Equilibrium of species' distributions with climate

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The degree to which species' distributions are at equilibrium with current climate is an important issue in the ecological literature (Davis 1986, Gaston 2003). Distinguishing the relative roles of present and past climates in determining species' distributions is not only of theoretical interest, but is key to understanding responses of species to climate change. Recent work has demonstrated significant departures from equilibrium with current climate for tree distributions in Europe (Svenning and Skov 2004), yet differences in the degree of equilibrium can be expected across organisms whose dispersal abilities (and hence ability to track changing climate conditions) vary greatly. Here we assess differences in equilibrium between present-day climate and vascular plant, breeding bird, amphibian and reptile assemblages in Europe. Our analyses included all know European species of breeding birds (Hagemeijer and Blair 1997), amphibians and reptiles (Gasc et al. 1997), and ca 20% of the European vascular flora (Jalas and Suominen 1972–1996, Lahti and Lampinen 1999). Assemblages of plants and breeding birds were found to be relatively closer to equilibrium than assemblages of reptiles and amphibians. Results suggest that responses of plant and bird species to climate change are more likely to be accurately forecasted by models correlating present-day distributions with climate, and that reptile and amphibian species will be least capable of shifting distributions, making them most vulnerable to rapid environmental changes.

Species are said to be at equilibrium with climate if they occur in all climatically suitable areas whilst being absent from all unsuitable ones (Hutchinson 1957). The observation that species are absent from many suitable areas is trivial. The critical question is how distant from equilibrium are current distributions. Accurate estimates of species' limits of tolerance to climate can be obtained by means of controlled experiments (Chuine and Beaubien 2001). However, these are expensive and time consuming and attempts to measure departures from equilibrium for large numbers of species have previously used the "bioclimatic envelope" approach, whereby observed species' distributions are correlated with environmental variables to approximate the ecological requirements of organisms (for review see Pearson and Dawson 2003). With this approach, the ratio between observed and modelled distributions is interpreted as indicating departures of species distributions from equilibrium (Svenning and Skov 2004). By relying on observed distributions (which inherently reflect multiple range determinants, both historical and ecological) to determine ecological requirements, this methodology is likely to underestimate the true range of climate variation that species are able to tolerate.

An alternative approach consists of measuring patterns of covariation between species assemblages and climate (Ferrier et al. 2002). It is assumed that if species are at equilibrium with current climate, then patterns of covariation between assemblage composition and climate will be high. A weak covariation between climate and biota may indicate that species tend not to occupy all available climate spaces due to historical and/or ecological factors (notably competition and limited dispersal ability). In some cases it could also imply that the selected climate parameters do not adequately describe the climatic determinants of the distribution of assemblages. However this possibility is inherent to any correlational approach (including bioclimate-envelope modelling) and the choice of climate variables needs to be supported from existing knowledge of species ecologies.
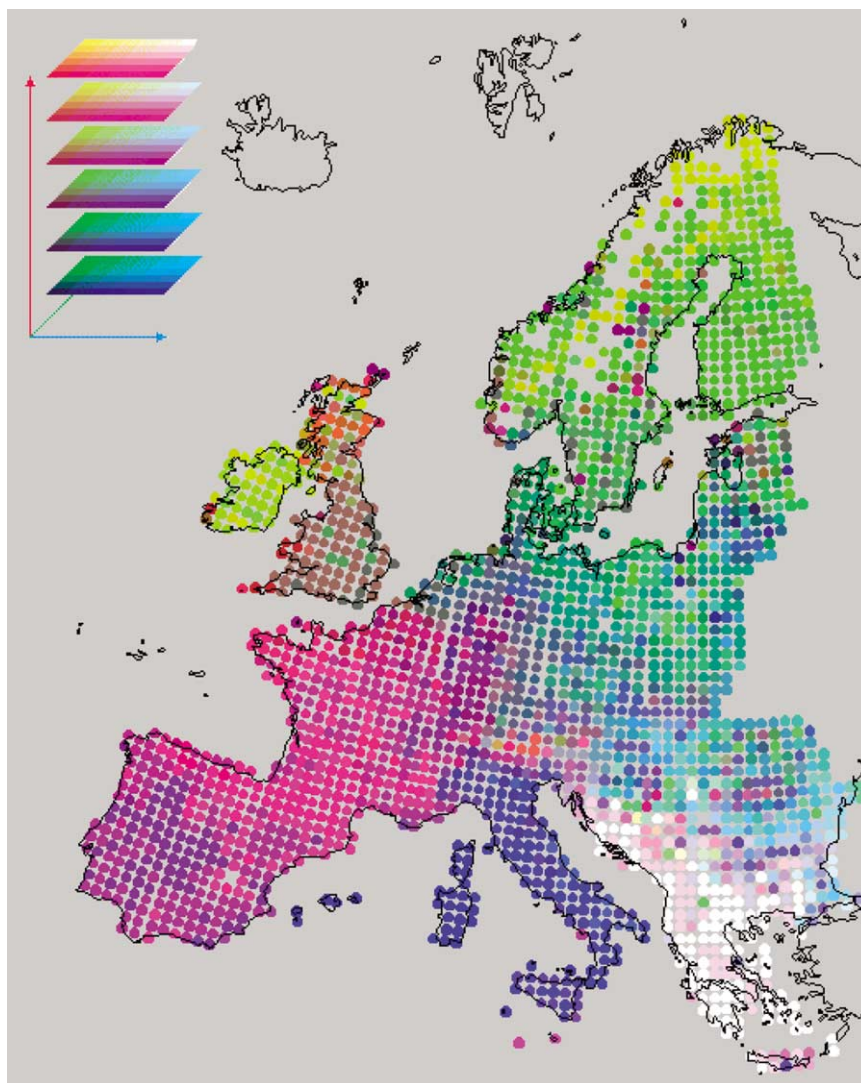
Fig. 1. Distribution of herpetological regions in 50-km grid cells in Europe. Variation in faunal composition was summarized as DCA (detrended correspondence analysis) ordination scores for grid cells on the first three axes. Scores on each axis are divided into sixteen colour-scale classes of equal score intervals, with increasing scores on the first axis shown in increasing intensities of green, increasing scores on the second axis shown in increasing intensities of blue, and increasing scores on the third axis shown in increasing intensities of red. The resulting "fuzzy" classification differentiates the three major ice age refugia in Iberia (showing post glacial colonisation in France; purple), Italy (dark blue), and the Anatolian peninsula (white). Variation in colours in central Europe indicates overlapping distributions of species from different ice age refugia.

This pattern-based approach can be explored by measuring the degree of association between two dissimilarity matrices using a suitable correlation coefficient (also known as mantel tests, see Manly 1998). Here we use Spearman's rank correlation coefficients (ρ) to measure the degree of association between species (Bray-Curtis) dissimilarity matrices and (standardised Euclidean) distances in a climate matrix. The climate matrix was constructed with seven climate variables (described in Araújo et al. 2004a) identified from the literature as being key determinants of physiological processes limiting distributions of plant (Prentice et al. 1992), bird (Lennon et al. 2000) and amphibian (Carey and Alexander 2003) distributions. An exploratory analysis of the potential impacts of climate change on European herptile species distributions (Araújo et al. unpubl.), also shows that climate variables selected by models tend to be similar for reptiles and amphibians.

The significance of the climate-biota relationship can be determined by comparison with the distribution of ρ found by randomly reallocating the order of the elements in one of the matrices. Under the null hypothesis of no relation between two matrices, ρ will be approximately zero. Here, its null distribution, either side of zero, was obtained by permutating 999 times one set of sample labels at random and recalculating ρ, to build up a frequency histogram with which the true value of ρ was compared. Departures from the null hypothesis indicate the degree of association between matrices. Our results show that co-variation between plant species composition and climate is highest ($\rho = 0.70$, $p < 0.001$), immediately followed by birds ($\rho = 0.69$, $p < 0.001$), then reptiles ($\rho = 0.55$, $p < 0.001$) and amphibians ($\rho = 0.47$, $p < 0.001$).

Higher co-variation, and thus equilibrium, for plant and bird assemblages are most likely to reflect greater

dispersal abilities. Whilst continental-scale post-glacial bird dispersal is well documented (Newton 2003), the potential for plants to undertake rapid large-scale migrations is more controversial (Nathan et al. 2002, Svenning and Skov 2004). Our results, combined with palaeoecological evidence of rapid plant migrations during the Quaternary (Huntley 1990, Prentice et al. 1992), support the hypothesis that plants are often more mobile than is conventionally thought (Nathan et al. 2002). In contrast, reptiles and amphibians are notoriously poor dispersers, leading to lower levels of equilibrium with current environmental conditions. Although dispersal ability may vary substantially within taxa (Smith and Green 2005), the generally low dispersal ability of "herptiles" is reflected in higher rates of endemism in comparison with other terrestrial vertebrate or plant groups in Europe (Williams et al. 2000), and can explain why major faunal regions in Europe are determined more by the location of three glacial refugia than by current climate gradients. This idea is illustrated in Fig. 1, where an ordination of European distributions of amphibians and reptiles (Araújo et al. 2004b) reveals the existence of three herpetological regions that coincide closely with the distribution of known past glacial refugia in Europe (Hewitt 2000), i.e., the Iberian, Italic and Anatolian peninsulas. Central and northern European herptile assemblages (greenish areas) include a few wide-ranging species that were able to disperse from post-glacial sources of colonisation.

These findings have important implications for projections of climate-change impacts on biodiversity (Araújo et al. 2004a, Thomas et al. 2004). Models generally assume that species' distributions are at equilibrium with current climate (Pearson and Dawson 2003), yet we show that the validity of this assumption varies substantially across different groups of organisms. Species-climate equilibrium is inversely related to species' ability to track future climate changes, suggesting that those species for which projections are least certain are in fact those most likely to be at risk. Further investigation of within-taxa dispersal differences would be interesting.

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