Adult activity and temperature preference drives region-wide damselfly (Zygoptera) distributions under a warming climate

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We analysed a recently completed statewide odonate Atlas using multivariate linear models. Within a phylogenetically explicit framework, we developed a suite of data-derived traits to assess the mechanistic distributional drivers of 59 species of damselflies in New York State (NYS). We found that length of the flight season (adult breeding activity period) mediated by thermal preference drives regional distributions at broad (10^5 km^2) scales. Species that had longer adult flight periods, in conjunction with longer growing seasons, had significantly wider distributions. These intrinsic traits shape species’ responses to changing climates and the mechanisms behind such range shifts are fitness-based metapopulation processes that adjust phenology to the prevailing habitat and climate regime through a photoperiod filter.

1. Introduction

Traits-based mechanistic approaches for understanding how climate change affects insect distributions have recently emerged, and when undertaken in a phylogenetic framework, reveal the biological mechanisms underlying landscape-level patterns. This is because the traits are known to affect individual fitness and therefore metapopulation processes such as extinction and colonization [1,2]. Yet, the fitness-based models that can test for the cause of observed range changes are very difficult to construct, in part because repeated presence–absence data are required at fine spatial resolutions and across large areas, in order to compile comprehensive up-to-date species inventories. Furthermore, intimate knowledge of species’ biological traits and how they relate to fitness, as well as robust phylogenetic frameworks, are practically non-existent for most freshwater macroinvertebrates [3].

Without clear identifiable biological outcomes to climate change effects, resource management decision-making is left largely to guesswork. Illustrating this, over the past century, the climate in New York State (NYS) has warmed up considerably [4]. Remnant boreal forests embedded within temperate zones, such as the iconic Adirondack massif, are projected to have very short climate residence times and fast velocities of temperature change [5,6]. Already this has translated into meaningful changes for resource managers because plant hardiness guidance has altered significantly since 1990, and flagship native coldwater sport fishes and some boreal birds have required interventions to stave off extirpations [7,8].

We know that longer growing seasons are having myriad effects on forested ecosystems in east-central North America including range shifts of Odonata (damsel- and dragonflies), and observations of new species arriving from the south are commonplace [9,10]. Damselflies have, in fact, demonstrated some of the fastest range margin movements, nearly tracking shifting isotherms [11,12], and a preliminary traits-based analysis [13] found that cold-adapted
stenothermic odonates would be the ‘losers’ under modern warmer climates. However, much uncertainty remains over the geographical scales at which certain traits like dispersal ability might predominate [3], or even whether we can predict the limits that intrinsic traits impose upon distributional shifts [14].

To investigate this problem, we developed a suite of phylogenetically explicit data-derived traits in order to test the mechanistic drivers (figure 1; electronic supplementary material, figure S1) that have shaped damselfly distributions in NYS, a large (141 000 km²) well-watered and ecologically diverse region, rising from sea level to 1630 m. As predators in both aquatic and terrestrial systems, damselflies play a strong role in structuring communities, providing tangible ecosystem services in the form of insect pest control. Based on their hypothesized ability to track isotherms, we highlight the uniquely suited aspects of this taxon as barometers [12] of rapid ongoing landscape-scale climate and habitat changes.

2. Material and methods

We gained an understanding of the fine-scale distributions of all odonates ever documented from NYS during our 5 year Atlas [17]. This citizen science effort involved hundreds of volunteers following a standardized protocol designed to locate breeding populations. Nearly 4400 geo-referenced surveys were conducted at approximately 2170 unique site locations (March to November, 2005–2009) across the state. Data were submitted to a coordinator to ensure standardization and expert verification of vouchers. For this analysis, we focused on the 59 known damselflies, many of whom are on their overall North American range margins here (electronic supplementary material, figure S1); see [9,17] for further details.

We measured distribution as the total number of individual site records. This metric integrated a species’ range extent and frequency of occurrence across the state over the 5 year period (table 1). When logarithmically transformed, it was strongly correlated to coarser measures of distribution such as latitudinal extent and number of occupied counties ($r = 0.88$). We coded five explanatory variables known to be related to damselfly distributions including proxy traits for dispersal, physiology, habitat and phenology. For consistency, we used the same three broad larval habitat designations (lentic, lotic and generalist) in [18] to categorize a species’ aquatic habitat type. Adult breeding affinity was scored by reviewing our raw site records, first determining which were marked by the surveyor into each of five broad habitat types: (i) seeps (lotic), (ii) streams and creeks (lotic), (iii) rivers (lotic), (iv) ponds and lakes (lentic), and (v) bogs, fens, marshes and swamps (lentic). Lentic and lotic habitat subtypes were then collapsed and species occurring in both broad types were considered generalists.

We determined the number of flight days from the species’ phenology charts in [17] modified to remove extraneous exuvial records. This adult flight season is a terrestrial activity period that varies widely among species (a few days to several months) centred around the breeding cycle. Traits correlated with dispersal ability (wing loading) were taken from the literature. For thermal preference we extracted the geo-referenced elevations [17] for each species’ records and used the maximum elevation which was strongly correlated ($r = 0.98$) with the entire occupied elevational range. So a higher maximum elevation...
Table 1. Five proxy measurements for damselfly species’ traits known to be related to distributions.

<table>
<thead>
<tr>
<th>species trait</th>
<th>measurement</th>
<th>reference</th>
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<tbody>
<tr>
<td>physiological tolerance</td>
<td>max. elevation detected 2005 – 2009 (m)</td>
<td>[13,17]</td>
</tr>
<tr>
<td>habitat preference</td>
<td>larval morphology: lentic, lotic, generalist (lentic and lotic)</td>
<td>[18,19]</td>
</tr>
<tr>
<td>aquatic</td>
<td>adult breeding affinity: lentic, lotic, generalist</td>
<td>[17]</td>
</tr>
<tr>
<td>terrestrial</td>
<td></td>
<td></td>
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<tr>
<td>breeding season phenology</td>
<td></td>
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</tr>
<tr>
<td>length of flight season (2005 – 2009)</td>
<td>max. site record date minus min. site record date in any year, 2005 – 2009 (no. days)</td>
<td>[17]</td>
</tr>
<tr>
<td>dispersal ability</td>
<td>max. length female hindwing (mm)/max. total body length of female (mm)</td>
<td>[19]</td>
</tr>
<tr>
<td>wing loading</td>
<td></td>
<td></td>
</tr>
<tr>
<td>distribution (response)</td>
<td>no. overall site records total no. of unique site × date surveys of species’ presence (2005 – 2009)</td>
<td>[17]</td>
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Demonstrated population viability across a much broader range of thermal microclimates compared with a stenothermic damselfly that is only found within a narrow elevation zone [13].

Using a generalized linear model with a Gaussian error distribution, we explored the strength of these five key predictors on the distribution of 54 damselflies (we omitted species with no records) documented during our Atlas. The continuous variables were untransformed, with the exception of distribution (log[number site records]). We also regressed predictors on an independently assembled dataset of pre-Atlas county-level damselfly distribution records in NYS [20]. All analyses were conducted in R v. 3.02.

3. Results

Number of flight days and maximum elevation were the only significant predictor variables in our analysis. A linear regression model with only these two factors explained 71% of the variation in the distribution ($F_{50.2} = 64.04$, adj. $r^2 = 0.71$) of damselflies in NYS (figure 2). These physiologically proxy traits for adult breeding season length and temperature preference also explained most of the pre-Atlas variation in distribution ($F_{50.3} = 49.61$, adj. $r^2 = 0.65$). The inclusion of family as a phylogenetic control variable did not appreciably alter any of the $r^2$ values. As a further check, we mapped traits onto the phylogeny (electronic supplementary material, figure S1) and though damselflies demonstrate strong biogeographic phylogenetic structuring [9], trait states were not clustered in certain clades, but instead were well represented across the tree.

4. Discussion

Damselflies possess traits such as more efficient wing designs that presumably confer greater dispersability within groups, thus shaping range sizes [21]. However, we detected no significant effects of wing loading on species’ distributions. Nor did we find a significant relationship for larval or adult habitat preference, whether or not covariates and phylogeny were accounted for.

By contrast, a large body of work [18,22,23] posits that stronger dispersal tendencies arise in lentic odonates because of greater habitat instability compared with lotic habitats; thus they have larger ranges and should be able to track climate change more closely. Unlike the above studies, we retained the generalists in our analysis and still we did not find any effect of habitat type on distribution because in this system at least, dispersal does not appear to be limiting. Yet as a region, the size of NYS is large enough that differences in dispersal ability are thought to play a strong role in freshwater macroinvertebrate species’ distributions [3], and this does appear to be the case at larger continental scales [18,21–23]. However, at more tractable resource management-oriented scales where most decisions are made (up to approx. $10^5$ km$^2$), damselflies would seem to have more than enough inherent capacity to move around.

Rather, we found strong support for length of the adult flight season (figures 1 and 2) as modulated by thermal preference to be the prime drivers of damselfly distributions. This is because a species’ adult breeding season phenotype results from natural selection to optimize the period of activity and reproduction in a given environment (figure 1; [24]). Flight duration during the breeding season integrates many fitness-based life-history traits that are ultimately temperature driven; however damselfly reproductive activity might conceivably be limited by predators or senescence. But fig. 11.68 in [16] clearly details instead how adult survival is controlled mostly by ‘random’ weather events such that more adult activity leads to greater lifetime reproductive success.

Two studies [14,23] found only weak support for flight season as a distributional driver in odonates, but eco-physiological traits were not included in the analyses, which we argue for these ectothermic insects is essential [2]. Others have found thermally mediated [1] activity-driven results for terrestrial ectotherms [25], and it is well known that thermal tolerance is a primary driver of range size for many insects, including odonates [2,12]. But because larval activity (diapause) in Odonata is also a function of photoperiod (especially in north-temperate nates) [2,12]. However, larval activity (diapause) in Odonata is also a function of photoperiod (especially in north-temperate latitudes), photoperiodism acts as a filter for the solely temperature-driven phenological outcomes (figure 1; [15,16]). It would nevertheless be instructive to test our novel findings over varying geographical areas and against finer scale traits like $CT_{\text{max}}$, known dispersal distances and finer oviposition–habitat associations, but these detailed measurements currently exist in only a few cases.

As NYS’s colder boreal ecoregions slide towards a more temperate climate regime, they become largely thermally
unsuitable for many of the cold-adapted specialists, forcing them into micro-refugia [7,8]. This pattern was evident during our surveys because the boreal (rear edge) damselflies were primarily confined to places with relatively short growing seasons. Boreal odonate community reassembly can happen on fast (decadal) time scales, meaning that even large temperate-embedded boreal ecosystems in the mid-latitudes could see notable changes in their insect fauna in the coming years [26].

Data accessibility. See [17].

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Conflict of interests. No competing interests.

References


Figure 2. Semi-log scatterplot of the number of flight days (adult breeding season length) versus damselfly distribution in NYS (2005–2009). Each data point is a species.