

Habitat stability affects dispersal and the ability to track climate change

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Habitat persistence should influence dispersal ability, selecting for stronger dispersal in habitats of lower temporal stability. As standing (lentic) freshwater habitats are on average less persistent over time than running (lotic) habitats, lentic species should show higher dispersal abilities than lotic species. Assuming that climate is an important determinant of species distributions, we hypothesize that lentic species should have distributions that are closer to equilibrium with current climate, and should more rapidly track climatic changes. We tested these hypotheses using datasets from 1988 and 2006 containing all European dragon- and damselfly species. Bioclimatic envelope models showed that lentic species were closer to climatic equilibrium than lotic species. Furthermore, the models over-predicted lotic species ranges more strongly than lentic species ranges, indicating that lentic species track climatic changes more rapidly than lotic species. These results are consistent with the proposed hypothesis that habitat persistence affects the evolution of dispersal.

Keywords: bioclimatic envelope models; damselflies; dragonflies; freshwater; odonata; range-filling

1. INTRODUCTION

Habitat is an important determinant of the evolution of life-history traits and hence the ecological characteristics of species [1]. Broadly classified, freshwater habitats can be divided into standing (lentic habitats) and running water bodies (lotic habitats). Lentic habitats are, on average, less persistent over time than lotic habitats [2,3], and this should have consequences for the evolution of dispersal abilities of lentic and lotic species. Specifically, we hypothesize that if their habitats are more likely to disappear within shorter

periods of time, lentic species should have evolved a higher propensity for dispersal than lotic species [3]. Support for this hypothesis—hereafter referred to as the habitat–stability–dispersal hypothesis (HSDH)—comes from several studies, which showed that lentic species have larger range sizes [4] and a lower genetic diversity among populations [5,6] than lotic species. Furthermore, post-glacial re-colonization of northern Europe was probably faster for lentic than for lotic species [7–9].

Here, we test the HSDH for European dragonflies using bioclimatic envelope models (BEMs). BEMs are useful for projecting potential ranges based on distribution data, and are extensively used for projecting future species distributions under climate change [10]. If contemporary climate is an important determinant of species distributions, distributions of species with stronger dispersal abilities should be closer to equilibrium with contemporary climate [11]. Therefore, these species should show higher levels of range filling and should be able to track climatic changes more rapidly. Range filling, the ratio of the observed versus potential range size given by BEMs (O/P ratio), has been used to infer the degree of climatic equilibrium [12–14]. According to the HSDH, lentic species should show a higher degree of climatic equilibrium (indicated by higher O/P ratios), and a higher ability to track climatic changes, than lotic species. If so, then BEMs should over-predict lotic species ranges more strongly than lentic species ranges when comparing range changes with climatic changes between two distinct time periods.

2. MATERIAL AND METHODS

We used digitized distribution maps drawn in 1988 and 2006 for all European dragon- and damselfly species [15,16] ('dragonflies' hereafter; electronic supplementary material, table S1). Maps were transferred into a Universal Transfer Mercator 50 × 50 km grid of Europe (<http://www.ibiochange.mncn.csic.es/>; [17]). We further compiled larval habitat preferences (lentic and lotic) and phylogenetic data for all species. The final dataset included 88 species (see the electronic supplementary material for details).

We ran BEMs for all species using BioMod [18] with mean annual temperature and total annual precipitation as climatic variables [19], and using seven different modelling techniques (see figure 1 for the BEMs used and electronic supplementary material, figure S1 for climate maps and details on data preparation). Model outputs were translated into presence–absence maps using receiver-operating-characteristic- (ROC-) and Kappa-optimizing thresholds (for more details on BEM techniques and standard features of BioMod, see [18]).

To compare the levels of range filling between lentic and lotic species, we calculated the O/P ratio for each species and time period [12,13] (see the electronic supplementary material, figure S2 for an illustration of the modelling steps and calculations). To calculate the O/P ratio for a species in 1988 for example, we used its observed distribution in 1988 and climatic data for 1988 to calibrate a BEM, from which we obtained the potential distribution in 1988. Then the observed range size was divided by the potential range size, to obtain the O/P ratio (electronic supplementary material, figure S2a). The effects of habitat type on O/P ratios were assessed with Wilcoxon rank sum tests.

To assess how well species tracked climatic changes between 1988 and 2006, we also projected potential distributions for 2006 based on the models calibrated in 1988. To test whether lotic species showed a stronger tendency to over-prediction, we calculated model sensitivities and specificities comparing projected and observed distributions for 2006 (see the electronic supplementary material, figures S2b and S3 for further details).

We also accounted for possibly confounding effects of phylogeny and range size (see the electronic supplementary material). All analyses were run in R (v. 2.12.0; [20]).

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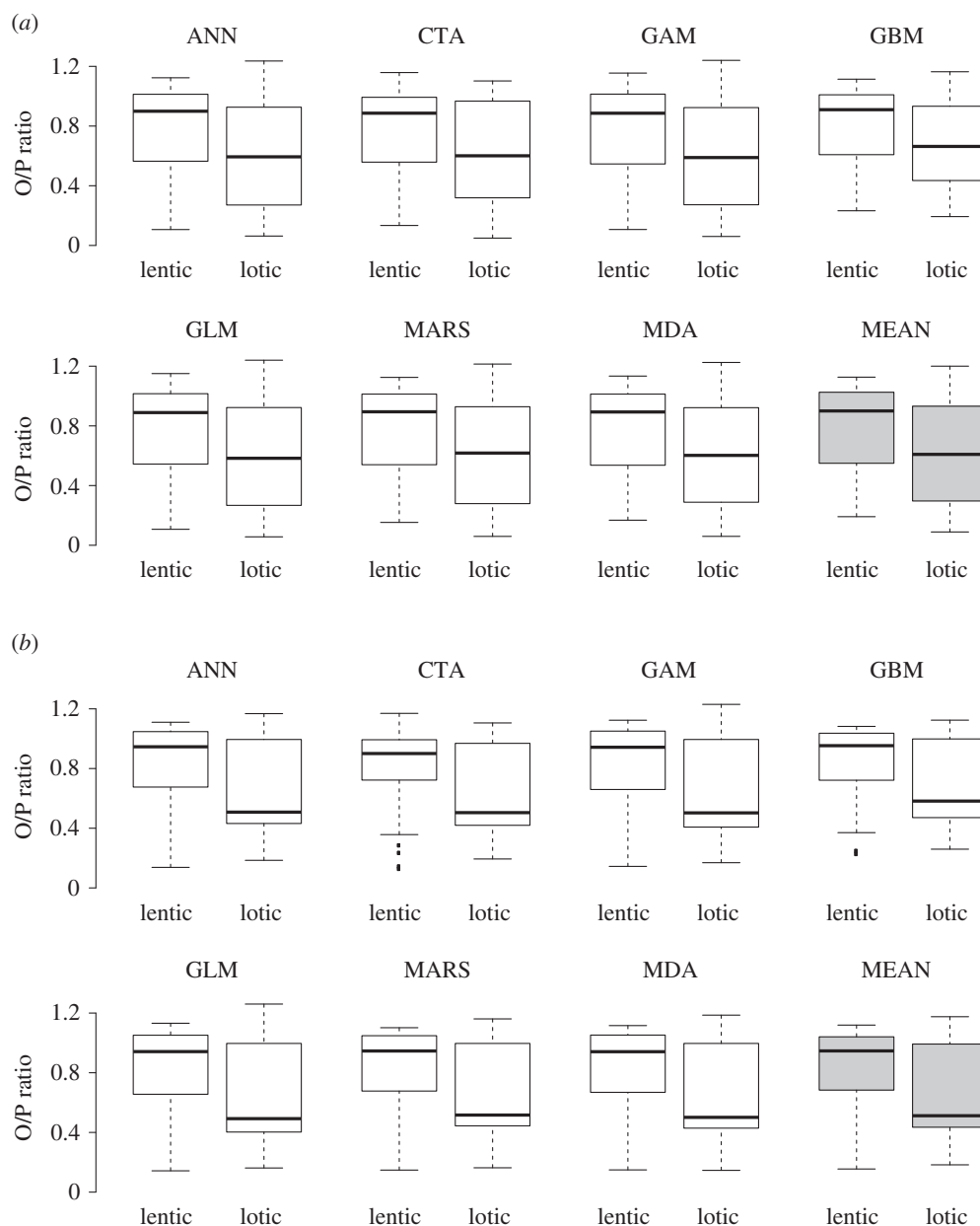


Figure 1. Effect of habitat type on O/P ratios of European dragonflies using different BEM techniques ((a) 1988 and (b) 2006). O/P ratios were averaged across all lotic and lentic species, respectively. Differences were significant ($p < 0.05$, Wilcoxon rank sum test) in all cases except CTA in 1988 ($p = 0.068$). Arithmetic means across the seven BEM techniques are indicated in grey ('MEAN'). Projected range sizes were transformed into presences and absences from probabilities of occurrence using ROC-optimizing thresholds. BEM technique acronyms: ANN, artificial neural networks; CTA, classification tree analyses; GAM, generalized additive models; GBM, generalized-boosting models; GLM, generalized linear models; MARS, multiple adaptive regression splines; MDA, mixture discriminant analyses. See the electronic supplementary material, figure S4 for calculations using Kappa-optimizing thresholds, and an explanation of box-and-whisker plots.

3. RESULTS

O/P ratios were higher for lentic than for lotic species (figure 1); this pattern was largely independent of the BEM method used, even though the strength of the difference may vary in some cases, especially depending on the threshold technique used (electronic supplementary material, figure S4). When accounting for phylogeny, the effect of the habitat type on O/P ratio remained significant in only a few cases, but the overall trend (higher O/P ratio for lentic species) remained consistent in most comparisons (electronic supplementary material, table S2). Range size had an influence on

O/P ratio, but in most cases, especially in the first to third range-size quartiles, lentic species still showed higher O/P ratios (electronic supplementary material, figures S5–S8).

Comparisons of observed and projected distributions for 2006 showed a stronger tendency for over-prediction (smaller specificities) for lotic than lentic species ranges in the vast majority of cases (figure 2). When accounting for range size, this tendency towards a stronger over-prediction for lotic species was mostly supported (electronic supplementary material, figures S9–S10).

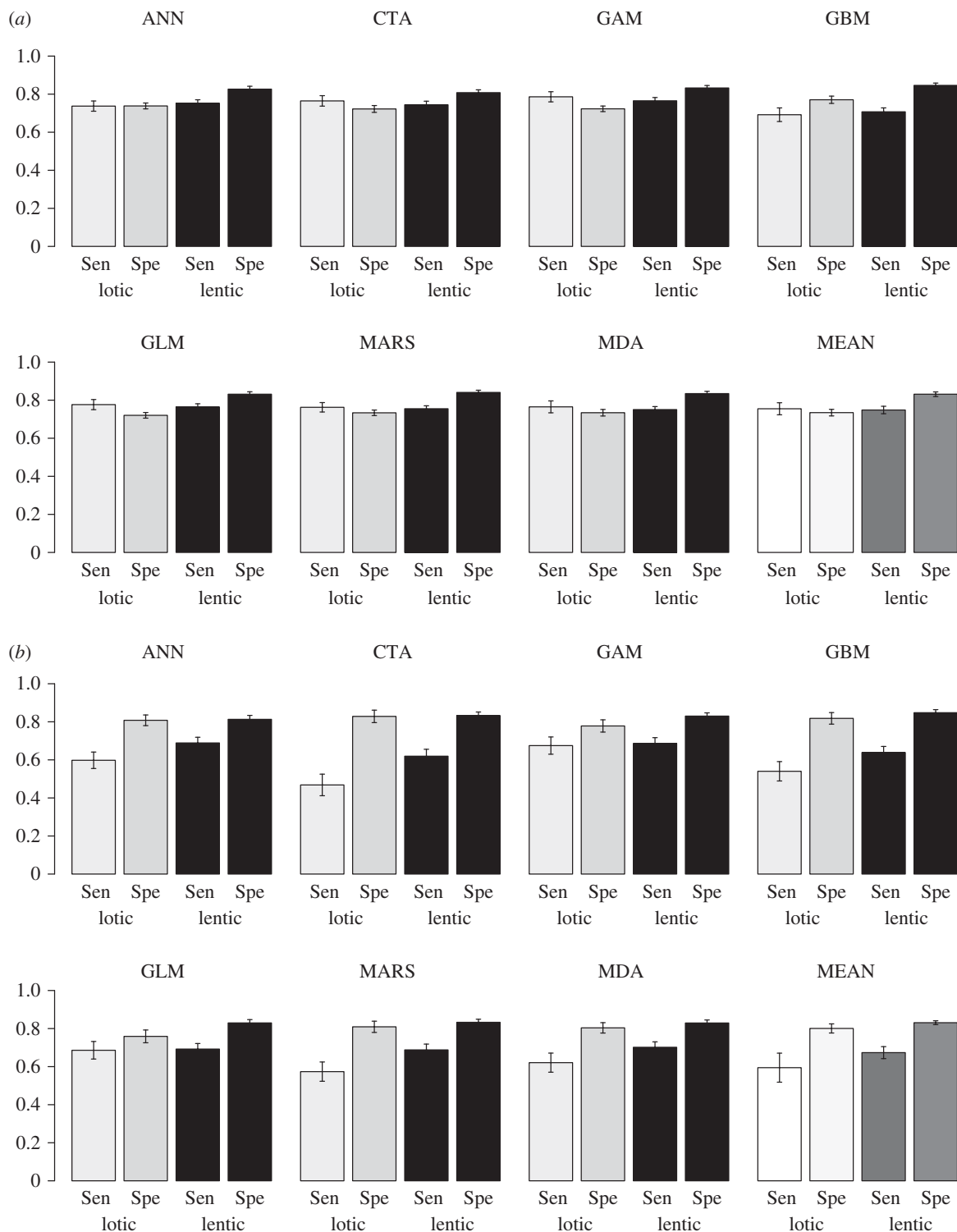


Figure 2. Sensitivity (Sen) and specificity (Spe), averaged across all lotic (grey bars) and lentic (black bars) dragonflies, for different BEM techniques, using (a) ROC- and (b) Kappa-optimizing thresholds (error bars indicate the s.e. of the mean; see §2, electronic supplementary material, methods and figures S2b and S3 for further details). Arithmetic means across the seven BEM techniques are presented in the last panels ('MEAN', error bars here indicate the s.d.).

4. DISCUSSION

Higher O/P ratios in lentic dragonflies support the hypothesis that lentic species distributions are closer to climatic equilibrium than lotic species distributions. This is underlined by the tendency towards stronger over-prediction of lotic species ranges when comparing projected and observed ranges for 2006. Both findings support the HSDH, suggesting that lower habitat

stability selects for stronger dispersal abilities [3,4] (see the electronic supplementary material, discussion for details on the effects of range size, phylogeny, threshold technique and on other deviances from the overall pattern).

The observed differences in range filling could be confounded by habitat availability, e.g. in cases where climatic conditions are suitable but no freshwater

habitats are present. This is assumed to be the case if habitat availability is a strong predictor of freshwater species richness. However, for the geographical extent and resolution of our study, the distribution of freshwater bodies is a weak predictor of dragonfly species richness [21]. Furthermore, the explanatory power of habitat availability for species richness of lotic habitats is exceptionally low [9]. Therefore, the confounding effect of habitat availability should be rather negligible. The influence of other factors such as pollution, anthropogenic land-cover changes or predator occurrence [22] could also affect the results. However, as these factors either should not differentially affect lotic and lentic habitats (land-cover changes) or most likely act at finer scales than the scale of our analyses (pollution and predators), we assume such effects to be of minor importance for the extent and resolution of our analyses [23].

Our results support the findings of previous studies that lotic species are weaker dispersers than lentic species [4–6]. If true, lentic species should be able to track climatic changes more rapidly than lotic species [24]. Our analyses support this prediction, along with studies that relate contrasting large-scale diversity patterns in lentic and lotic species to their post-glacial re-colonization capacity [3,7,8]. It is widely accepted that the glacial–interglacial cycles of the Pleistocene are still mirrored in contemporary patterns of species richness in Europe [25]. As dragonflies are assumed to be strong dispersers compared with other invertebrates, they are also expected to be able to track climatic changes more successfully [26,27]. The differential dispersal abilities of dragonflies adapted to different habitat types suggest that similar generalizations for entire taxa may be misleading, though.

Dispersal ability is of major importance for species to respond successfully to climate change (but see [28]). BEM studies projecting species distributions under climate-change scenarios usually adopt very coarse dispersal assumptions, i.e. unlimited or no dispersal. That these assumptions are unrealistic is widely acknowledged, but as long as species-specific dispersal data are vastly lacking, multi-species BEMs rely on such simplifications. If habitat is indeed a generally important determinant of dispersal ability [1], establishing even simplified links between habitat preferences, habitat stability and dispersal ability may, with an accordant model parameterization, help to overcome the over-simplistic dispersal assumptions currently used in models that project species responses to climate change.

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