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The coincidence of climatic and species rarity: high risk to small-range species from climate change

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Why do areas with high numbers of small-range species occur where they do? We found that, for butterfly and plant species in Europe, and for bird species in the Western Hemisphere, such areas coincide with regions that have rare climates, and are higher and colder areas than surrounding regions. Species with small range sizes also tend to occur in climatically diverse regions, where species are likely to have been buffered from extinction in the past. We suggest that the centres of high small-range species richness we examined predominantly represent interglacial relict areas where cold-adapted species have been able to survive unusually warm periods in the last *ca* 10 000 years. We show that the rare climates that occur in current centres of species rarity will shrink disproportionately under future climate change, potentially leading to high vulnerability for many of the species they contain.

Keywords: hot spots; refugia; range shifts; extinction

1. INTRODUCTION

Large numbers of species with small geographical ranges are concentrated in a small proportion of the Earth's land surface (Orme *et al.* 2005; Lamoreux *et al.* 2006), making these regions of particular conservation concern (Malcolm *et al.* 2006). Recent work suggests that current climate can explain much of the variation in global patterns of total species richness but only small amounts of the variation in species richness of small-range species (Jetz & Rahbek 2002; Rahbek *et al.* 2007). The relative role of historic versus contemporary climate as determinants of small-range species richness patterns is still a matter of controversy, as is the likely response of these areas to future climate change (Jansson 2003; Malcolm *et al.* 2006; Araújo *et al.* 2008).

Using three taxa from two regions, we test three hypotheses that could explain why areas containing small-range species are located where they are. (i) Current climatic conditions in these areas could be unusual (compared with the surrounding regions); species adapted to these conditions are more likely to have restricted ranges (*climatic rarity hypothesis*). (ii) The current climates in these locations could be cooler than the surrounding areas; cool conditions would have been more widespread during past glacial periods, such that cool-adapted species have become confined to them during warm (interglacial) conditions (*climatic relict hypothesis*; e.g. Willis & Whittaker 2000). (iii) Higher environmental heterogeneity in these areas promotes local survival (by short distance dispersal during climate shifts), adaptation and diversification (*climatic buffer hypothesis*; e.g. Qian & Ricklefs 2000; Jetz & Rahbek 2002). Here, we show that areas with high numbers of small-range species are climatically unusual, and assess how the species in these areas might be affected by future climate change.

2. MATERIAL AND METHODS

(a) *Species and climate data*

We used published species distribution data on 4087 Western Hemisphere (WH) bird species, 2294 European plant and 418 European butterfly species at a 0.5° grid resolution. We considered species as being rare if they were part of the 25% of species with the smallest range sizes (Gaston 1994). Climates of the reference (1961–1990) and future time periods (HadCM3 climate model; A1FI, A2, B1 and B2 emission scenarios; 2021–2030 and 2051–2060) were used to characterize the climate in each grid cell, for five biologically relevant variables. See the electronic supplementary material for details on species and climate datasets.

(b) *The three hypotheses*

(i) *Climatic rarity hypothesis*

Under this hypothesis, we expect centres of high species rarity to coincide with climates that are unusual. Unusual climates are those that are different from the dominant climate types of the region and isolated from analogous climates elsewhere. For each grid cell, we calculated the climatically analogous area (total area of similar climate within 1000 km), distance to the nearest cell with analogous climate and average distance to all cells with analogous climate within 1000 km (Ohlemüller *et al.* 2006). All 10′ grid cell climate values were averaged over 0.5° grid cells to match the resolution of species data.

(ii) *Climatic relict hypothesis*

Under this hypothesis, we expect small-range species not only to be restricted to unusual climates, but also for these climates to resemble conditions that were more widespread in the past (i.e. colder than the neighbouring areas). For each grid cell, we quantified the deviation in climate and elevation between the target cell and the average of cells within 1000 km (200 km radius results were similar; not shown).

(iii) *Climatic buffer hypothesis*

Under this hypothesis, we expect small-range species to survive best in regions containing a wide diversity of climates. For each grid cell, we quantified the range of the five climate variables within a 200 km radius and elevation range within each cell. See the electronic supplementary material for details.

3. RESULTS

(a) *The three hypotheses*

Consistent with the climatic rarity hypothesis, we found that grid cells containing small-range species of all three taxa are located in areas with high climatic

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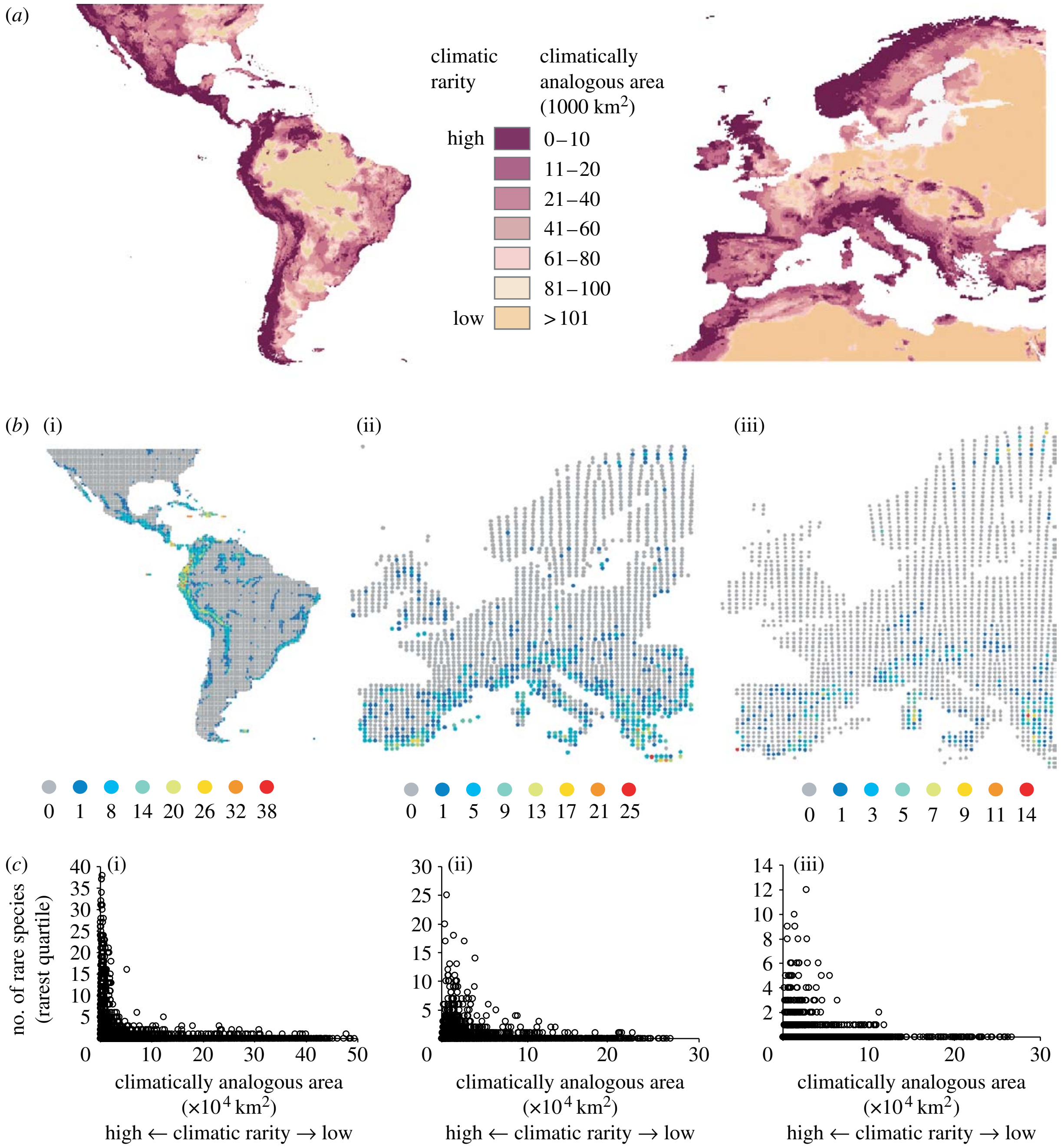

Figure 1. Climatic and species rarity. (*a*) Climatic rarity expressed as area with analogous climate conditions within a radius of 1000 km. (*b*) Species rarity expressed as the number of species ((i) birds, (ii) plants and (iii) butterflies) in the smallest range quartile; numbers indicate the upper bound of each richness class; for example, for butterflies, the red colour class represents grid cells containing 12–14 small-range species. (*c*) Relationship between climatic and species rarity ((i) birds, (ii) plants and (iii) butterflies): small-range species are generally found in areas of high climatic rarity. For butterflies, 36 species richness grid cells are excluded from (*c*) (see the electronic supplementary material).

distinctiveness and isolation (both $p<0.001$; figure 1; table 1). These results are not affected by total species richness. We found little or no correlation between small-range and total species richness and very similar patterns are observed when considering mean inverse range size rarity, a measure of species rarity that is not sensitive to total richness (see the electronic supplementary material).

As predicted from the relict hypothesis, high species rarity cells were also significantly higher and cooler than the surrounding area for WH birds and European butterflies (all $p<0.001$). Similarly, for European plants, these areas were at relatively higher altitudes than the surrounding areas ($p<0.001$); summer temperatures tended to be cooler (n.s.) and winter temperatures warmer ($p=0.002$), suggesting that these areas were also less seasonal than the surrounding areas (table 1). Centres of high species rarity for WH birds were drier than the surrounding areas ($p<0.001$), whereas those of European butterflies and plants were wetter than the surrounding areas (both $p<0.001$).

As expected by the climatic buffer hypothesis, high species rarity cells predominantly lie in regions with high climatic gradients, and the cells also contain a wide range of elevations within them (table 1). These

Table 1. Climatic characteristics of grid cells. (Characteristics of centres of high species rarity (grid cells containing at least one small-range species) and other cells, in relation to variables associated with the three climatic hypotheses; *p*-values indicate significance of differences between centres of species rarity and other cells (Kruskal–Wallis tests). Bonferroni-corrected significance levels (15 tests) are indicated as $^{*}p<0.05$, $^{***}p<0.001$. Deviations are calculated as the climate variable in the target cell minus the average value for the same variable in all cells within a 1000 km radius: for example, for WH birds, centres of species rarity have, on average, 99.89 mm less rainfall than the surrounding cells within 1000 km, whereas the other cells have, on average, 3.32 mm more rainfall than the surrounding cells. Negative temperature scores indicate that the target cells are colder than the surrounding areas and positive elevation scores indicate that they are higher.)

	Western Hemisphere birds			European plants			European butterflies		
	mean			mean			mean		
	species rarity cells	other cells	*p*	species rarity cells	other cells	*p*	species rarity cells	other cells	*p*
climatic rarity									
climatically analogous area (10^3 km^2)	30.44	72.61	$<0.001^{***}$	27.33	58.90	$<0.001^{***}$	25.06	49.15	$<0.001^{***}$
distance to the nearest analogous cell (km)	28.76	17.67	$<0.001^{***}$	15.88	12.06	$<0.001^{***}$	16.05	12.88	$<0.001^{***}$
mean distance to all analogous cells (km)	232.86	227.11	0.211	280.24	229.27	$<0.001^{***}$	277.03	235.63	$<0.001^{***}$
climatic relict									
average deviation within a 1000 km radius:									
elevation (m)	251.13	−24.73	$<0.001^{***}$	72.46	−40.72	$<0.001^{***}$	247.98	−50.14	$<0.001^{***}$
mean temperature of the warmest month (°C)	−1.56	0.08	$<0.001^{***}$	−0.32	−0.16	0.492	−1.26	−0.03	$<0.001^{***}$
mean annual temperature (°C)	−1.33	0.05	$<0.001^{***}$	0.10	0.23	0.894	−0.95	0.43	$<0.001^{***}$
mean temperature of the coldest month (°C)	−1.05	0.03	$<0.001^{***}$	1.03	0.67	0.002^{*}	−0.14	1.00	$<0.001^{***}$
annual precipitation (mm)	−99.89	3.32	$<0.001^{***}$	96.23	26.69	$<0.001^{***}$	95.25	42.58	$<0.001^{***}$
number of dry days (d yr^{-1})	3.36	−1.05	0.031	0.09	−2.94	0.130	−4.25	−1.78	0.006
climatic buffer									
average range within a 200 km radius:									
mean temperature of the warmest month (°C)	13.88	8.08	$<0.001^{***}$	10.83	7.56	$<0.001^{***}$	11.65	8.30	$<0.001^{***}$
mean annual temperature (°C)	13.39	7.67	$<0.001^{***}$	10.63	7.45	$<0.001^{***}$	11.48	8.08	$<0.001^{***}$
mean temperature of the coldest month (°C)	13.52	7.77	$<0.001^{***}$	11.32	8.58	$<0.001^{***}$	12.20	8.84	$<0.001^{***}$
annual precipitation (mm)	2298	990	$<0.001^{***}$	951	946	0.001^{*}	1007	1022	0.002^{*}
number of dry days (d yr^{-1})	89.59	54.86	$<0.001^{***}$	72.15	68.53	$<0.001^{***}$	78.43	68.09	$<0.001^{***}$
elevational range within a cell (m)	1461.3	531.7	$<0.001^{***}$	1270.4	542.8	$<0.001^{***}$	1515.5	631.2	$<0.001^{***}$

grid cells were more strongly associated with variation in precipitation for WH birds than for European plants and butterflies (table 1).

(b) *Future changes*

Most grid cells containing high numbers of small-range butterfly and plant species in Europe will experience reductions in area with climate analogous to the reference period by 2051–2060 (figure 2). Trends are similar for B1 and A1FI greenhouse gas emission scenarios, although losses are greater for the more severe A1FI scenario. The area with climate conditions of high species rarity grid cells is predicted to shrink more than the area with climate of other grid cells between the 1961–1990 baseline and two future time periods for the emission scenarios investigated here (table 2). Hence, the types of climate experienced in 1961–1990 in high species rarity cells are disproportionately likely to be lost in the future.

4. DISCUSSION

(a) *Centres of high species rarity*

Species with small range sizes tend to occur in areas with rare, i.e. localized, climatic conditions. This suggests that the boundaries of many of the constituent species are not independent of current climate and gives support to the notion that current climate is likely

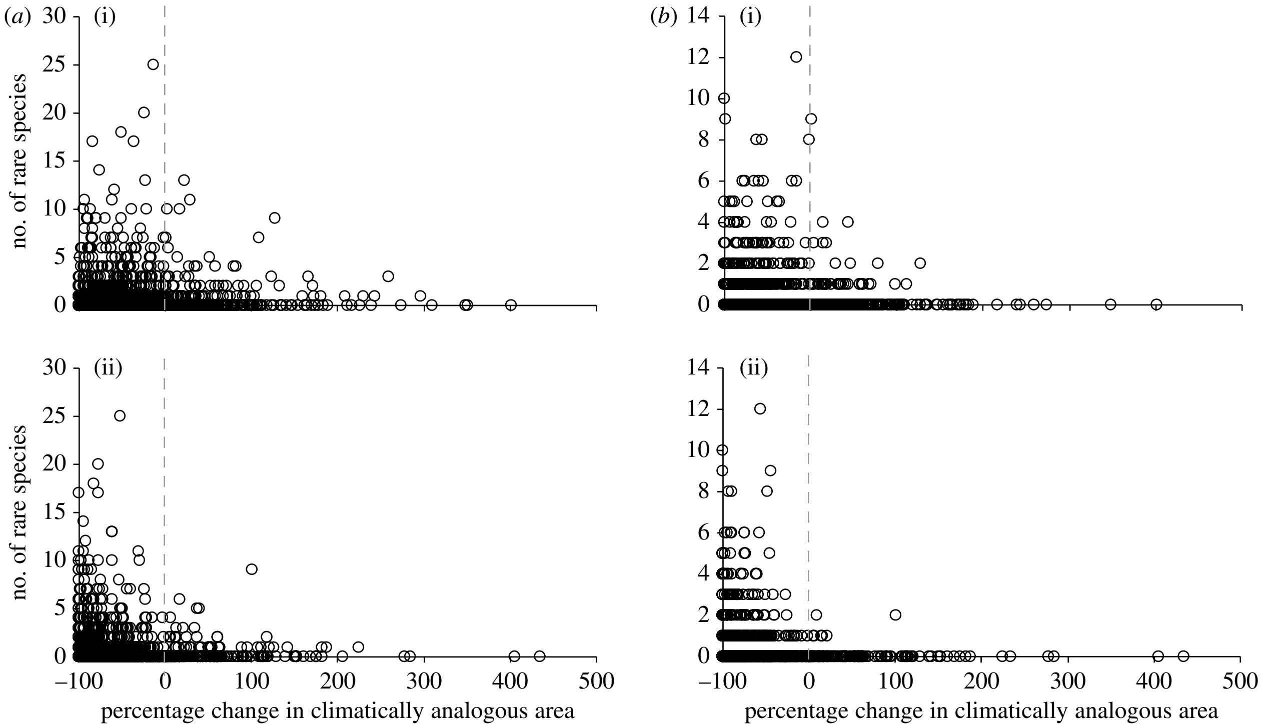

Figure 2. Relationship between the number of small-range species ((*a*) plants and (*b*) butterflies) and projected future changes in climatically analogous area between reference (1961–1990) and future (2051–2060) time periods. Climate projections are based on the HadCM3 climate model with (i) B1 (moderate) and (ii) A1FI (severe) emission scenarios. Each point represents one European 0.5° grid cell. Dashed line indicates no change in climatically analogous area; −100% represents a complete loss of grid cells with climate analogous to the reference period 2051–2060.

to have at least some role in shaping present-day patterns of species rarity. Not all rare climates, however, contain rare species. We interpret these as rare climates that might not have (i) existed in the past (and hence species are not specifically adapted to them), (ii) been colonized by specialized species with appropriate adaptations from elsewhere, or (iii) sufficient areas to maintain viable populations of specialized species.

Under the climatic relict hypothesis, we would expect small-range species not only to be restricted to unusual climates, but also for these climates to resemble conditions that were more widespread in the past. Most of the last million years has been colder than average Holocene temperatures (Willis & Whittaker 2000), so we would expect relict areas to be relatively cold compared with the neighbouring cells. Our data show this for WH birds and European butterflies, and to some extent for European plants (table 1). Centres of high species rarity appear to contain cool-adapted species that would have occurred at lower elevations and presumably have been more widespread during colder glacial periods.

Under the climatic buffer hypothesis, we would expect species to survive best in regions containing a wide diversity of climates, where they could survive rapid environmental change, such as glacial cycles, by dispersing relatively short distances. For all taxa and regions analysed here, we find a higher range of environmental conditions in the local neighbourhood of high species rarity cells compared with other cells (table 1). A large elevation gradient is a good predictor of the occurrence of small-range species of African as well as WH birds (Jetz & Rahbek 2002; Hawkins & Diniz-Filho 2006; Rahbek *et al.* 2007).

Table 2. Significance tests to compare declines in climatically analogous area between grid cells with at least one small-range species and other grid cells, for European plants and butterflies: Kruskal–Wallis tests; $^{*}p<0.05$, $^{***}p<0.001$ (Bonferroni-corrected for eight tests). (All comparisons show a greater loss of analogous climates under 2021–2030 and 2051–2060 climate conditions for species rarity grid cells than for other cells (for all four emission scenarios (A1FI, A2, B1 and B2)).)

	2025	2055
(*a*) *plants*		
A1FI	*	***
A2	*	***
B1	*	***
B2	***	***
(*b*) *butterflies*		
A1FI	***	***
A2	***	***
B1	*	***
B2	***	***

Support for the buffer and relict hypotheses is consistent with the interpretation that areas of high endemism represent locations with historically low rates of extinction: both recent and past extinction rates have been reduced in topographically (and climatically) diverse regions. It seems likely that both high levels of speciation and low levels of extinction contribute to the accumulation of large numbers of species in climatically heterogeneous regions (Qian & Ricklefs 2000; Cowling & Lombard 2002; Jetz & Rahbek 2002).

(b) *Impact of climate change*

Because most of the centres of high species rarity we examined are cool, relative to the surrounding region, the climatic conditions recently found within these centres are predicted to shrink as the climate warms. For European butterflies and plants, grid cells containing small-range species showed significantly greater reductions in area with analogous climate conditions by 2021–2130 and 2051–2060 than did other cells (table 2; figure 2). Future climate warming is likely to be increased at high elevations and may threaten small-range montane species there (Bradley *et al.* 2004; Thuiller *et al.* 2005). Even if endemic-rich areas were to warm less than other regions (Jansson 2003), the impact of warming would be greater because they disproportionately lose climatically analogous area (figure 2; table 2). Evidence from other continents also suggests that endemic species of various taxa are likely to be threatened by climate change (Williams *et al.* 2003; Bomhard *et al.* 2005). Shrinking areas of currently rare climates may result in globally important centres of conservation interest becoming hot spots of extinction.

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