonomic uncertainties exist for both the *Erebia* and *Parnassius* species groups. Within the *Erebia tyndarus* complex, very different numbers of species were recognized by different authors (Descimon & Mallet, 2009). Here, we adopted a conservative approach, considering the *tyndarus* complex composed by only two taxa: the Ponto-Mediterranean (*Erebia* PM) clade and the Euro-Siberian (*Erebia* ES) clade (*sensu* Albre *et al.*, 2008). A recent re-analysis of *E. tyndarus* complex, limited to the ES 'terminal' clade (*E. tyndarus*, *E. cas-*

sioides, *E. nivalis* and *E. calcaria*) based on nucleotide sequence variation at genome-wide markers and morphometry, confirmed the 'traditional' four-species taxonomy (Gratton *et al.*, 2016). However, all these taxa show a strictly parapatric distribution with overlaps confined to narrow contact zones, indicating that some degree of competitive exclusion is likely and, hence, also some niche similarity. Regarding *Parnassius*, the close relationships between *P. apollo* and *P. phoebus* have been corroborated by molecular studies (Omoto *et al.*, 2004; Todisco *et al.*, 2010). Within the *Parnassius* group some discrepancies emerged between the traditional taxonomy of the *P. phoebus* complex and mtDNA data (Todisco *et al.*, 2012). These authors highlighted the existence of only two geographically structured clades: the first including Palaearctic and Alaskan populations (*P. phoebus* PA), the other including the Nearctic populations inhabiting the Rocky Mountains, Coast Range, Klamath Mountains and Sierra Nevada (*P. phoebus* NA). In contrast, the highly divergent haplogroups identified in the wide range of *P. apollo* (Todisco *et al.*, 2010) did not lead to a taxonomic revision of this species.

To assess which species assemblages can be considered as operational units during the modelling phase, we tested niche divergence and niche conservatism hypotheses within both *Erebia* and *Parnassius* species groups, using the methodological framework proposed by Broennimann *et al.* (2012). Specifically, by means of a principal component analysis calibrated on the environmental space (PCA–env) enclosed by a 100-km buffer around each species record, we measured niche overlap and niche similarity between *Erebia* ES and *Erebia* PM, *P. apollo* and the whole *P. phoebus* complex and between *P. phoebus* PA and *P. phoebus* NA.

Climatic modelling procedure

Multicollinearity was tested by examining cross-correlation among all climatic variables, according to the Select method proposed by Dormann *et al.* (2013). The R code was obtained from http://horizon.science.uva.nl/scge2010-wiki/doku.php?id=parmat. To assess correlations within the environmental predictor data, we used the non-parametric Spearman correlation coefficient (ρ). Within each pair of predictor variables exhibiting a correlation greater than 0.85, the univariate importances were calculated fitting generalized additive models (GAMs) with a binomial error structure. Based on the deviances of univariate regressions of the single predictors against the response variable, the less important variable was identified within each pair and removed from the data set. For each operational unit only variables showing a ρ of 0.85 or less were retained (see Appendix S1 in Supporting Information).

To prevent spatial autocorrelation between training and testing samples to inflate model predictive performances (Veloz, 2009), we used the approach proposed by Harris (2015), modified to take into account spatial heterogeneity. Harris's method is based on the selection of a set of evenly spaced coordinates across the geographical space. Two different threshold distances from these coordinates are chosen to separate training records from testing records. However, given the highly fragmented ranges of the study taxa, a coordinate selection based on a regular grid sampling appeared unsuitable. Consequently, for each taxon we identified centroids via a k-means clustering of records' geographical coordinates (nstart = 1000, iter.max = 1000). Records within 20 km from each centroid were considered testing samples, whereas all the records beyond 40 km were considered training samples. All the records between 20 and 40 km from each centroid were discarded (*Erebia* ES = 224, *Erebia* PM = 11, *P. apollo* = 531, *P. phoebus* PA = 179 and *P. phoebus* NA = 59). For each taxon, the analysis was run iteratively by increasing the number of clusters until the ratio between testing samples and total remaining samples was greater than 0.25 (testing/total respectively: *Erebia* ES = 94/370, *Erebia* PM = 17/63, *P. apollo* = 255/1002, *P. phoebus* PA = 90/359 and *P. phoebus* NA = 61/228).

Combining the outputs of different modelling techniques has been proposed as an approach to reduce the intermodel variations and to determine an optimal solution from an ensemble of models, hence producing more robust and ecologically correct estimates of species distribution (Araújo & New, 2006; Thuiller *et al.*, 2009). Ensemble models and potential distribution maps were generated using the R package biomod2, version 3.1-64 (Thuiller *et al.*, 2014). We used all the modelling techniques implemented in biomod2: artificial neural networks (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), GAM, generalized boosting model (GBM), generalized linear models (GLM), Maxent, multiple adaptive regression splines (MARS), random forest (RF) and surface range envelope (SRE). The area under the receiver operating characteristic curve (AUC; Fielding & Bell, 1997) and the true skill statistic (TSS; Allouche *et al.*, 2006) were used to evaluate the predictive performances of both single models and ensemble models. Since AUC scores highly depends on the spatial extent (in terms of environmental distance too) used to calibrate the model (Lobo *et al.*, 2008), we used a random subset of the environmental space enclosed by a 100-km buffer around each species record as pseudo-absences. Five different sets of pseudo-absences ($N = 10 \times$ number of training presences) were generated within the buffer; to increase model predictive accuracy, in each run presences and pseudo-absences were weighted to give a prevalence of 0.5 (Barbet-Massin *et al.*, 2012).

A total of 250 models were computed (5 operational units × 5 different sets of pseudo-absences × 10 different algorithms). Models with AUC values below 0.8 (see Appendix S1) were excluded and ensemble predictions were generated using a weighted (proportional) average consensus method between the remaining models. The resulting ensemble models were finally projected through time, obtaining the potential distributional ranges at present, HCO and LGM (see Appendix S1). Binary transformations were carried out using the threshold maximizing simultaneously the number of presences and absences correctly predicted. This threshold was shown to produce the most accurate predictions (Jiménez-Valverde & Lobo, 2007). As a conservative approach, the suitability of all cells showing variable values not experienced during the model training (values greater than zero in the clamping mask) was set to zero. Similarly, the suitability of all cells covered by glaciers or ice sheets at LGM (Ehlers *et al.*, 2011; maps available at http://booksite.elsevier.com/9780444534477) was set to zero in the LGM maps. Summary predictions at HCO and LGM were calculated by summing the binary (presence/absence) ensemble maps based on different GCMs. All the cells predicted as suitable (presence) by at least one ensemble model were retained. This allowed us to take into account the contribution of single predictions, upweighting at the same time the areas in which both predictions agree.

Testing bias towards NSAs

Niche stability areas represent regions whose climate remains suitable for the species through time, potentially ensuring long-lasting survival for the inhabiting populations. We assigned a stability value to each grid cell as the product of the ensemble suitability maps calculated for the three time frames (present, HCO and LGM). As we used different GCM projections for HCO and LGM, the stability value for each grid cell is in the set {0,1,2,4} (present * HCO * LGM = {0,1} * {0,1,2} * {0,1,2}), where the maximum value of 4 stands for predicted suitability under all GCMs and time frames. All areas covered by glaciers or ice sheets at LGM were assigned a stability value of 0. We produced binary maps of niche stability under all possible thresholds (i.e. defining NSAs as cells with stability value ≥1, ≥2 and =4 respectively).

To quantify the bias of current realized distributions towards NSAs, and, thus, the degree of species–climate disequilibrium, we (1) calculated, for the occurrences data set of each taxon, the average stability and the average geographical distance to the nearest NSA (under all binary stability maps); (2) used a randomization approach to test the null hypothesis that the observed average values for stability and distance to NSAs did not differ from those expected under species–climate equilibrium (the condition where the occurrence of a taxon is entirely predicted by the current climate suitability). To generate expectations under the species–climate equilibrium, we simulated 999 random occupancies within the current potential range by sampling the same number of occupied cells observed for the *i*-th operational unit and using the ensemble current predictions as the sampling probability surface (i.e. the probability of each cell to be sampled as occupied was proportional to its suitability value in the ensemble prediction, with all cell values below the threshold simultaneously maximizing the number of correctly predicted presences and absences set to zero). For each randomized occupancy, we calculated both the average stability and the average geographical distance to the nearest NSA and obtained the two-tailed *P*-value for the null hypothesis of species–climate equilibrium as $\min(N_{\leq obs} + 1, N_{\geq obs} + 1) * 2/(N + 1)$, where $N_{\leq obs}$ and $N_{\geq obs}$ are the number of randomized occupancies with average values smaller than or equal to and greater than or equal to the observed mean, respectively, and N is the total number of randomizations. Occupancy randomizations were limited to different portions of the study area for each taxon, according to species realized distributions (e.g. the whole Holarctic for *Erebia* ES and *P. phoebus* PA, the Nearctic for *P. phoebus* NA and the Palaearctic for *Erebia* PM and *P. apollo*). By doing so, we prevented randomizations from occupying areas that were not potentially colonizable during the post-glacial migration process. All the analyses were performed using the R programming environment (R Development Core Team 2015, http://www.R-project.org/) and associated packages. Data sets and R scripts used to run the analyses are available upon request from the corresponding author.

RESULTS

Identifying population groups and ensemble model predictions

A PCA performed only on presence records showed low levels of niche differentiation within both the *Erebia* group (Fig. 3a) and the *Parnassius* group (Fig. 3b). In both species complexes, no clear pattern was evident in the contribution

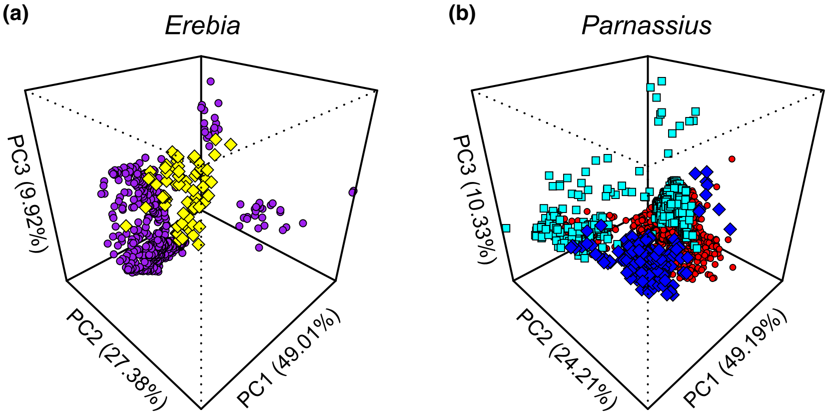

Figure 3 PCA plots obtained by using the complete set of climatic variables, for (a) *Erebia* and (b) *Parnassius*. (a) *Erebia tyndarus* species complex: circles = Euro-Siberian (*Erebia* ES) clade and diamonds = Ponto-Mediterranean (*Erebia* PM) clade (*sensu* Albre *et al.*, 2008). (b) *Parnassius apollo–P. phoebus* species complex: circles = *P. apollo*; squares = Palaearctic + Alaskan populations (*P. phoebus* PA) and diamonds = Nearctic populations of the *P. phoebus* species complex (Todisco *et al.*, 2012).

Table 1 Results of niche shift analysis (PCA–env; Broennimann *et al.*, 2012) within both *Erebia* and *Parnassius* species groups. Observed niche overlap (*D* metric) corrected for environmental availability and significance levels for niche equivalency and niche similarity tests. Within the *E. tyndarus* species complex we tested for niche shifts between the Euro-Siberian (*Erebia* ES) and the Ponto-Mediterranean (*Erebia* PM) clades (*sensu* Albre *et al.*, 2008). Within *Parnassius* we tested for shifts between both *P. apollo* and the whole *P. phoebus* species complex and within this last group, between Palaearctic and Alaskan populations (*P. phoebus* PA) and Nearctic populations (*P. phoebus* NA) (Todisco *et al.*, 2012).

Pairs tested	*D* metric	Niche equivalency	Niche similarity (range 1→range 2)	Niche similarity (range 2→range 1)
Erebia ES–*Erebia* PM	0.161	< 0.05	ns	ns
P. apollo–*P. phoebus* complex	0.617	< 0.05	< 0.05	< 0.05
P. phoebus PA–*P. phoebus* NA	0.138	< 0.05	ns	ns

of the single climatic variables to the first three principal components. According to Broennimann *et al.* (2012), niche similarity test yielded significant differences ($P < 0.05$) only between *P. apollo* and the *P. phoebus* complex (Table 1), leading to nonrejection of the null hypotheses of niche similarity due to chance for *Erebia* ES–*Erebia* PM and *P. phoebus* PA–*P. phoebus* NA. Niche equivalency hypothesis, on the other hand, was rejected in all cases ($P < 0.05$), revealing significant differences between species ranges. Consequently, we considered each group (*Erebia* ES, *Erebia* PM, *P. apollo*, *P. phoebus* PA and *P. phoebus* NA) as a different operational unit during the modelling phase.

For each operational unit, all models with AUC > 0.8 (*Erebia* ES = 45, *Erebia* PM = 39, *P. apollo* = 25, *P. phoebus* PA = 14 and *P. phoebus* NA = 25) were used for deriving the ensemble model, being RF and SRE the algorithms which more and less contributed to it respectively (see Appendix S1). All final ensemble models showed good to excellent predictive abilities (AUC/TSS respectively: *Erebia* ES = 0.954/0.779, *Erebia* PM = 0.907/0.719, *P. apollo* = 0.940/0.715, *P. phoebus* PA = 0.965/0.886 and *P. phoebus* NA = 0.907/0.666).

Testing bias towards NSAs

For all taxa, NSAs occupy a fraction of the current potential distribution (Fig. 4). Within *Erebia* ES and *P. phoebus* PA, the average stability of actually occupied cells is significantly higher than expected under the null model of species–climate equilibrium. All other operational units showed no significant bias ($P > 0.05$; *Erebia* PM and *P. phoebus* NA) or, in the case of *P. apollo*, a significant bias towards values lower than expected (Table 2). The distributions of distances from each occupied cell to the nearest NSA displayed a different pattern: with the exception of *P. apollo*, all operational units showed a significant ($P \leq 0.05$) bias towards short distances, compared to occupancies simulated under species–climate equilibrium (Table 2). As using different thresholds to create binary maps of stability did not return differences in the patterns of significance, but only in the distance values, we hereafter considered all those cells with a value greater than zero as stable (i.e. all cells predicted as suitable by at least one model in each time frame were considered stable).

The vast majority of occupied cells in the *Erebia* group are within a 100 km radius from NSAs (*Erebia* ES = 91.58%; *Erebia* PM = 75.68%), and very few are more than 500 km away from the nearest NSA (*Erebia* ES = 7.24%; *Erebia* PM = 1.35%). Within the *Parnassius* group, on the other hand, the distribution of the minimum distances (Fig. 5c–e) is less concentrated around NSAs (cells closer than 100 km from stability: *P. apollo* = 76.97%; *P. phoebus* PA = 65.99%; *P. phoebus* NA = 19.86%). Distances greater than 500 km are much more common than in the *Erebia* group, especially for *P. phoebus* PA (32.16%) and *P. phoebus* NA (60.63%). *P. apollo* shows an intermediate behaviour: with respect to the other taxa within the *Parnassius* group, departures greater than 500 km are less frequent (16.05%), but its distribution is still less concentrated around NSAs than in *Erebia*. The analysis of the scatterplots representing latitudinal and longitudinal shifts from stability (Fig. 5f–j) confirms these patterns and indicates both substantial northward movements and large longitudinal shifts for all *Parnassius* taxa.

DISCUSSION

Reduced habitat tracking and species–climate disequilibria

Our results highlight different influences of niche stability both between the *Erebia* and *Parnassius* groups and within each group of species. Maps of niche stability point out that NSAs occupy a small portion of the current potential distributions (Fig. 4). This narrowness is partly due to glaciers and ice sheets occupying the higher latitudes and altitudes at the LGM and partly to the spatial mismatch of suitable unglaciated areas during the LGM and/or the HCO with respect to present conditions. As we stated in the introduction, both the *Erebia* and the *Parnassius* groups have a largely overlapping Holarctic distribution (Fig. 2). The most evident difference lies in their presence at high latitudes: *Erebia* is almost absent at high latitudes, whereas all the three operational units within *Parnassius* moved northward during the Post-glacial, colonizing broad areas unsuitable at LGM (i.e. *P. apollo* colonized Scandinavia, *P. phoebus* PA the Polar Urals and the central and eastern Siberia and *P. phoebus* NA the Northern Rocky Mountains). Even when downscaled at

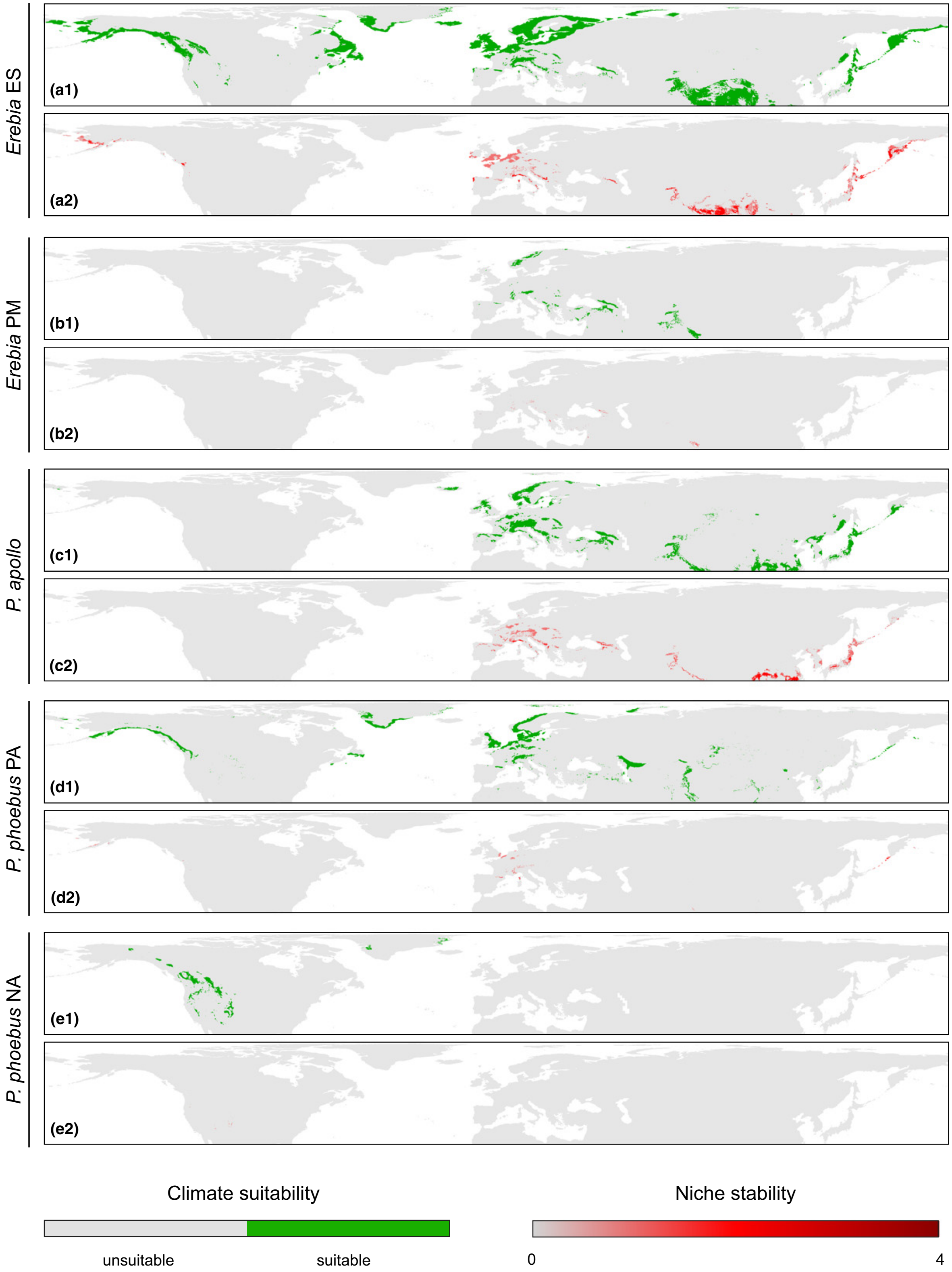

Figure 4 Maps of current climate suitability (ensemble models; a1, b1, c1, d1 and e1) and niche stability (a2, b2, c2, d2 and e2) for each operational unit. Niche stability areas (NSAs) were defined as those grid cells for which climate remained constantly suitable for the species through time and were obtained by multiplying the summary maps from each time frame (present, Holocene climate optimum and Last Glacial Maximum). *Erebia* ES and *Erebia* PM: respectively, Euro-Siberian and Ponto-Mediterranean clades within the *E. tyndarus* species complex; *P. phoebus* PA and *P. phoebus* NA: respectively, Palaearctic + Alaskan populations and Nearctic populations within the *P. phoebus* species complex. Map projection: Behrmann Cylindrical Equal Area.

Table 2 Results of the randomizations to test biases towards niche stability areas (NSAs). For each distributional data set we measured the average stability and the average geographical distance (in kilometres) of each record from the nearest NSA. Within each operational unit, average observed stability and average observed distance are reported. Expected stability and distance refers to the distribution (mean; standard deviation) of the mean values obtained simulating 999 random occupancies of the species potential range under the null hypothesis of species–climate equilibrium. The average distances from the nearest NSA were calculated applying all possible thresholds (1, 2 and 4) to stability maps. Values indicating significant species–climate disequilibria (stability values significantly higher – distance values significantly lower than expected by a random occupancy) are marked in bold. *Erebia* ES and *Erebia* PM: respectively, Euro-Siberian and Ponto-Mediterranean clades within the *E. tyndarus* species complex; *P. phoebus* PA and *P. phoebus* NA: respectively, Palaearctic + Alaskan populations and Nearctic populations within the *P. phoebus* species complex.

	Stability		Distance					
			Stability ≥ 1		Stability ≥ 2		Stability $= 4$	
Operational unit	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
Erebia ES	**0.63****	0.51; 0.05	**95***	575; 41	**114***	590; 41	**317***	848; 47
Erebia PM	0.18ns	0.20; 0.08	**65***	246; 61	**85***	431; 77	**373***	896; 110
P. apollo	0.63*	0.92; 0.03	200*	60; 7	206*	68; 7	553*	340; 16
P. phoebus PA	**0.26***	0.10; 0.02	**471***	910; 48	**706***	1019; 49	**1497***	2439; 70
P. phoebus NA	0.02ns	0.02; 0.01	**624***	979; 77	**681***	1056; 77	**1102***	1416; 74

P-values: ns = not significant; * = $0.01 < P \leq 0.05$; ** = $P \leq 0.01$.

high-resolution, GCMs provide a coarse-grained reconstruction of past climate and cannot account for local, microclimatic conditions. This implies that small areas effectively allowing species persistence through time may escape identification by GCM-based SDMs (Pearson, 2006). Therefore, some latitudinal and longitudinal shifts between presence records and the nearest NSA (see Fig. 5f–j) could be overestimated because of unidentified microrefugia. However, substantial colonizations of previously glaciated areas can be confidently interpreted as the result of post-glacial dispersal. The distribution of *Erebia* (Fig. 5a, b, f and g) is highly concentrated around NSAs, with rare exceptions in *Erebia* ES

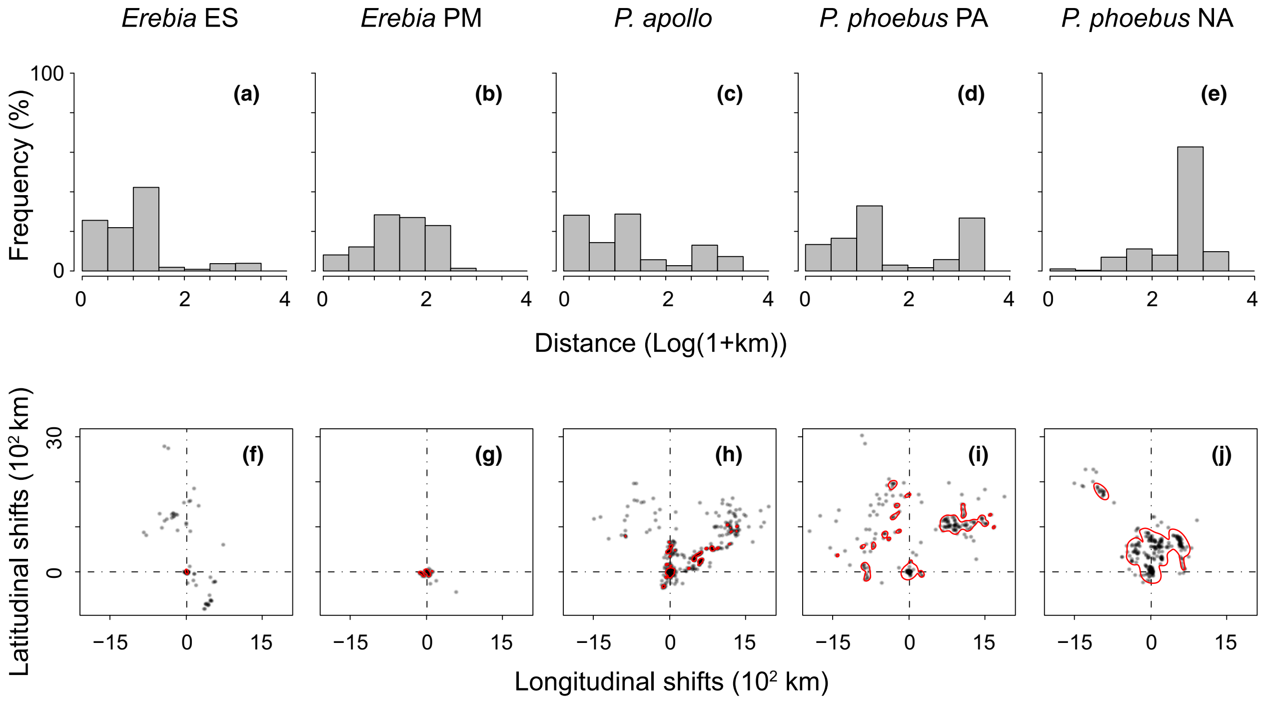

Figure 5 Spatial configuration of occurrences with respect to niche stability areas (NSAs). Histograms (a–e) show the distribution of the minimum distances between each record and the nearest NSA. Biplots (f–j) represent latitudinal and longitudinal shifts between each record and the nearest NSA, with grey shadings indicating the density of occurrences and solid contour lines enclosing 90% of the distribution, according to kernel density estimates. *Erebia* ES and *Erebia* PM: respectively, Euro-Siberian and Ponto-Mediterranean clades within the *E. tyndarus* species complex; *P. phoebus* PA and *P. phoebus* NA: respectively, Palaearctic + Alaskan populations and Nearctic populations within the *P. phoebus* species complex.

that could be interpreted as the result of model failure in identifying suitable microrefugia (Fig. 5a, f). In contrast, the distribution of distances in *P. apollo*, *P. phoebus* PA and *P. phoebus* NA is more continuous (Fig. 5h–j), and involves massive occupancy of previously glaciated areas in both Scandinavia and North America, suggesting that these patterns result from post-glacial northward dispersal waves. Our analyses indicate that *Erebia*'s post-glacial colonization mostly consisted of small-distance movements, that is, essentially upward shifts to track climate changes within topographically heterogeneous areas (as attested by the occurrence of these species at previously glaciated high elevations in the Alps and other mountains). It is well known that populations or species inhabiting topographically heterogeneous areas should be less influenced by climate changes (Lobo *et al.*, 2001; Tzedakis *et al.*, 2002; Svenning & Skov, 2007b). Given the slower climate change velocities in these areas, these populations/species do not need as strong dispersal abilities as those living in homogeneous landscapes to track climate change (Nogués-Bravo *et al.*, 2010; Sandel *et al.*, 2011). Within *Parnassius*, however, upward shifts could have been frequently accompanied by northward movements, sometimes across topographically homogeneous areas (e.g. central and northern Europe for *P. apollo*). Analogous to what has been reported for some widespread European trees (e.g. *Alnus glutinosa*, *Betula pendula*, *B. pubescens*, *Picea abies* – Svenning & Skov, 2004), these movements allowed *Parnassius* to colonize previously glaciated regions and indicates a greater ability to respond to post-glacial climate variations. *Erebia*, on the contrary, as with some other small-range species (e.g. *Abies alba*, *Larix decidua*, *Pinus cembra* – Svenning & Skov, 2004) is currently restricted to fragmented areas in the southern part of its potential range.

Analysing the European tree flora, Svenning & Skov (2004, 2007a,b) reported strong disequilibria between potential and realized species' distribution, and provided evidence on how geographical accessibility to putative glacial refugia explains a great part of the geographical variation in species diversity at the regional scale. Similarly, our randomizations on the influence of NSAs in shaping species' realized distribution show highly significant associations between the realized distribution and the areas that allowed the survival of viable populations throughout the Lateglacial and the Post-glacial. Excluding *P. apollo*, for which randomizations seem to indicate an almost complete filling of the species' potential range (as expected from the scenario A in Fig. 1), the current realized distributions of the studied species are more concentrated around NSAs than expected if species were in equilibrium with climate (the null hypothesis), suggesting species–climate disequilibria. Several factors could account for the differences in post-glacial habitat tracking, namely the species' dispersal ability (Graham *et al.*, 2006; Araújo & Peterson, 2012), the number and location of NSAs (Pearson, 2006) and the environmental permeability to migration between these areas and the current potential range (Svenning & Skov, 2007a). Finally, habitat tracking could be constrained by biological interactions (Araújo & Luoto, 2007; Araújo & Peterson, 2012). For butterflies, in particular, colonization could be prevented by the absence of the larval foodplants (Araújo & Luoto, 2007; Schmitt & Haubrich, 2008). In our case, however, foodplant limitations should not take place either within *Erebia* or *Parnassius*. According to the HOST database (Robinson *et al.*, 2010), at the larval stage *Erebia* ES feeds on, among others, the widely distributed *Festuca ovina* and *Poa annua* in Europe. *Parnassius apollo*, as well as *P. phoebus*, feeds on several genera of Crassulaceae (e.g. several widely distributed species of *Sedum* and *Sempervivum* such as *Sedum album*, *Sedum lanceolatum* and *Sempervivum tectorum*). Consequently, we could assume that the species' dispersal ability, mediated by both the location of NSAs and the environmental permeability, played a major role in shaping the post-glacial range dynamics in both *Parnassius* and *Erebia*. Very importantly, our conclusions about post-glacial demographic histories of *Parnassius* and *Erebia* butterflies in this study are consistent with independent phylogenetic and phylogeographical data. Todisco *et al.* (2012) found that populations of *P. phoebus* NA (*P. smintheus*) from the northern Rocky Mountains are genetically homogenous, consistently with a northward post-glacial colonization. Similarly, Scandinavian *P. apollo* were found to be genetically similar to south-eastern European populations (Todisco *et al.*, 2010), and clearly derive from a Holocene expansion into previously glaciated areas. Conversely, mtDNA data indicated that the small-ranged species within the *Erebia tyndarus* complex derive from multiple cladogenetic events spanning about one million years (Albre *et al.*, 2008), suggesting that range fragmentation played a paramount and continued role in the evolutionary history of this taxon.

Consequences of climate warming on alpine species

Alpine species offer a straightforward model for understanding the effect of climate fluctuations on species range: we have the chance to study the dynamics associated with an in-progress survival in unsuitable climates (Stewart *et al.*, 2010). Most species adapted to cold environments are indeed expected to suffer range reduction following climate warming (Thuiller *et al.*, 2005; Parmesan, 2006). Stewart *et al.* (2010) argued that the current realized distributions of cold-adapted species would roughly correspond to the location of the interglacial refugia, as their range should be at its minimum during Interglacials. According to our results, however, this view may be improved by looking at the current realized distributions as the result of the whole set of post-glacial range dynamics: that is, *in situ* survival within NSAs coupled with different degrees of northward dispersal. In fact, even for cold-adapted species, populations living at the northern edge of the species range have a high probability of going extinct during glacial periods (e.g. because of the advance of glaciers), and usually contribute only marginally to the long-term evolution of the species (Stewart *et al.*, 2010).

The net balance of local survival within NSAs and small-distance dispersal events is an increase in insularization, mainly in the southern portion of the species range (Fig. 1, scenario B). If the species, as in the case of *Erebia*, completely fails to move northward colonizing newly available areas, its survival would be restricted to disjunct southern mountain refugia, the so-called sky islands (*sensu* Heald, 1951). Metapopulation dynamics in fragmented habitats are mainly influenced by island dimension and isolation (Hanski & Gilpin, 1991), consequently the wider and less isolated the southern sky islands, the higher both the carrying capacity and the migration rate will be and, hence, the probability for the local populations to overcome adverse climatic conditions will be higher. Future climate changes, by directly reducing suitable habitats and decreasing inter-habitat connectivity, could therefore strongly influence these dynamics. Moreover, as NSAs, which have a mainly southern distribution, represent the core of species ranges and host the highest intraspecific genetic uniqueness, ongoing climate warming, is expected to cause severe genetic depauperation (Alsos *et al.*, 2012). The effects of future climate changes on metapopulation dynamics in the southern portion of the species range could therefore cause even much more than just a reduction in suitable areas: they may lead to the definitive loss of essential centres of biological diversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Variables importance, model performances and EM predictions.

BIOSKETCH

Silvio Marta undertook this research as a post-doc in the lab of Professor Valerio Sbordoni at the University of Rome 'Tor Vergata'. Silvio is currently a post-doc at the Institute of Ecosystem Study (National Research Council – Italy). He has strong interests in historical biogeography, especially in the comprehension of the mechanisms shaping species' geographical ranges over broad time-scales.

Author contributions: S.M. conceived the idea; S.M., D.C. and V.S. collected the data; S.M., F.L. and P.G. analysed the data; all authors contributed to the writing.

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