# Dispersal, niche breadth and population extinction: colonization ratios predict range size in North American dragonflies

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## Summary

**1.** Species' range sizes are shaped by fundamental differences in species' ecological and evolutionary characteristics, and understanding the mechanisms determining range size can shed light on the factors responsible for generating and structuring biological diversity. Moreover, because geographic range size is associated with a species' risk of extinction and their ability to respond to global changes in climate and land use, understanding these mechanisms has important conservation implications.

**2.** Despite the hypotheses that dispersal behaviour is a strong determinant of species range areas, few data are available to directly compare the relationship between dispersal behaviour and range size. Here, we overcome this limitation by combining data from a multispecies dispersal experiment with additional species-level trait data that are commonly hypothesized to affect range size (e.g. niche breadth, local abundance and body size.). This enables us to examine the relationship between these species-level traits and range size across North America for fifteen dragonfly species.

**3.** Ten models based on *a priori* predictions about the relationship between species traits and range size were evaluated and two models were identified as good predictors of species range size. These models indicated that only two species' level traits, dispersal behaviour and niche breadth were strongly related to range size. The evidence from these two models indicated that dragonfly species that disperse more often and further had larger North American ranges.

**4.** Extinction and colonization dynamics are expected to be a key linkage between dispersal behaviour and range size in dragonflies. To evaluate how extinction and colonization dynamics among dragonflies were related to range size we used an independent data set of extinction and colonization rates for eleven dragonfly species and assessed the relationship between these populations rates and North American range areas for these species.

**5.** We found a negative relationship between North American range size and species' extinction-to-colonization ratios. Our results indicate that metapopulation dynamics act to shape the extent of species' continental distributions. These population dynamics are likely to interact with dispersal behaviour, particularly at species range margins, to determine range limits and ultimately species range sizes.

**Key-words:** dispersal limitation, extinction–colonization, freshwater connectivity, geographic distribution, niche breadth, Odonata, range limits, range size

## Introduction

Among extant species geographic range sizes vary over 12 orders of magnitude (Brown, Stevens & Kaufman 1996). This extraordinary level of variation in range area reflects important differences in species' traits resulting from their evolutionary and ecological history. Consequently, a better understanding of the mechanisms causing variation in range size could provide insight into the fundamental processes that structure and maintain biological diversity. Understanding factors determining range size is also increasingly critical in the face of widespread habitat destruction and climate change. Range size is an important predictor of global extinction risk (Purvis *et al.* 2000; IUCN 2001; Gaston 2009) and the factors determining species range limits likely affect the capacity of species to alter ranges in response to climate change (Thomas *et al.* 2001). Thus, an understanding of factors limiting species' range areas can provide important insights for evolutionary ecology and for conservation biology.

Despite the obvious importance of understanding the association between species traits, population characteristics and range size, we know remarkably little about the relative importance of these factors limiting species ranges for most taxa (Gaston 2003, 2009). Studies that have examined the relationship between species traits and range size report mixed results with some finding that species traits are predictive of range size (Juliano 1983; Gutierrez & Menendez 1997; Rundle, Bilton & Foggo 2007; Rundle *et al.* 2007) while others find no relationship (Lester & Ruttenberg 2005; Lester *et al.* 2007). The relationship between species traits and range expansions in recent decades can also provide insights into how these traits may act on determining range size. Recent work suggests that while species traits, including measures of species mobility (Pöyry *et al.* 2009), can be related to the extent of range expansion, clear patterns about what those traits are and how they act to determine the extent of spread remain elusive (Angert *et al.* 2011; Chessman 2012).

Key traits expected to be related to range size include species niche breadth, body size, abundance and dispersal ability (Gaston 2003). Among these traits, however, the role of dispersal has rarely been directly tested (Gaston 2003; but see: Gaston & Blackburn 2003). This results in part from the difficulties associated with acquiring comparable data on dispersal behaviour in a sufficient number of species to make robust comparisons. Consequently, previous tests examining the relationship between dispersal and range size have primarily utilized proxy measures of dispersal ability, most commonly based on morphology (e.g. dispersal mode: Juliano 1983; Gutierrez & Menendez 1997; or body size: Rundle *et al.* 2007; Rundle, Bilton & Foggo 2007), but also time available for dispersal (Lester & Ruttenberg 2005; Lester *et al.* 2007; Paul *et al.* 2009). These proxies for dispersal ability generally have exhibited some (Paul *et al.* 2009) but relatively limited success in predicting species range sizes (Lester *et al.* 2007). However, studies using such proxies rely on the implicit assumption that dispersal ability is the dominant limiting factor in dispersal patterns, but species capable of extensive movement may nonetheless exhibit a limited behavioural propensity to disperse (e.g. migratory birds Gaston & Blackburn 2003; Wheelwright & Mauck 1998). In species where dispersal ability and dispersal behaviour are even partially decoupled, tests of the relationship between dispersal proxies that reflect primarily dispersal ability and range size may be weak tests of this relationship. We addressed this gap by examining the relationship between range size across North America and dispersal behaviour measured for fifteen species (Table S1, Supporting information) of dragonfly in a common landscape using an experimental habitat approach (McCauley 2007). We also examined how other species traits including niche breadth, body size, population abundance and relative wing size was related to the size of species' North American ranges for the same species set. The latter trait, relative wing size, allowed us to evaluate the relative extent to which morphology and behaviour predicted patterns of range size.

Dispersal is expected to be positively related to range size because it facilitates species reaching and colonizing suitable habitat (Gaston 2009). Across long temporal scales, dispersal determines the rate at which species spread into suitable habitats following speciation (Paul *et al.* 2009) or recovery from major disturbance events such as glaciation (McLachlan, Clark & Manos 2005; Bialozyt, Ziegenhagen & Petit 2006). Dispersal limitation can also restrict species ranges by limiting their ability to maintain their populations in regions where patch colonization rates are lower than extinction rates (Holt & Keitt 2000; Gaston 2009). This latter effect may especially important in taxa such as dragonflies, which occupy inherently patchy habitats (water-bodies set within an unsuitable terrestrial matrix), which are often temporally unstable through much of the life cycle. Many of these habitats experience relatively high levels of disturbance, principally from drying and long-term surveys of larval dragonfly populations indicate that their populations are highly dynamic, experiencing frequent local extinction and recolonization events (McCauley *et al.* 2008). We used a data set, independent of the data set on species traits discussed above (Table S1, Supporting information), to evaluate the relationship between extinction and colonization dynamics and range size. This data set has extinction and colonization rates for 11 species of dragonflies, sampled as larvae in 36 lakes and ponds surveyed across 13 years. We used these data to test for a relationship between species North American range areas and their observed extinction-to-colonization ratios. This analysis provided insights into the relationship between population dynamics and range size, which can provide insights into how species traits might link these dynamics to range size.

The combination of data from these two independent data sets (Table S1, Supporting information) allowed us to make two unique tests about how species traits and population dynamics are related to species range extents. In the first, we examined the relationship between North American range size and species characteristics, including local dispersal behaviour for 15 dragonfly species. The second data set allowed us to evaluate whether a putative mechanism relating dispersal behaviour and range size, the dynamics of colonization and extinction, was correlated with range size for 11 species of dragonflies (Table S1, Supporting information).

## Materials and methods

### MEASURING RANGE AREA

Dragonfly distributions across North America have been well documented, and these have been compiled in a central data base, OdonataCentral (Abbott 2007). Range size was measured across North America for each of the 17 species included in the two data sets (Table S1, Supporting information) using these records. A minimum convex polygon was fitted around distribution records to measure each species' range area. Ranges excluded outliers, which we defined as single collection records that fell at least 500 km from another set of points. Whether species had outlier points was noted and if so how many outliers (number of outliers varied between 0 and 2). There were no correlations between the number of outliers and range size or any of the variables expected to be related to range size explored in this study (all $P > 0.1$).

### QUANTIFYING SPECIES TRAITS

We compiled species-level traits for the 15 species in the first data set (Table S1, Supporting information). Species niche breadths were calculated based on larval distributions across two characteristics of local habitats, the range of habitat permanence and the number of top predators with which larvae coexisted. Both of these are major environmental axes shaping the local habitat distributions of odonates (McCauley *et al.* 2008) and many other freshwater taxa (Wellborn, Skelly & Werner 1996). Habitat permanence was defined by hydroperiod, the portion of the year a water body contained standing water (permanent = 1). Species niche breadth along this axis was defined as the difference between the mean hydroperiod for the most permanent water body in which the species was found and the mean hydroperiod of the least permanent site in which it occurred. Species varied in their breadth of distribution across top predator communities, with some species only coexisting with a single top predator type and others having broader distributions. These lake and pond habitats can be classified as having one of three top predator types: invertebrates, small-bodied fish or large-bodied fish. The breadth of the larval distributions of these dragonfly species across these predator communities varied between 1 and 3 (McCauley *et al.* 2008). These two variables, hydroperiod and top predator range, were combined into a single measure of niche width using a principal components analysis. This PCA extracted a single axis that explained 70% of the variation in these data. The breadth of hydroperiod levels species occupy and the number

of top predator communities in which species occur both loaded positively on this axis each with loadings of 0.84. A PC-score reflecting niche breadth was retained for each species and used in regression analyses. Data on species' distributions across both axes were taken from multiyear surveys of 57 water bodies within the same landscape where the dispersal study was conducted (McCauley *et al.* 2008).

Measures of body size (adult total length and hind-wing length) were taken from the literature (Walker & Corbet 1978) and combined in a summary measure of body size using a PCA. A single axis explained 98% of the variation in the data and both total length and hind-wing length had strong positive loadings of 0.99 on this axis. Species' PC scores from this analysis were used as measures of body size in subsequent analyses.

Three alternative morphological proxies for dispersal ability were examined (hind-wing length / total length, hind-wing length/ total length[3] and residuals from the regression of hind-wing length on total length). We examined the relationship between each of these variables and range size in three separate linear regressions. None of these three measures of morphological dispersal capacity was significantly related to range size and all three had roughly equivalent and low predictive power ($R^2$ values between 0.019 and 0.037). Of the three morphological proxies for dispersal ability, the value of the residual from the regression of hind-wing length on total length was the most biologically interpretable and so the regression relating this measure of dispersal capacity to species range size was retained for use in the AICc analysis.

Data on dispersal behaviour were taken from a previously published landscape-level experiment that followed dispersal to and colonization of artificial ponds (cattle watering tanks) by multiple species of dragonflies over 2 years in a landscape where source habitats were known (McCauley 2007). This experiment allowed us to measure how far species travelled from source ponds and how frequently they dispersed. Our analyses were restricted to species within the most species-rich dragonfly family in lentic systems, Libellulidae (Odonata: Anisoptera). A PCA was used to derive a summary measure of dispersal behaviour from three measures of dispersal, mean dispersal distance, maximum dispersal distance and the mean rate of arrival (across 2 years) at newly created patches for each species. A single axis was extracted and all three dispersal measures loaded positively (loadings: maximum dispersal distance = 0.93, mean dispersal distance = 0.75, arrival rate = 0.59) on this axis which explained 59% of the variation in these data. Higher PC scores indicate increasing dispersal distances (maximum and mean) and higher rates of arrival at cattle tanks.

Population abundance for our landscape was determined using catch-per-unit effort (CPUE) for each species. This was calculated for 22 water bodies that were surveyed for 2 years with a standard protocol (McCauley *et al.* 2008). The mean of the CPUE for the species was used as a measure of its local abundance.

### EXTINCTION-TO-COLONIZATION RATIOS

A second data set (Table S1, Supporting information) from a long-term survey of 36 ponds on the E.S. George Reserve in southeast Michigan was used to assess how extinction–colonization dynamics across habitat patches were related to species range sizes. Rates of colonization ($c$) or extinction ($e$) were calculated as the number of each event type divided by the total number of

ponds in which the species was observed. This approach allowed a comparison of colonization and extinction rates among species, which differ in the breadth of habitats they occupy and consequently the number of sites within this landscape. These analyses included 11 species of libellulid dragonflies (found in at least three ponds at the site), nine of which were also included in the previous analyses testing the relationship between species characteristics and range size. When extinctions exceed colonizations ($e/c > 1$), the metapopulation is declining and will go extinct if this trend is not reversed, while when extinctions are less frequent than colonizations ($e/c < 1$), the metapopulation will grow (Hanski 1999).

### ROLE OF PHYLOGENY

The Blomberg's K (Blomberg & Garland 2002; Blomberg, Garland & Ives 2003) test for phylogenetic signal was performed in order to assess whether phylogeny plays a role in determining range area, dispersal behaviour and niche breadth. MRBAYES (Ronquist *et al.* 2012) and BEAST (Drummond *et al.* 2012) was used to generate a phylogeny and ultrametric tree, respectively, on a set of available concatenated gene sequences: 5·8S rDNA, 12S rDNA, 16S rDNA, 28S rDNA, tRNA-Val, cytochrome oxidase subunit 1 and elongation factor 1α (See Table S2, Appendices 1–4, and Fig. S1, Supporting information).

### STATISTICAL ANALYSIS

To assess the relationship between range size and species characteristics a linear regression for each model was used (see Table 1 for all models evaluated). A comparison of the level of support for these regressions was conducted using AICc (Burnham & Anderson 2002). A linear regression was used to assess the relationship between species extinction-to-colonization ratio and species range size.

## Results

### SPECIES TRAITS AND RANGE SIZE

Among the five species traits or population characteristics examined only two were significantly related to North American range size, dispersal behaviour ($F_{1,13} = 10.59$,

$P = 0.006$, $R^2 = 0.45$, Fig. 1) and niche breadth ($F_{1,13} = 7.02$, $P = 0.02$, $R^2 = 0.35$). Analysis of the support for all the models evaluated using AICc found that two regression models receive strong, and nearly equivalent support, dispersal behaviour alone and the regression combining dispersal behaviour and niche breadth ($F_{1,12} = 8.06$, $P = 0.006$, $R^2 = 0.57$, Table 1).

### EXTINCTION : COLONIZATION RATIOS AND RANGE SIZE

Species extinction-to-colonization ratios were negatively related to species' range area in North America (linear regression: $F_{1,9} = 5.79$, $P = 0.04$, $R^2 = 0.39$, Fig. 2). Extinctions and colonizations are common in this system (McCauley *et al.* 2008) and were often associated with drought events during the time period in which these data were collected (Werner *et al.* 2009). These values, many of which differ from 1, therefore reflect population trends following perturbations and the natural flux of habitat occupancy, rather than an equilibrial state.

### PHYLOGENETIC SIGNAL

Phylogeny (Fig. S1, Supporting information) played no significant role in shaping range area, dispersal behaviour and niche breadth among the taxa studied. The *P* values for Blomberg's K were 0·34, 0·745 and 0·507, respectively, indicating that phylogenetic relatedness has little bearing on the behavioural traits analysed in this study. Additionally, inspection of the relationship between range size and both dispersal behaviour and the extinction-to-colonization ratio finds species within a given genera distributed across the full breadth of this relationship (Figs 1 and 2).

## Discussion

Our results indicate that species traits can be important predictors of range size; in the dragonfly species we studied, we found two traits, dispersal behaviour and niche breadth (defined by habitat usage), that were both

**Table 1.** Results from calculations of support for ten regression models based on AICc

| Model | K | $n$ | Residual SS | AIC | AIC$_c$ | $\Delta_i$ | Exp ($-\Delta_i/2$) | $w_i$ | Evidence ratio | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Niche breadth (A) | 3 | 15 | 28·98 | 15·88 | 18·06 | 2·48 | 0·289 | 0·109 | 3·46 | 0·35 |
| Body size (B) | 3 | 15 | 43·56 | 21·99 | 24·17 | 8·60 | 0·014 | 0·005 | 73·54 | 0·02 |
| Morphological dispersal capacity (C) | 3 | 15 | 43·78 | 22·07 | 24·25 | 8·67 | 0·013 | 0·005 | 76·38 | 0·02 |
| Dispersal behaviour (D) | 3 | 15 | 24·59 | 13·41 | 15·60 | 0·02 | 0·991 | 0·374 | 1·01 | 0·45 |
| Local population abundance (E) | 3 | 15 | 43·93 | 22·12 | 24·30 | 8·72 | 0·013 | 0·005 | 78·36 | 0·02 |
| A+C | 4 | 15 | 27·89 | 17·30 | 21·30 | 5·73 | 0·057 | 0·022 | 17·51 | 0·38 |
| A+D | 4 | 15 | 19·04 | 11·58 | 15·58 | 0·000 | 1·000 | 0·377 | 1·00 | 0·57 |
| C+E | 4 | 15 | 43·6 | 24·01 | 28·01 | 12·43 | 0·002 | 0·001 | 499·63 | 0·02 |
| D+E | 4 | 15 | 22·67 | 14·20 | 18·20 | 2·62 | 0·270 | 0·102 | 3·70 | 0·49 |
| A+B+C+D+E | 7 | 15 | 14·09 | 13·06 | 29·06 | 13·49 | 0·001 | 0·000 | 847·19 | 0·68 |

K, number of parameters in the model; $n$, sample size; SS, sum of squares; AIC, Akaike Information Criteria; AIC$_c$, Akaike Information Criteria for small sample sizes; $\Delta_i$, (AIC$_{ci}$) −(AIC$_c$ of best model); $w_i$, AICc weights; $R^2$, regression coefficient of determination.
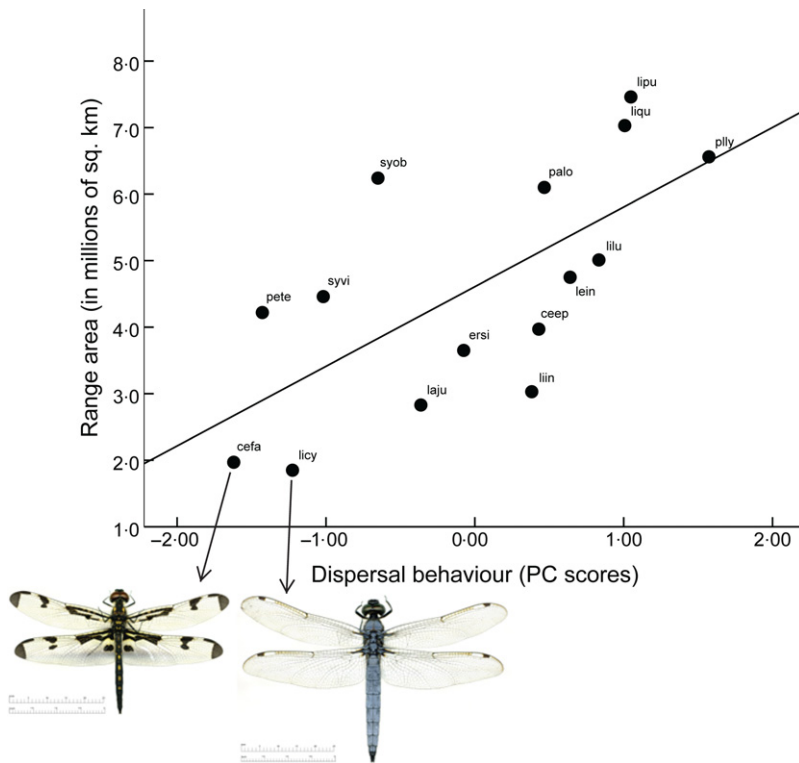
**Fig. 1.** Dispersal behaviour predicts North American range size (linear regression: range area = 4·61 + 1·12(dispersal), $F_{1,13}$ = 10·59, $P$ = 0·006, $R^2$ = 0·45). Symbols are labelled with species abbreviations (Table S1, Supporting information). Species with the same first two letters in their abbreviation are in the same genus. Examples of species in the study pictured with their average adult lengths indicated to right of each picture (Images courtesy of Ed Lam).
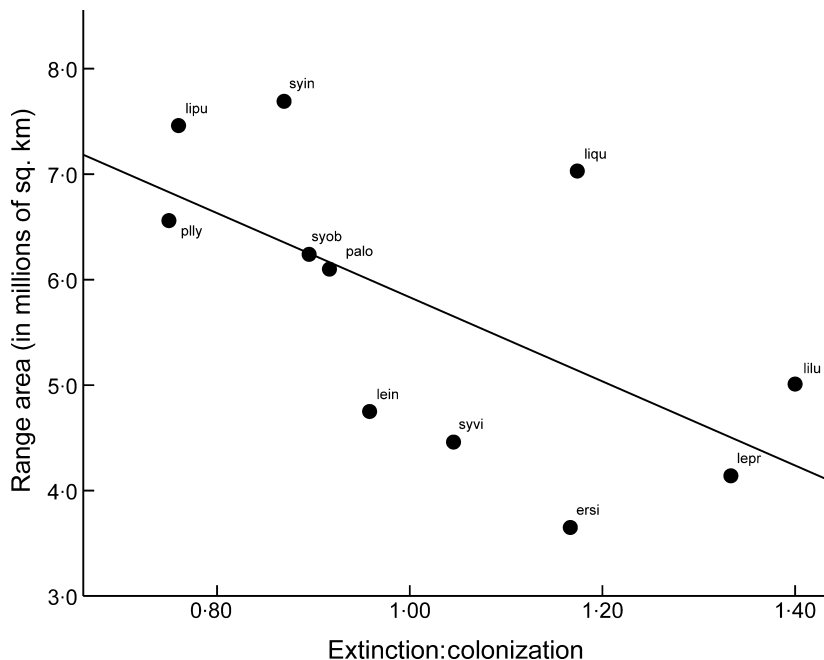


**Fig. 2.** North American range size is related to colonization and extinction dynamics, species with higher rates of colonization than extinction within one landscape of lakes and ponds have larger range sizes (linear regression: range area = 9·82 + −3·99 (extinction : colonization ratio), $F_{1,9}$ = 6·79, $P$ = 0·028, $R^2$ = 0·43). Colonization and extinction rates were from a 13 year survey of 36 lakes and ponds on the E.S. George Reserve in south-east Michigan. Symbols are labelled with species abbreviations as in Fig. 1 (Table S1, Supporting information).

positively related to species' North American range size. However, none of the other species traits examined were significant predictors of range size. Dispersal behaviour was most strongly related to range size with those species that have limited dispersal at the landscape scale also having smaller range areas than those species that are more dispersive. Niche breadth was also positively related to range area, explaining a proportion of the variation between species' range sizes. This trait, however, had less explanatory power than dispersal behaviour in predicting range area.

Our study represents one of the first direct tests of the connection between species dispersal behaviour and range size. Only one previous study used empirically measured dispersal, measured from radiotelemetry studies, to assess how dispersal behaviour was related to range size (Gaston & Blackburn 2003). In that study, the authors assessed the relationship between dispersal distances and the distributional

extent of 67 birds across the UK. Unlike our results, they found no relationship between dispersal behaviour and species' ranges across this region. However, the geographic scale of these studies differs dramatically, and no previous study has related empirical measures of dispersal behaviour to species range size at the continental scale.

Evidence from studies of translocations moving species beyond their current range margins (Marsico & Hellmann 2009) and species' range expansions also connect dispersal with range limits. For example, in butterflies species' mobility is positively related to ability to expand their ranges (Warren *et al.* 2001; Pöyry *et al.* 2009) and populations derived from recent expansions show evidence of the evolution of increased dispersal capacity (Hill, Thomas & Blakeley 1999). Although such range expansions have been documented in odonates (Hickling *et al.* 2005), there has been limited data on species dispersal behaviour to test the relationship with range expansions. Angert *et al.* (2011) examined the relationship between range expansions and migrant status and flight behaviour during daily activities (percher or flier) in the British odonates and neither were related to the extent of range expansion. However, these movement behaviours are distinct from the interhabitat dispersal behaviours we examined and likely not predictive of interhabitat dispersal.

Previous studies in another odonate taxon, *Enallagma* damselflies, found a positive correlation between wing length (both absolute and relative) and range size suggesting dispersal ability (as indexed by flight capacity) may shape range size in these species (Rundle *et al.* 2007). In our regression analyses of the dragonflies, however, no morphological measures were significantly related to range area (body size: $F_{1,13} = 0.405$, $P = 0.536$; relative wing size: $F_{1,13} = 0.173$, $P = 0.684$). While results from the *Enallagma* suggest that for these damselflies flight capacity is critical in determining range size, differences in flight capacity may be less important among the dragonflies we studied. The difference between these suborders of Odonata likely arises because dragonflies are generally stronger fliers than damselflies (larger thoraces that house more flight musculature and wings shapes suited for longer distance flight compared with the petiolate wings of damselflies, Corbet 1999). Thus, the role of behavioural propensity to disperse becomes the dominant factor restricting distributions of dragonflies, especially when species distributional extents are determined by movements at the regional or landscape scale rather than long-distance dispersal events an issue we return to in our discussion of extinction-to-colonization ratios. Distinguishing the effects of behaviourally mediated dispersal limitation from dispersal capacity may be especially important in animals where the traits affecting dispersal capacity (e.g. flight musculature and wing morphology) are also used in other life-history functions (e.g. foraging or territory defence). In these systems, disconnects between dispersal ability and the behavioural propensity to disperse may be especially likely.

Another species trait we found positively correlated with range size was niche breadth, specifically how broadly they were distributed across a habitat gradient of hydroperiod and top predator type that is an important structuring force in lentic freshwater systems (Wellborn, Skelly & Werner 1996; McCauley *et al.* 2008). Species that can occupy a greater range of habitat types had larger range sizes. This trait could act independently, as the ability to utilize a broader set of habitats would enable species to persist in regions where the full gradient of habitats is either not present or some of these habitats become rare. Additionally, the interaction of niche breadth and dispersal behaviour may be important in shaping species geographic distributions. Previous work with several of these dragonfly species also found that niche breadth was related to dispersal behaviour; species whose larvae occupied a greater range of habitats were more dispersive than specialists that were confined to permanent lakes with fish (McCauley 2007). Correlations such as this between species traits are common, and these traits may interact to reinforce patterns of species' distributions. The relationship between niche breadth and dispersal behaviour in this system suggests a fundamental link encompassing a suite of traits linked as part of a life history, which act together to determine species geographic range sizes.

The analysis of our extinction–colonization data set uncovered a negative relationship between species' North American range size and the extinction-to-colonization ratio of their population sites surveyed in Michigan. Although these extinction-to-colonization ratios are for a single landscape, which does not encompass a range boundary for any of these species, it suggests that the factors driving these population dynamics also play a role in shaping species range limits. Among these factors, dispersal is likely to play a prominent role. Dispersal determines the frequency of colonization attempts, and local populations can be buffered from extinction by dispersers arriving at and colonizing a site (Hanski 1999; Vandewoestijne *et al.* 2004). These mechanisms mean that dispersal rates will be strongly linked to observed extinction-to-colonization ratios. Dispersal behaviour can therefore act on range size through its effects on extinction and colonization dynamics, determining the ability of species to maintain regional populations through regions where habitat density declines and recovery from local extinction is likely to be limited by the infrequent arrival of dispersers. Dragonflies and other species occupying lentic habitats such as lakes, ponds and impoundments confront a clear gradient in habitat availability across the North American continent. The frequency of these habitats strongly declines on an east-west gradient, with the lowest densities in the centre-west of the continent (Downing *et al.* 2006), a region in which many of these species reach one of their range boundaries. Insufficient habitat availability can limit ranges (Holt & Keitt 2000; Holt *et al.* 2005), but the conditions that represent an inadequate habitat density varies

between species based at least partially on their ability disperse to and colonize habitat patches. In systems where local extinctions are common (McCauley *et al.* 2008), the maintenance of a regional population will require relatively frequent recolonization of previously occupied sites to counterbalance these extinctions and prevent the entire regional population from spiralling to zero. Our findings on the negative relationship between range size and extinction-to-colonization ratios suggest that species with smaller ranges may be less able to quickly recolonize sites in which local extinctions have occurred. As interhabitat distances increase these species may be subject to regional extinctions that result in the development of range boundaries.

Taken together, analyses of both species traits and e : c ratios suggest that dispersal behaviour plays a central role in structuring the geographic distributions of North American libellulid dragonflies. These two independent tests of range size prediction do not have a strong overlap in the species included (Table S1, Supporting information), limiting our ability to assess the direct connection between dispersal behaviour and extinction-to-colonization ratios. Nonetheless, the finding that both dispersal behaviour and extinction–to-colonization ratios are good predictors of the size of species ranges is highly suggestive of a connection mediated through the effects of dispersal on population dynamics and the ability to maintain regional populations across the extent of North America. Our results also provide an impetus for further studies that can draw on empirically measured dispersal behaviour (e.g. extinction : colonization ratios), rather than rely on dispersal proxies (e.g. the measures of relative wing size we examined here), to evaluate the role of dispersal in determining species geographic distributions and provide an example of how we can employ results of studies at smaller scales to elucidate macroecological properties of species. A better understanding of the forces shaping species range extents is vital in the context of the combined effects of climate and landscape change. Climate change is associated with range shifts across a wide array of species (Parmesan 2006), and these shifts may be critical for species persistence, allowing organisms to track suitable environmental conditions and facilitate species persistence. The relationship between range sizes and species traits or population dynamics can provide insights into the forces structuring ranges and potentially limiting the capacity of species to shift these ranges.

## Acknowledgements

## Data Accessibility

Data used in analyses relating range size to species traits and population dynamics are available through Dryad at: doi:10·5061/dryad.b79v5.

Additional information on phylogenetic analyses is available in Supporting Information: Table S2, Fig. S1 and Appendices 1–4.

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## Supporting Information

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

**Appendix S1.** MrBayes (Ronquist *et al.* 2012) alignment and partition information in NEXUS format.

**Appendix S2.** BEAST (Drummond *et al.* 2012) XML file. Contains input data and run parameters.

**Appendix S3:** Raw text file containing input data and commands used for analyses performed within R (R Development Core Team, 2013).

**Appendix S4.** A detailed description of the protocol used to construct a Libellulidae phylogeny and subsequent tests for the detection of phylogenetic signal on various traits.

**Fig. S1.** Phylogenetic consensus tree obtained via MrBayes (Ronquist *et al.* 2012). Values at the nodes represent posterior probability support.

**Table S1.** Key to species abbreviations used in figures. Species are abbreviated by combing the first two letters of the genus name with the first two letters of the species name. Superscripts identify species as belonging to the species traits data set (1), extinction–colonization data set (2) or both (1,2).

**Table S2.** Key to GenBank (Benson *et al.* 2005) Accessions used for phylogenetic analysis. NA denotes genes not available or usable for analysis. Asterisks denote outgroup taxa.