RESEARCH PAPER

Habitat type mediates equilibrium with climatic conditions in the distribution of Iberian diving beetles

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ABSTRACT

Aim The contrasting habitat permanence over geological time-scales of lotic and lentic habitats may impose different constraints on the dispersal ability of their macroinvertebrate populations, and ultimately on the degree of equilibrium with current climate. We aim to test for differences between species typical of either habitat type in their potential versus realized distributions as a surrogate measure of degree of climate equilibrium, both in refuges and more recently deglaciated areas.

Location Western Europe.

Methods We focus on 99 Iberian diving beetles (family Dytiscidae). A multidimensional envelope procedure was used to estimate their potential distributions, which were projected for different spatial scales. At the continental scale we calculated the percentage of countries with climatically suitable conditions for each species over those actually occupied (range filling). At the regional scale, we estimated realized distributions using: (1) convex hull polygons for Sweden and the Iberian Peninsula; and (2) generalized linear models for the Iberian Peninsula.

Results In the Iberian Peninsula, differences in the degree of equilibrium with climatic conditions between lotic and lentic species were few, if any. However, at the continental scale we found significant differences, with lentic species closer to equilibrium than lotic species. In the recently deglaciated area (Sweden) the subset of species with ranges wide enough to encompass Iberia and Scandinavia were mostly lentic, and all were closer to climatic equilibrium without significant differences between habitat types.

Main conclusions Our results show that, at continental scales, climate equilibrium is not concordant between the habitat types across western Europe. We hypothesize that: (1) the differences between refuge areas in dispersal ability are erased probably due to long-term climatic stability, allowing enough time to reach equilibrium, and (2) the species with wide geographical ranges able to recolonize recently deglaciated areas should have the highest dispersal abilities, and are closer to climatic equilibrium.

Keywords

Climate equilibrium, diving beetles, Dytiscidae, Iberian Peninsula, lentic species, lotic species, post-glacial recolonization, potential distribution, realized distribution, western Europe.

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INTRODUCTION

Current species distributions are determined by a mixture of contemporary and historical filters acting at several spatial and temporal scales. The degree to which species distributions are at equilibrium with current climate is an important issue in the ecological and biogeographical literature and has spurred long debates (Davis & Scholtz, 2001; Gaston, 2003; Ricklefs, 2004;

Araújo & Pearson, 2005; Bonada *et al.*, 2005; Svenning & Skov, 2005). Hutchinson (1957) suggested that if a species' actual and potential distribution match perfectly, then its distribution is likely to be limited mainly by climatic parameters. However, if the actual distribution fills the potential distribution only partially then other factors, such as biotic interactions or limited dispersal abilities, are more likely to shape its distribution. A key question of this approach is how the potential distribution is estimated or modelled. When only the environmental conditions of the observed occurrences are available, we need procedures that are able to maximize the spatial representation of the species' fundamental niches (Jiménez-Valverde *et al.*, 2011).

Several studies have examined the differences between potential and realized distributions in the context of the effect of Pleistocene glaciations in Europe. Svenning & Skov (2004) suggested significant departures from equilibrium with current climate for tree distributions in Europe, probably owing to limited dispersal capability during post-glacial range expansions. While post-glacial recolonization of Europe seems to have proceeded rapidly for some tree species (Huntley, 1990; Kullman, 1998), dispersal limitation may continue to pose a large-scale constraint on the composition and richness of native tree species (Svenning & Skov, 2005). These historical constraints could be at least of a strength comparable to that of current environmental factors. Araújo & Pearson (2005), using data for European plants, birds, reptiles and amphibians, concluded that species that are notoriously poor dispersers have lower levels of equilibrium with current environmental conditions, due to lagged recolonization of northern latitudes following Holocene warming. At continental scales, differences in the degree of equilibrium are always related to differences in dispersal abilities (Araújo & Pearson, 2005), with successful northward migrants more in equilibrium than the poor disperser species that persisted in refugial areas. Northern species are thus a biased subset of the regional species pool, filtered by their higher dispersal ability.

The question remains as to what factors determine the dispersal ability of a species, and in particular if they can be used as predictors of the response of the species when confronted with changes in local or global conditions. For freshwater invertebrates it has been suggested that habitat type, a surrogate of long-term habitat persistence, is a good predictor of dispersal ability (Ribera & Vogler, 2000; Ribera *et al.*, 2001, 2003; Hof *et al.*, 2006, see Ribera, 2008, for a review). Species typical of geologically short-lived ponds or small lakes need to migrate when their habitat disappears, while species in more stable streams or rivers can persist in place over longer periods. This asymmetry in habitat preferences is repeated multiple times in many phylogenetically independent lineages (Ribera & Vogler, 2000), thus providing a set of independent replicas to test any predicted macroecological and macroevolutionary pattern. It has been shown that lotic species have generally smaller and more southerly range sizes (Ribera & Vogler, 2000; Hof *et al.*, 2006, 2008) and higher evolutionary turnover rates (Abellán *et al.*, 2009) than lentic species. Latitudinal diversity gradients of lentic and lotic species in Europe also differ, with lotic species

more dependent on historical factors such as distance to glacial refugia (Ribera *et al.*, 2003).

If habitat type can be considered a good predictor of the ability of freshwater macroinvertebrates to migrate and trace habitat or climatic change, it should be possible to detect differences between the species typical of running or standing waters in the degree of equilibrium with current climatic conditions. In areas less affected by the Pleistocene glacial cycles, like the unglaciated southern European peninsulas, it is expected that, due to the longer periods of climatic stability, both lotic and lentic species are largely in equilibrium with current climatic conditions. On the contrary, the same species would show differences in the speed at which they expand to occupy areas more severely affected by Pleistocene climatic fluctuations, like central and northern Europe. In these areas, the southern lentic species may occupy a larger portion of their potential range than the southern lotic species, which, due to their generally more limited dispersal abilities, have not had enough time to expand to occupy all suitable habitats. In the extreme situation of an area that has been recently fully glaciated, like Scandinavia, it is expected that only the best dispersers among the southern species could be present, i.e. mostly lentic species.

Here, we test these predictions using western European diving beetles present in the Iberian Peninsula, whose taxonomy and western European distributions are well known. We aim to compare the role of climatic variables in explaining current distributions in species adapted to running and standing water in areas differently affected by the Pleistocene glaciations (i.e. recently deglaciated and refuge areas). More specifically, we expect to find greater disequilibrium with climate conditions (measured as differences in the realized versus the potential distribution) for lotic than for lentic species.

METHODOLOGY

Source of biological data

We concentrated on 99 species and well-established subspecies of diving beetles from the family Dytiscidae (see Appendix S1 in Supporting Information). This family was selected because it is taxonomically stable and its species biology and life history are generally well known, including genetic phylogeographical data for most of the European species to validate current species concepts. The selected species are those with five or more records in the Escarabajos Acuáticos Ibéricos (ESACIB) database, which compiles all the available taxonomic and distributional data from Iberian water beetles (Sánchez-Fernández *et al.*, 2008). A total of 6382 Iberian Dytiscidae records were used. The habitat specificity of each species was assigned following Ribera & Vogler (2000), updated whenever necessary. The Iberian fauna of Dytiscidae is a heterogeneous assemblage including examples of many of the major lineages within the family, and in all of them there are both lentic and lotic species (Ribera & Vogler, 2000; Ribera *et al.*, 2008). In some genera, all species are either lentic or lotic, but due to the widespread occurrence of species of both habitat types (sometimes in very closely related species, e.g.

Table 1 List of variables used to obtain potential and realized distributions.

Type of variable	Denomination
Climatic	Annual mean temperature
	Isothermality
	Temperature seasonality
	Maximum temperature of warmest month
	Minimum temperature of coldest month
	Temperature annual range
	Mean temperature of wettest quarter
	Mean temperature of warmest quarter
	Mean temperature of coldest quarter
	Annual precipitation
	Precipitation of wettest month
	Precipitation of driest month
	Precipitation seasonality
	Precipitation of wettest quarter
	Precipitation of driest quarter
	Precipitation of warmest quarter
	Precipitation of coldest quarter
Spatial	Latitude
	Longitude
Geological	Percentage of land with acidic rocks
	Percentage of land with basic rocks
	Percentage of land with acidic deposits
	Percentage of land with basic deposits

Abellán *et al.*, 2009), it is unlikely that any observed difference could be influenced by phylogenetic constraints. For species with geographical distributions including areas outside the Iberian Peninsula we estimated their potential distributions, compiling presence records through their ranges (1341 additional records), to obtain representative data of the climatic conditions they experience. Although these distributional records are incomplete and lack homogeneity, we assume that inclusion of these data will better represent the full spectrum of climatic conditions in which these species can be found (see Sánchez-Fernández *et al.*, 2011).

Environmental variables

Seventeen environmental variables (see Table 1) were obtained from WORLDCLIM (version 1.3, http://www.worldclim.org; see Hijmans *et al.*, 2005, for details). WORLDCLIM contains climate data (monthly precipitation and mean, minimum and maximum temperature) at a spatial resolution of 30 arcsec (*c.* 1×1 km cell resolution) obtained by interpolation of climate station records from 1950–2000.

Modelling potential distributions

The study of the equilibrium of species with climatic conditions is not straightforward, as in general species can potentially inhabit a wider set of climatic conditions than those defined by

their present localities. Furthermore, extreme tolerances cannot be known without performing experimental physiological studies, and even in this case potential distributions may be an underestimate due to acclimation and phenotypic plasticity. Potential distributions can be briefly defined as the regions in which the climatic conditions are suitable according to the observed occurrences (see Jiménez-Valverde *et al.*, 2011, for a more precise conceptual definition). Here we use an established procedure directed at maximizing the capacity to represent geographically the potential distribution of species niches when they are only based on distributional data (Jiménez-Valverde *et al.*, 2011). In any case, the estimated potential distributions should be considered partial and provisional, subject to the caveats of having been delimited from geographical data (see the Discussion).

We used multidimensional envelopes (MDEs) to estimate the potential distribution (PD) of each species (Jiménez-Valverde *et al.*, 2011). First, we estimated for each species the climatic values prevailing in the observed presence localities (both inside and outside Iberia), and then calculated the extreme climatic values. These extreme values were used to derive a distributional hypothesis on the areas with climatically suitable conditions (the potential distribution), assuming that these recorded occurrences are representative of the full environmental spectrum of climatic conditions in which the species may survive and reproduce. As the distributional simulations obtained by MDEs are highly dependent on the number and identity of the selected predictors (Beaumont *et al.*, 2005), we first tried to identify the minimum set of climatic variables related to the occurrence of each species by an ecological niche factor analysis (ENFA) procedure (Hirzel *et al.*, 2002). ENFA compares the climatic data of recorded localities against climatic conditions in the whole study area, thus computing uncorrelated factors able to explain both species marginality (M) (the distance between the species optimum and averaged climatic conditions in the study area) and specialization (S; the ratio of the ecological variance in the climate of the study area to that associated to the focal species). The number of retained factors was determined by comparing the eigenvalues with a 'broken-stick' distribution (Hirzel *et al.*, 2002). Finally, the relevant climatic variables selected as predictors were those showing the highest correlation values with the retained ENFA factors (≥ 0.30). This process was repeated for each species, selecting a number of climatic predictors ranging from six to two. Using these variables and a MDE procedure we finally obtained a map with the European PD for each one of the 99 considered species.

Equilibrium at the European extent

To test the degree of equilibrium of the Iberian species throughout their ranges, we used presence/absence data per country at a continental (European) extent. The use of country species lists, although varying in grain size, may be the only possible strategy for studying compositional and species richness patterns for some groups (see Ribera *et al.*, 2003, for water-beetle data, or Baselga, 2008, and Ulrich & Fiera, 2009). A recent study showed
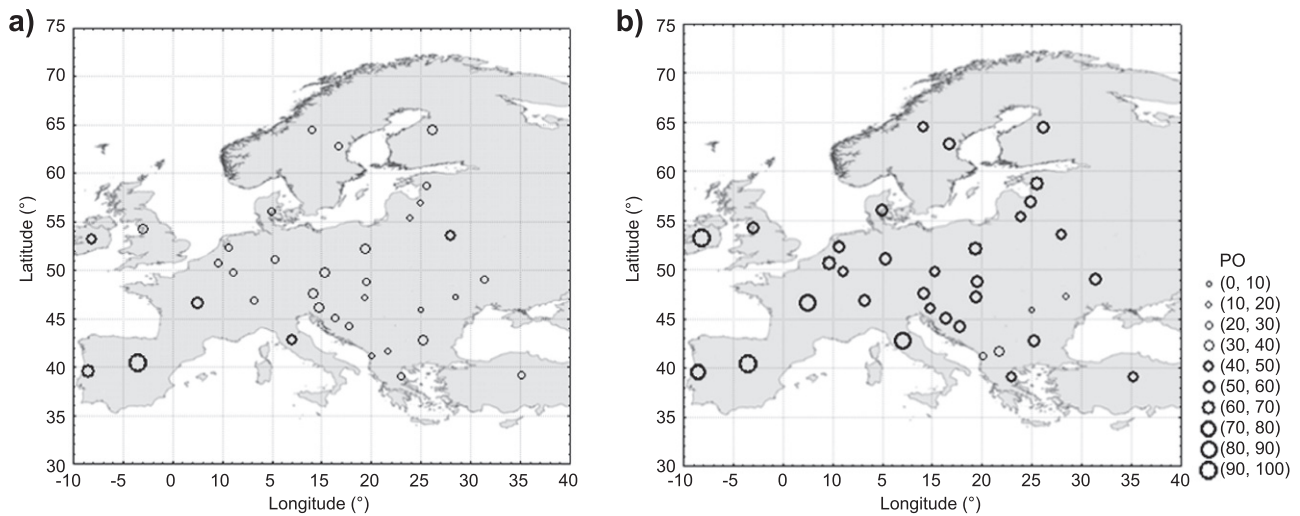
Figure 1 Geographical location of the number of recorded species in each country divided by the number of species with climatically favourable conditions (percentage of occupancy, PO). Each European country was represented by the centroid of its location, being the size of the circles proportional to PO values: (a) lotic species, (b) lentic species.

that the use of these data may provide reliable results at large resolutions and extents (Keil & Hawkins, 2009).

After estimating the PD of each species using all the available distributional information, we calculated both the number of countries with climatically suitable conditions for each species (N_C) and the number of species that could potentially inhabit each country (N_{PS}). The percentage of N_C over those countries actually occupied (according to Nilsson, 2003) was used as an estimate of the degree of non-equilibrium with the climatic conditions of each species, or range filling (RF). Thus, RF is defined as the percentage of climatically suitable areas (potential climatic range) that a species actually occupies (see Svenning & Skov, 2004). If the actual distribution fills the PD only partially then other factors, such as limited dispersal abilities, are more likely to limit its distribution (Svenning & Skov, 2004; Soberón & Peterson, 2005), indicating departures of species distributions from equilibrium.

The percentage of recorded species in each country over N_{PS} was used as an estimate of the degree of equilibrium of each regional inventory with regard to the Iberian elements (percentage occupancy, PO; see Fig. 1). We compared the PD, the realized distribution (RD), RF and PO values between the Iberian lotic ($n = 51$) and lentic ($n = 48$) species using a nonparametric Mann–Whitney U-test.

Equilibrium in the refuge area

For the comparisons at regional (Iberian Peninsula) extent we used both river sub-basins (SBs) and Universal Transverse Mercator (UTM) 100-km^2 grid cells. In the first case, PD was calculated as the number of well-surveyed sub-basins (WSSBs; see below) with suitable climatic conditions for each species, while RD was estimated as the number of WSSB with observed records according to the ESACIB database (Sánchez-Fernández *et al.*,

2008). RF was estimated as the percentage of climatically suitable WSSB that a species actually occupies, while PO was the percentage of observed species in each WSSB over the number species than potentially could occur in it. Similarly, we used a nonparametric Mann–Whitney U-test to compare PD, RD, RF and PO values between lotic and lentic species.

For the analyses using the number of UTM 100-km^2 grid cells as sampling units, PD was calculated as the number of cells with suitable climatic conditions for each species, while RD was estimated in two ways (see below): (1) using generalized linear models (GLMs) directed to estimate the realized distribution of each species and (2) estimating convex hull polygons from the distributional data. RF was estimated as the percentage of climatically suitable cells that a species actually occupies. For the comparison of PD, RD and RF values between lotic and lentic species we also used a nonparametric Mann–Whitney U-test.

Measure of RDs in the Iberian Peninsula

A clear distinction should be drawn between PDs and RDs within the species distribution model (SDM) framework (see Soberón, 2007). This is important, as many modelling exercises overlook the conceptual and methodological implications of discerning between PDs and RDs, as well as the influence of the kind and quality of the primary data used to build the models (Jiménez-Valverde *et al.*, 2008). While the PD is a hypothetical concept that refers to locations where a species could exist based on suitable environmental factors, the RD refers to locations where the species actually exists at a specific time, as constrained by environmental, biotic or/and dispersal limitations. Accounting for all these effects requires using data on the absence of the species to restrict model predictions (Soberón & Peterson, 2005; Václavík & Meentemeyer, 2009; Lobo *et al.*, 2010). If, on the contrary, the goal is to estimate the PD of a species, the absences

caused by non-climatic factors must be avoided (Chefaoui & Lobo, 2008; Jiménez-Valverde *et al.*, 2008; Lobo *et al.*, 2010).

We thus tried to obtain as many reliable absences as possible. We first overlaid each Iberian hydrological basin with a map representing the three main climatic Iberian subregions in order to divide each basin into climatically homogeneous SBs. The Iberian climatic subregions were estimated by a *k*-means procedure using the above-mentioned climatic variables. A total of 208 climatically similar SBs were thus obtained. We then assessed the sampling effort for each SB to identify those that could be considered to be well-surveyed and with reliable richness scores (the WSSBs). For that purpose we used collector's curves using the Estimate$S$ 8.0 software package (Colwell, 2006), using the number of database records (independently for lotic and lentic species) in each SB as a surrogate of sampling effort (Hortal *et al.*, 2004). This is generally considered to be a good approach for evaluating the quality of inventories (Hortal *et al.*, 2004). These curves represent the expected accumulated number of species encountered within a certain geographical area as a function of a measure of the effort (number of records in this case) invested to collect them (Gotelli & Colwell, 2001). The slope of the collector's curve determines the rate of species accumulation at a given level of sampling effort. This slope diminishes with the increase of sampling effort, reaching a hypothetical value of 0 when all species are detected. A Clench function was fitted to the smoothed data, and the asymptotic value for each SB (i.e. the predicted species richness for an ideally unlimited sample size) computed. The ratio of recorded to predicted species richness (the asymptotic score) was used as a measure of completeness of each SB inventory. A SB was considered to be adequately sampled (i.e. a WSSB) when the completeness values were ≥ 80%. We considered as 'reliable' the absences of species in these WSSBs. To include absence data from climatically unsuitable localities we also include all the absences outside the Iberian PD (see Chefaoui & Lobo, 2008).

The presence/absence data for each species was analysed with a stepwise logistic regression method using GLMs to obtain realized distribution hypotheses (RD$_{GLM}$). GLMs are an extension of classic linear regression models that allow for analysis of nonlinear effects among variables and non-normal distributions of the independent variables (McCullagh & Nelder, 1989). The relationship between the dependent and the explanatory variables (the link function) was logit, and we assumed a binomial distribution of the dependent variable. The presence/absence data for each of the 100-km^2 UTM cells was first compared with linear, quadratic and cubic functions of each environmental variable to account for possible curvilinear relationships. Then we built a model using all climatic variables, adding them sequentially according to their estimated deviance. Subsequently, the third-degree polynomial of the central latitude and longitude of each cell (trend surface analysis) as well as four geological variables (percentage of land with rocks or deposits, both acidic and basic) were included in the climatic model to account for other possible non-climatic factors. Significant variable functions ($P < 0.05$) were retained and results used to estimate the explanatory power of climatic variables

(%DevClim) and the combined explanatory power of the climatic, geological and other spatial variables (%DevTot). The difference in the percentage of deviance explained by both models (Dif-Dev = %DevTot − %DevClim) was calculated and used as a measure of the incapacity of the climatic variables to account for the RDs.

We also used a simple method of estimating RDs in the Iberian Peninsula (RD$_{CH}$) by building minimum convex polygons (i.e. the smallest polygon in which no internal angle exceeds 180° and contains all presence sites). The extension Convex Hulls v. 1.24 for Arcview 3.2 (ESRI Inc.) was used for this purpose. We used the statistica 6.0 package (StatSoft, Inc., 2004) for all statistical computations.

Equilibrium in a recently deglaciated area

To compare the degree of equilibrium of the current distribution with climatic variables for the subset of Iberian species that also occur in a recently deglaciated area we use Sweden, fully covered by the polar ice sheet during the Last Glacial Maximum and likely to had become available for recolonization only after the Younger Dryas, *c.* 12 ka (Lundqvist, 2004). The detailed distribution of the species of Dytiscidae occurring in both Sweden and Iberia was recorded on 50 × 50 km squares following Nilsson & Persson (1989). For each species the RD was estimated using convex hulls polygons, and the PD and RF of all species common to the two areas were computed as above.

RESULTS

Equilibrium at the European extent

When considering their entire known range, Iberian lentic species had significantly larger PDs ($U = 819.0$, $P = 0.003$), RDs ($U = 651.0 < 0.0001$) and RFs ($U = 754.5$, $P = 0.001$) than Iberian lotic species. The PO per country was also significantly higher for lentic than for lotic species ($U = 84.0$, $P < 0.0001$; Fig. 1).

Equilibrium in the refuge area

Well-surveyed sub-basins

Of the 208 defined Iberian SBs only 24 could be considered as WSSBs both for lotic and lentic inventories. These 24 WSSBs, ranging from 7 to 68 species, were mainly located in Iberian mountainous areas.

When the comparisons were made based on the distribution in these SBs there were no significant differences between Iberian lotic and lentic species for PD, RD and RF values ($P > 0.05$; Table 2). The PO for the SBs was also not significantly different between lotic and lentic species (Fig. 2).

UTM 100 km^2 cells

Lotic and lentic species were distributed uniformly across the UTM cells, without significant differences in the number of

presences and marginality (ENFA parameter). Species did differ significantly in the extent of their PDs, with lentic species having significantly larger PDs than lotic species, and marginally significant larger RD areas when estimated by convex hull polygons ($P = 0.052$). However, there were no significant differences in the

RF values, whatever the method used to estimate the RD of species (GLMs with reliable absences and convex hull polygons) ($P > 0.05$; Table 2).

The explanatory power of the climatic variables (%DevClim) was higher for lentic than for lotic species, although differences were only marginally significant ($P = 0.065$). The complete explanatory power of all the variables used (%DevTot) was significantly higher for lotic than for lentic species, as were the difference values (Dif-Dev) measuring the incapacity of climatic variables to explain RDs (Table 2).

Table 2 Comparison of different variables related with the distribution of lotic and lentic species at the regional (Iberian) scale (Mann–Whitney U-test).

	U	Z	P-level
N	1028.0	−1.372	0.170
M	1038.5	−1.299	0.194
T	1203.5	−0.144	0.886
PD	925.0	2.093	0.036*
RD_{GLM}	901.0	1.362	0.173
RD_{CH}	968.0	1.941	0.052
RF_{GLM}	1068.0	−1.092	0.275
RF_{CH}	956.0	1.876	0.061
%DevClim	938.0	−1.852	0.064
%DevTot	769.0	−3.054	0.002*
Dif-Dev	663.0	−3.928	0.000*

N, number of presences; M, marginality; T, tolerance; PD, potential distribution (km^2); RD_{GLM}, realized distribution using generalized linear models (GLMs) and reliable absences (in km^2); RD_{CH}, realized distribution using convex hull polygons (in km^2); RF_{GLM}, range filling using RD_{GLM} values; RF_{CH}, range filling using RD_{CH} values; %DevClim, percentage of deviance explained by GLMs using just climatic variables; %DevTot, percentage of deviance explained by GLMs using all the considered variables (climatic, geological and spatial variables); Dif-Dev, difference in the percentage of deviance explained by GLMs using climatic variables and models using all the considered variables.
The negative Z statistics indicates higher values for lotic than for lentic species.
*Significant differences at $P \leq 0.05$.

Equilibrium in a recently deglaciated area

Of the 99 Dytiscidae species occurring in the Iberian Peninsula included in the analyses (51 lotic and 48 lentic), 27 are also found in Sweden (20 lentic and 7 lotic). As predicted, the proportion of Iberian lentic species reaching Sweden is higher than lotic ones (exact Fisher 2×2 contingency table, $P < 0.015$). The average value of RF for the 27 species was 72.9%, and there were no significant differences between lotic and lentic species (Mann–Whitney U-test, $U = 51.0$; $P = 0.3$).

DISCUSSION

At a European scale, i.e. when a large part of the whole geographical range of the studied species was considered, we found clear differences between lotic and lentic species of Dytiscidae in the degree of equilibrium with current climate of the geographical distribution for all tested variables. These results were according to the expectations based on the assumed differences in dispersal ability (Ribera & Vogler, 2000; Ribera, 2008). Lentic species, hypothesized to have better dispersal abilities as they are forced to migrate when their more unstable habitat disappears, have better agreement between their PDs and RDs, and there are
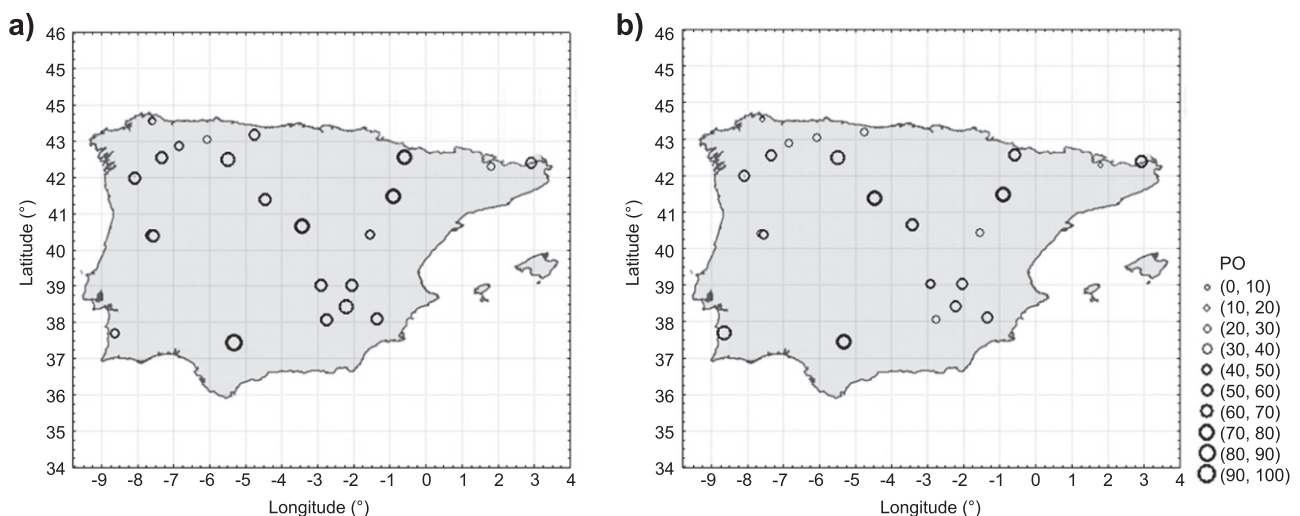
Figure 2 Geographical location of the number of recorded species in each Iberian well-surveyed sub-basin divided by the number of species with climatically favourable conditions (percentage of occupancy, PO). Each basin was represented by the centroid of its location, the size of the circles being proportional to the PO values: (a) lotic species, (b) lentic species.

fewer species missing from areas in which they could occur according to their PDs. This is in full agreement with differences found in Ribera *et al.* (2003) for the distribution of the whole European aquatic beetle fauna (*c.* 800 species), in which the species richness of lotic species was found to be related mostly to latitude (interpreted as a surrogate of 'time since deglaciation'), but that of lentic species to the extent of the land connection to adjacent considered regions (interpreted as a surrogate of the width of the 'gate' for faunal interchanges across the Pleistocene).

In the area less affected by Pleistocene climatic fluctuations (the 'refuge area') differences, if any, were much less pronounced, although results suggest a stronger influence of non-climatic factors in the distribution of the lotic, less-dispersive, species. A similar situation is found in the other extreme of the latitudinal gradient, in the recently deglaciated area, in which there were also no differences between the RF values of lotic and lentic species. This apparently paradoxical result is due to differences in the respective species pools which implies a significantly smaller proportion of lotic species: while in the Iberian Peninsula a complete regional fauna has persisted for long enough to have reached equilibrium, in Sweden we found a highly biased subsample of those species with dispersal abilities good enough to have reached a distant area that only recently became available for recolonization. The few lotic species with distributions large enough to encompass Iberia and Scandinavia are certainly good dispersers, and, as expected, show a high degree of equilibrium with environmental conditions through their range.

The lack of equilibrium of the current European distributions with environmental conditions has been proposed for different groups (e.g. Svenning & Skov, 2004; Araújo *et al.*, 2008; Munguía *et al.*, 2008), and is usually explained by post-glacial dispersal limitation. Detailed data for the southern peninsulas are far scarcer, but available results also suggest the determinant role of dispersal: groups with poor dispersal abilities, such as freshwater fishes, are further away from equilibrium than groups with better dispersal abilities, such as Trichoptera (Filipe *et al.*, 2009, and Bonada *et al.*, 2005, respectively). However, differences in dispersal ability have rarely been associated with general ecological or biological characteristics of the species, such as their habitat preference. We have shown that the preference of freshwater invertebrates for standing or running water habitats, a well-known and easily measurable ecological characteristic, may be associated with large-scale geographical patterns of response to climatic changes. Our conclusions are admittedly derived from indirect data (the current distribution of the species), and as such it is difficult to exclude alternative explanations. Future estimations of dispersal rates or the study of Quaternary fossil records to explore whether lentic species experience more frequent and intense range shifts than lotic species may provide further evidence. Although the available fossil data have serious limitations, both temporal (covering in their vast majority only the last glacial cycle) and geographical (with virtually no records from the most species-rich areas in the Mediterranean), a recent study on the Late Quaternary beetle data (Abellán *et al.*, 2011)

shows that most of the species belonging to the families Dytiscidae and Hydraenidae which are known to have experienced very large (continental scale) range shifts are exclusively lentic, in agreement with our conclusions.

Can we obtain an effective measure of the species fundamental niche from presence data?

Understanding environmental species limits is fundamental if we aim to estimate their PD (Soberón & Peterson, 2005). The estimation of the environmental limits of a species is not a simple task, as even if all current populations of a species were known (i.e. covering all observed environmental extremes), these estimated limits could be narrower than the real ones (Jiménez-Valverde *et al.*, 2011). This is especially the case when we consider areas where a species has become extinct for reasons other than climatic ones, or potentially suitable regions still not colonized due to limited dispersal.

When the objective is to obtain a geographical representation of the 'fundamental niche' it is necessary to consider that dispersal limitations, local extinctions, biotic interactions (Colwell & Rangel, 2009; Soberón & Nakamura, 2009) or the environmental conditions at any given time (Jackson & Overpeck, 2000) may mask the full spectrum of climatic requirements in which the species can maintain source populations (Araújo & Pearson, 2005; Welk & Bruelheide, 2006). These caveats are ultimately related to two of the main shortcomings of these modelling techniques when used to represent the PD: that the environmental conditions in the unoccupied localities are uninformative for estimating PDs (Jiménez-Valverde *et al.*, 2011), but mainly that the environmental conditions in the occupied localities can only provide a partial representation of the fundamental niche of the species (Colwell & Rangel, 2009). Due to these limitations there is some risk of bias; the estimated PD of species with lower dispersal capabilities could be underestimated, and thus it may be wrongly considered that they are closer to equilibrium than they really are. The smaller estimated PDs of the lotic species in the Iberian Peninsula could be a consequence of this methodological problem, suggesting that differences with lentic species may be larger than detected (i.e. the potential bias would run against our hypothesis). The fact that the non-climatic variables accounted for a higher percentage of deviance of the Iberian distribution of lotic species points to the same differences.

Therefore, the PD of a species is a hypothetical concept that could be partially evaluated using new presence information, or preferably with either physiological data (Kearny, 2006), translocation experiments or additional evidence from species invasions or fossil data (Dawson *et al.*, 2011; Jiménez-Valverde *et al.*, 2011). Although we have tried to minimize these biases by trying to include the environmental extremes that species can tolerate (including records of locations able to represent the climatically extreme conditions of each species; Sánchez-Fernández *et al.*, 2011), we could still have underestimated the PD of lotic species, generally with more restricted ranges (Ribera & Vogler, 2000). Therefore, results obtained from these approaches should be always considered with caution, especially if we aim to interpret

them in absolute terms. However, our aim is to compare between lotic and lentic species, and this potential bias, although to a different degree, appears in both groups. As stated above, the lack of differences could be caused by this methodological problem, but this bias will run against our hypothesis, so the fact that we did find that lotic species are significantly further from equilibrium than lentic species at a European scale is a conservative conclusion, and should be considered as strong evidence of the differences in dispersal ability of the two groups of species.

Equilibrium and the ability to cope with climate change

Although departures from equilibrium could reflect a number of phenomena, such as biotic interactions, edaphic or other non-climatic environmental factors (Pearson & Dawson, 2003), our results are congruent with other results found for different European groups (e.g. Svenning & Skov, 2004; Araújo *et al.*, 2008), and point to post-glacial dispersal limitation as a key factor in explaining the current distribution of the European biota (Johnstone & Chapin, 2003; Svenning & Skov, 2005). This is not only an important theoretical issue, but also an issue of crucial importance for predicting the effects of the impending near future climatic changes (Araújo *et al.*, 2004; Thomas *et al.*, 2004). Models directed to estimate the RDs of species generally assume that species distributions are at equilibrium with current climate (Pearson & Dawson, 2003), yet the validity of this assumption varies substantially across different groups of organisms (Araújo & Pearson, 2005). We show here that for freshwater invertebrates this variation could be linked to dispersal differences mediated through habitat preferences.

Concluding remarks

Present-day species distributions are determined by a mixture of ecological and historical filters acting on several spatial and temporal scales. In a context of the palaeoclimatic history of Europe, the historical factors seem to play a more important role in shaping species distributions, and especially at large scales. The Iberian Peninsula, as well as other Mediterranean regions, can be considered the starting line of a process of post-glacial recolonization. In this context, our results show that large-scale historical constraints have a stronger effect on Iberian lotic species than on lentic species. We hypothesize that in glacial refuges, as the Iberian Peninsula, species could have persisted for long enough under largely stable conditions to erase the difference in RF caused by their different dispersal abilities. As species climate equilibrium is inversely related to species abilities to track future climate changes, it should be expected that Iberian lotic species, among which are most of the narrow-range endemics, will have more difficulties in coping with rapid climate change.

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SUPPORTING INFORMATION

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

Appendix S1 List of species, indicating their habitat preferences.

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BIOSKETCH

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