Niche versus neutrality in structuring the beta diversity of damselfly assemblages

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SUMMARY

1. Differences among communities in taxonomic composition – beta diversity – are frequently expected to result from taxon-specific responses to spatial variation in ecological conditions, through niche partitioning. Such process-derived patterns are in sharp contrast to arguments from neutral theory, where taxa are ecologically equivalent and beta diversity results primarily from dispersal limitation.

2. Here, we compared beta diversity among assemblages of damselflies (Odonata: Zygoptera), for which previous experiments have shown that niche differences maintain genera within a community, but patterns of relative abundance for species within each genus are shaped primarily by neutral dynamics.

3. Using null-model and ordination-based methods, we find that both genera and (in contrast to neutral theory) species assemblage composition vary across the landscape in a deterministic fashion, shaped by environmental and spatial factors.

4. While the observed patterns in species composition conflict with theory, we suggest that this a result of weak ecological filters acting to produce spatial variation in assemblages of ecologically similar species undergoing ecological drift within communities. Such patterns are especially likely in systems of relatively weak dispersers like damselflies.

Keywords: community assembly, metacommunity, neutral, niche, odonate

Introduction

In any given locality, species composition is often governed by the abiotic and biotic limitations of potential colonists from the regional species pool (Ricklefs, 2004). Many species are excluded because they are unable to live under the abiotic regime found at a given site (Dunson & Travis, 1991), because interactions with other local species actively exclude them (Connell, 1961; Paine, 1966; McPeek, 1990), or because of the interactive effects of abiotic and biotic factors (Dunson & Travis, 1991; Jackson *et al.*, 2001). Similarly, the abundance of species that are present is influenced by their interactions with the local abiotic environment and with other species, as well as by dispersal from nearby communities (MacArthur & Wilson, 1967; Shmida & Wilson, 1985; Leibold *et al.*, 2004; Cadotte, 2006).

Differences among communities in species composition and abundance are frequently expected to result from how component species respond to spatial variation in ecological conditions (MacArthur, 1972; Chase, 2010; Kraft *et al.*, 2011). Many species differ in their ability to perform under various abiotic conditions or in interactions with other species, and so their abundances are expected to change along ecological gradients in ways that reflect their ecological performance capabilities (Chesson, 2000; Chase & Leibold, 2003). As a result, changes in community composition across local communities (beta diversity; Whittaker, 1960) should be associated with environmental gradients, and this beta diversity may represent the scaling between local and regional diversity. Variation in species turnover among communities could be driven by ecological, niche-based differences among the different taxa in the regional species pool. For example, ecological

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filters may result in some taxa co-occurring with one another more often than expected by chance, producing highly similar communities under similar environmental conditions (Leibold *et al.*, 2004; Holyoak *et al.*, 2005; Chase, 2010; Chase *et al.*, 2011; Logue *et al.*, 2011). These predictions, however, are based on the underlying assumption that the various species differ ecologically such that their ability to persist in a local community, and thus changes among communities, is a consequence of how the species respond to environmental heterogeneity (e.g. Chase & Leibold, 2003; Ricklefs, 2004; Gaston *et al.*, 2007). Many of these models thus assume that changes in community composition across the landscape are shaped by the same factors that affect local community composition, which may not necessarily be the case.

In contrast, the neutral view of community structure postulates that many species in local communities are effectively ecologically equivalent. While the total number of individuals of all these ecologically equivalent species may be strongly regulated, local species composition and relative abundance are expected to vary unpredictably as a result of demographic stochasticity and ecological drift through time (Hubbell, 2001). However, changes in community composition and abundance patterns in neutrally structured communities are not expected to be without pattern. For instance, limited dispersal among local communities will tend to cause community similarity to be inversely associated with spatial proximity (Hubbell, 2001; Chave & Leigh, 2002; Condit *et al.*, 2002), but community similarity should not change consistently along ecological gradients.

While niche and neutral processes have distinct signatures (Chesson, 2000; Hubbell, 2001), much progress on understanding local community structure has been made by showing that both processes can act simultaneously in a community (Chesson, 2000; Gravel *et al.*, 2006; Leibold & McPeek, 2006; Thompson & Townsend, 2006; Adler, HilleRisLambers & Levine, 2007; Ellwood, Manica & Foster, 2009; Siepielski *et al.*, 2010). What remains unclear is how the joint operation of niche and neutral processes may affect beta diversity within a given region (Legendre, Borcard & Peres-Neto, 2005; Thompson & Townsend, 2006; Chase & Myers, 2011; Kraft *et al.*, 2011; Swenson, Anglada-Cordero & Barone, 2011).

Our previous works on the damselflies that inhabit fish with lakes of eastern North America have shown that niche and neutral processes operate at different taxonomic levels. Commonly co-occurring damselfly genera (*Enallagma*, *Ischnura* and *Lestes*) are ecologically quite distinct (e.g. Chesson, 2000; Adler *et al.*, 2007; Siepielski & McPeek, 2010), which should facilitate their coexistence

in lakes. For example, *Enallagma* species grow slowly but experience low levels of mortality from fish, whereas *Ischnura* species grow rapidly but are vulnerable to fish predation (McPeek, 1998). These ecological differences are consistent with mechanisms of coexistence under keystone predation (Holt, Grover & Tilman, 1994; Leibold, 1996; McPeek, 1996). Although *Lestes* species suffer similar (low) rates of mortality from fish predation as *Enallagma* (Stoks & McPeek, 2003), their larger size appears to allow them to eat larger prey (Siepielski *et al.*, 2011). As a result, individual growth rates of these three genera declined strongly with increased intrageneric densities but not intergeneric densities in field experiments (Siepielski *et al.*, 2011). In addition, the relative abundances of these three genera respond differently to various environmental gradients across lakes (Siepielski *et al.*, 2011). These results all indicate that damselfly genera are ecologically distinct and likely to fill different niches within littoral food webs.

Each of these three genera, however, also has several co-occurring species in every lake (McPeek, 1990, 1998; Stoks & McPeek, 2003). The results of both observational and experimental field studies suggest that *Enallagma* species (the most speciose of the three genera) found within fish lakes are essentially ecologically equivalents (Siepielski *et al.*, 2010). Specifically, no species gained a demographic advantage (i.e. a higher growth rate or lower mortality rate from predators) when perturbed to low relative abundance (a defining feature of ecological equivalence; see Chesson, 2000; Adler *et al.*, 2007), and the relative abundance of *Enallagma* species varied randomly among lakes with respect to the same environmental gradients that explained genus-level structure (Siepielski *et al.*, 2010). Ecological drift (*sensu* Hubbell, 2001) thus seems the best explanation for variation in composition and abundance patterns of species within the genus *Enallagma*.

Damselfly assemblages across lakes thus provide an ideal opportunity to evaluate whether the expected patterns of beta diversity are observed for niche-structured or neutrally structured communities. Given the above results (McPeek, 1998; Siepielski *et al.*, 2011), we predicted that beta diversity measured at the generic level should be non-random and correlate with ecological gradients. In contrast, turnover among lakes for species within the genus *Enallagma* should be driven primarily by spatial effects and not covary with environmental gradients (McPeek, 1990; Siepielski *et al.*, 2010). To test these predictions, we compared turnover among genera and among the *Enallagma* species using an occurrence-based measure of beta diversity coupled with a null-model approach to examine the extent to which beta diversity varied deterministically. We also used a variance partitioning ordina-

tion approach to quantify the relative importance of spatial and environmental variation for taxonomic turnover.

Methods

Study sites

We conducted this study at 40 ponds and lakes throughout New Hampshire and Vermont, U.S.A., during 2008 and 2009 (Fig. 1; Appendix S1). Waterbodies were chosen based on the following criteria: (i) easy access, (ii) the presence of fish as the top predators in the system (i.e. no fishless lakes were included) and (iii) a well-developed littoral zone, where damselfly larvae are found clinging to the plants.

Damselfly community composition

We sampled larval damselflies to quantify the presence and abundance of genera and species. Larvae were

Fig. 1 Map of study locations. The small inset map shows the overall location, denoted by a black rectangle, of the study region throughout NH and VT, U.S.A. Individual study sites are designated by grey circles.

sampled from the littoral zone of each lake using 10 replicate, standardised 1-m-long sweeps through the macrophytes with a D-frame dip net (28-cm net opening, 1×1 mm mesh) at a depth between 0.25 and 0.50; this method gives highly repeatable estimates of odonate abundances and detectability (Crowley & Johnson, 1992; Stoks & McPeek, 2003). We also recorded the abundances of other large odonates (e.g. dragonflies) captured.

In these samples, we captured damselflies in five genera: *Argia, Enallagma, Ischnura* and *Nehallenia* in the Coenagrionidae, and *Lestes* in the Lestidae. *Argia violacea* was the only representative of this genus at these lakes. Based on adult surveys, we know that both *Ischnura verticalis* and *Ischnura posita* were present at most lakes we sampled, but these two are indistinguishable as larvae at the time of sampling. Similarly, *Nehalennia irene* and *Nehalennia gracilis* were present at most of these ponds, but these two are also indistinguishable as larvae during our sampling periods. *Lestes* was represented by *Lestes vigilax* and *Lestes inaequalis*. Ten *Enallagma* species were represented in our samples, all of which except two, *Enallagma hageni* and *Enallagma ebrium*, are easily distinguished to species (Westfall & May, 2004).

Environmental gradients

We quantified a set of abiotic and biotic variables to characterise major environmental gradients that appear to be important for regulating damselfly abundances in these lakes (McPeek, 1998; Stoks & McPeek, 2003; Siepielski *et al.*, 2010, 2011). Here, we describe only briefly methods associated with each variable; complete descriptions of methods can be found elsewhere (Siepielski *et al.*, 2010, 2011).

We used hand-held digital probes to record dissolved O_2 (per cent saturation), conductivity (μs cm^{-1}) (model YSI 85 hand-held probe; YSI incorporated, Yellow Springs, OH, U.S.A.) and pH (Milwaukee model SM102 hand-held probe; Milwaukee Instruments incorporated, Rock Mount, NC, U.S.A.). Total nitrogen and total phosphorus in water taken from the littoral zone were estimated using standard methods following persulphate digestion. Particulate carbon was estimated using a gravimetric approach, based on filtering littoral lake water through glass filters.

We quantified the net primary productivity of the littoral food web of each lake by estimating the growth rates (mg C $\times$ day^{-1}) of attached algae on clay tiles. We also estimated standing stock of chlorophyll-*a* in the water column by filtering littoral lake water across glass filters, extracting chlorophyll-*a* on the filters with methanol and
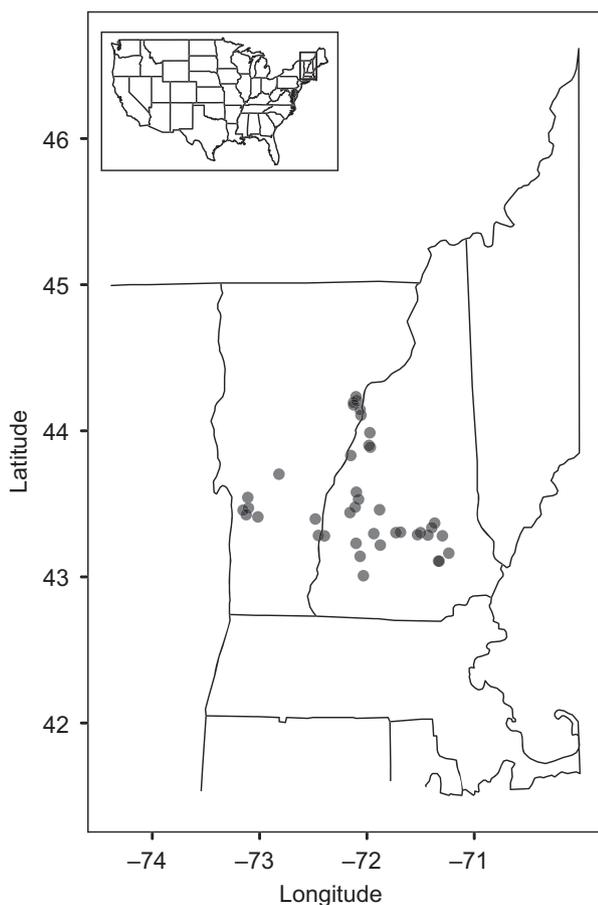
then quantifying the fluorescence of the chlorophyll-*a* extractant using a fluorometer (Turner Designs, Sunnyvale, CA, U.S.A.).

Macrophytes provide cover and are the main foraging surface for damselfly larvae (Crowley & Johnson, 1992), but also the primary oviposition site for adult damselflies (Butler & deMaynadier, 2008). We quantified macrophyte density and species composition in 0.5×0.5 m quadrats randomly placed along transects through the littoral zone of each lake.

Damselfly prey abundances in each lake were quantified by taking 10 replicate samples with a 6 L box sampler (100-μm mesh) placed over the macrophytes (e.g. where damselflies forage) (Downing, 1986). All captured prey were identified to the lowest possible taxonomic unit (family in most cases). Mean taxon abundances across replicates for each lake were used in analyses. To reduce the dimensionality of the prey data set, we combined all taxa that were potential prey of damselflies and conducted a principal components analysis (PCA) on the covariance matrix. The first and second PCs of the prey PCA accounted for 62 and 12%, respectively, of the total variation. Cladoceran abundances loaded positively on PC1, and so lakes with higher PC1 scores had higher abundances of cladocerans. Gammarid and ostracod abundances loaded positively and annelid abundances loaded negatively on PC2, and so PC2 quantifies a contrast between the abundances of these groups (see Siepielski *et al.*, 2011, for details).

We also estimated the densities and diversity of predatory fish and newts (*Notophthalmus viridescens*) (Blois-Heulin *et al.*, 1990; McPeek, 1998) in each lake by taking four standardised seine hauls (using a 4.5×1.5 m beach seine, with 5-mm mesh), each separated by 10 m, through the macrophytes in the littoral zone of each lake (means were used in the analyses). All fish and newts were counted, identified to species and immediately returned alive to the lake.

Spatial variation in damselfly assemblage composition

Considerable debate has emerged regarding how to quantify spatial components of community structure and how to determine the extent to which such patterns can be explained by spatial and environmental components (see Anderson *et al.*, 2011). Here, we take a pluralistic approach to comparing assemblage composition using several recent methods. For all of the approaches, the same procedures are conducted using assemblage matrices of either site × genera or site × species within

Enallagma. The genus-level assemblage matrix was constructed by collapsing the presence or abundance of all species of each genus into genus-level data.

To quantify beta diversity, we used a modified Raup–Crick index (β_{RC}; Raup & Crick, 1979), which is calculated using presence–absence data (Chase *et al.*, 2011). Although numerous beta indices have been developed (e.g. Anderson *et al.*, 2011), β_{RC} has two advantages. First, β_{RC} is a null-model approach that quantifies the deviation of pairwise comparisons of assemblage dissimilarity from the null expectation under purely random assembly. It varies between −1 and 1, with values close to −1 indicating that assemblages are more similar than expected by chance and values close to 1 indicating that assemblages are more dissimilar than expected by chance; values close to 0 indicate the observed data do not deviate from the null expectation. Second, β_{RC} explicitly accounts for sampling effects due to differences in alpha diversity among sites (Chase *et al.*, 2011), which if not taken into account can potentially lead to erroneous interpretations regarding the importance of stochastic or deterministic processes (e.g. Kraft *et al.*, 2011). The null expectation was generated using 999 randomisations; implementation of this metric was performed using R code described in Chase *et al.* (2011).

To evaluate whether the average beta diversity differed between genera and *Enallagma* species, we used a bootstrapping approach to calculate the 95% confidence interval for the mean difference of β_{RC} between these two groups. If the 95% confidence interval of this difference did not contain zero, we rejected the null hypothesis of no difference in mean β_{RC} between genera and species within *Enallagma*. This approach was necessary because the values within a matrix are not independent of one another, and the two matrices are also, themselves, not independent of one another as they arise from the same data set (see Anderson, Ellingsen & McArdle, 2006).

Statistical analyses of spatial and environmental components

We used a variance-partitioning approach to determine what proportion of variation in assemblage composition could be accounted for by variance components associated with environment, space, coupled spatial–environmental components and unexplained variation (see Borcard, Legendre & Drapeau, 1992; Legendre & Legendre, 1998). This approach used three matrices: the damselfly assemblage composition matrix, the environmental matrix and a spatial matrix. Two different analyses

were performed. In all cases, adjusted fractions of variation were used (Peres-Neto *et al.*, 2006).

In the first approach, we used the matrix of β_{RC} values as the assemblage composition matrix. This analysis allowed us to examine how changes in β_{RC} among sites change with spatial or environmental distance. For this approach, we used multiple regressions of distance matrices (Tuomisto, Ruokolainen & Yli-Halla, 2003; Gilbert & Bennett, 2010). The environmental matrix was represented as the multivariate Euclidean distances among lakes for the log-transformed environmental variables. The spatial matrix consisted of the pairwise latitude and longitude coordinate distances among lakes. Variance partitioning was accomplished using the general methods outlined in Legendre & Legendre (1998).

In the second approach, we used partial redundancy analysis (RDA) on the site × genus or site × *Enallagma* species presence/absence assemblage composition matrix. We also present the results of identical analyses using the site × genus or site × *Enallagma* species abundance assemblage composition matrix in the Supporting Information and note differences in the results of this abundance-based analysis versus the presence/absence analysis. The Hellinger transformation was applied to the species or genus matrix to reduce the influence of outliers (Legendre & Gallagher, 2001). In this analysis, the spatial component was represented using a third-order polynomial of the latitude and longitude coordinates. We initially attempted to use principal components of neighbourhood matrices (Borcard & Legendre, 2002; Dray *et al.*, 2006) to model the spatial components, as it allows one to quantify spatial variation over a range of spatial scales, but no significant overall spatial structure was detected in the global model. Thus, we used a simpler third-order spatial representation. The set of environmental variables was log transformed. We used a forward selection procedure to reduce the set of spatial and environmental variables in the models (Blanchet, Legendre & Borcard, 2008). Forward selection was performed with $\alpha = 0.1$ for acceptance of variables into the model and $\alpha = 0.05$ to evaluate the statistical significance of the full models. Variance partitioning was again accomplished using the methods outlined in Legendre & Legendre (1998). Only the fractions of variation attributed to pure space (i.e. controlling for environment) and pure environment (i.e. controlling for space) can be tested for statistical significance (Legendre & Legendre, 1998), and it is those fractions that we present in the results and discussion. Significance of the explanatory variables was determined using permutation tests. All statistical analyses were performed in R 2.14.1 (R Development Core Team, 2011)

Results

Two to five damselfly genera were captured at each lake in our samples (Appendix S1). *Enallagma* and *Ischnura* species were taken at all 40 lakes in our survey, while *Lestes* were captured at 17, *Nehalennia* at nine and *Argia* at six. Within *Enallagma*, *E. hageni/ebrium* was captured at 32 lakes, *Enallagma vesperum* at 29 and *Enallagma geminatum* at 26, with the remaining six species being captured at 10 or fewer lakes.

Damselfly assemblage dissimilarity, as quantified using β_{RC}, revealed that assemblages composed of both genera and *Enallagma* species were more similar, albeit weakly, among lakes than expected if assemblages were randomly assembled. Assemblage composition of genera was also more similar among lakes (β_{RC} mean = −0.337) relative to *Enallagma* species composition among lakes (β_{RC} mean = -0.238). The difference (0.098) in mean β_{RC} between genera and *Enallagma* species was significantly different (bootstrapped 95% CI of the difference: 0.057, 0.142).

Multiple regression of the assemblage (β_{RC}), spatial and environmental distance matrices coupled with variance partitioning revealed that assemblage dissimilarity was associated with the spatial arrangement of lakes for both genera and *Enallagma* species. Significant pure effects of environmental variation accounted for the dissimilarity in *Enallagma* species composition only, not genera (Fig. 2a). For both *Enallagma* species and generic composition, variance partitioning of β_{RC} showed small but significant components due to pure space (Fig. 2a). For both groups, shared spatial and environmental variation was also important, but most of the spatial variation in β_{RC} was unaccounted for by the measured spatial and environmental variables (Fig. 2a).

Among genera and *Enallagma* species, the partial RDA and variance-partitioning analyses showed that spatial turnover in their presence/absence among lakes was consistently associated with pure environmental components and, for genera only, a significant pure spatial component (Fig. 2b). Ordination results of these partial RDAs indicate that, for both *Enallagma* species and genera, variation in pH and total phosphorus were important factors, although there was little segregation of communities across space (Fig. 3). For *Enallagma* species, only Chlorophyll-*a* and the abundance of newts were also important, whereas for genera only the density of fish predators was important. Again, most of the spatial variation in damselfly assemblage composition was unexplained by any of the measured variables (Fig. 2b). Spatial variation in the partial RDA for *Enallagma* species was mainly along longitudinal axes (although not statistically
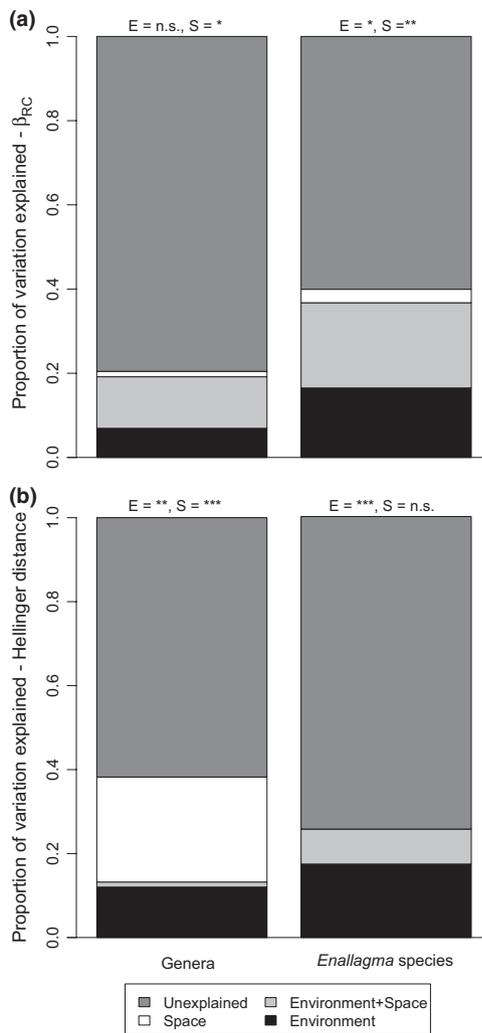
Fig. 2 Variance partitioning of (a) β_{RC} and (b) the Hellinger-transformed presence–absence distance matrix for damselfly genera and species of *Enallagma* among lakes into spatial and environmental effects. The explained variances are based on either multiple regressions of distance matrices (a) or a partial redundancy analysis (b). Only the pure spatial (S) and pure environmental (E) components are testable. The unexplained variation refers to variation not accounted for by the S, E or ES. $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; N.S. $P > 0.05$.

significant), whereas for damselfly genera the combination of latitude and longitude was important, as well as a more complicated third-order term capturing further variation in community composition with latitude (Fig. 3).

Similar variance partitioning and ordination results were obtained using the abundance-based assemblage matrices (Fig. S1), although different sets of environmental factors were important relative to the presence-/absence-based analysis. Ordination results of the partial RDAs based on the abundance data indicate that, for both *Enallagma* species and genera, the abundance of newts and variation in conductivity ($\mu s\ cm^{-1}$) were important

explanatory factors, although there was limited segregation of assemblages across space (Fig. S2). For *Enallagma* species, only pH was also important, whereas for genera only the density of other invertebrates was important. Thus, results from these two sets of analyses indicate that although there is some similarity in what factors shape spatial variation in assemblage composition and differences in abundance among lakes (namely pH), different environmental factors may be important for shaping differences in damselfly community composition versus differences in their abundances across the landscape.

Discussion

Our results indicate that damselfly genera and *Enallagma* species assemblage composition varies across the landscape in a somewhat deterministic manner. These findings are consistent with predictions made based on our previous studies of damselfly genera showing them to be ecologically differentiated, but seemingly discordant with our earlier studies of *Enallagma* species showing them to be ecologically equivalent within lakes. If taxa are ecologically differentiated in ways that affect their abilities to exploit variation in environmental conditions, this should generate a covariance between spatial variation in assemblages and environmental variation. By contrast, if taxa are not ecologically differentiated in such ways, such covariation should be absent. However, it could also be that the factors that affect the distribution of taxa across the landscape, and thus community assembly, are not the same factors that regulate the persistence and thus diversity of taxa once in a given location. We explore these alternatives to address how damselfly assemblages are organised across the landscape.

Spatial turnover for both genera and *Enallagma* species, as captured by β_{RC}, revealed greater assemblage similarity than would be expected if assemblages were randomly assembled. Although the strength of there patterns was weak, assemblages of genera were also slightly more similar among lakes than *Enallagma* species. As noted by Chase *et al.* (2011), when β_{RC} (and almost any beta index) is calculated in systems with low alpha diversity, these low values of alpha diversity will tend to pull the overall index closer to 0. However, both genera and *Enallagma* species had similarly low alpha diversity, so this should not bias the comparison between these two groups (and genera had the higher β_{RC} but fewer taxonomic groups). Regardless of the performance of the beta metric *per se*, these results imply that the distributions of both genera and *Enallagma* species across the landscape may be shaped by environmental factors to produce assemblages
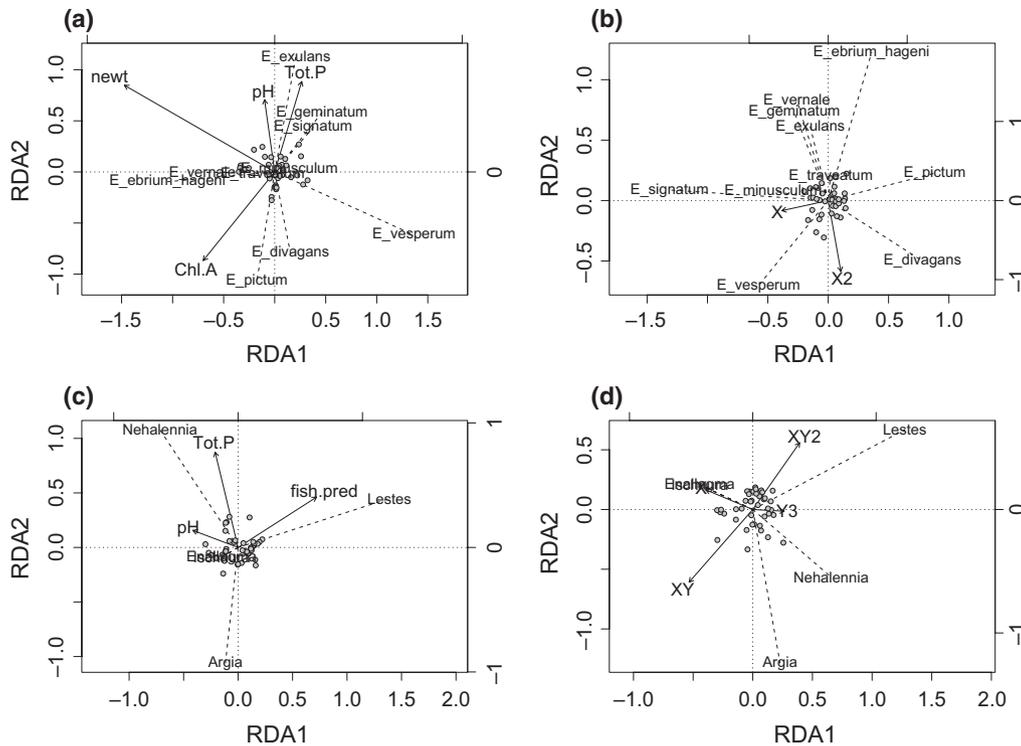
Fig. 3 Ordination plots from the partial redundancy analysis (RDA) of genera and *Enallagma* species composition of Hellinger-transformed presence–absence distance matrices among lakes. Significance of spatial and environmental fractions is given in Fig. 2. Panels (a) and (c) are *Enallagma* species and genera, respectively, ordinations of the environmental RDA controlling for space, whereas panels (b) and (d) are *Enallagma* species and genera, respectively, ordinations of space controlling for environment. Taxa (dashed lines) or sites (grey circles) aligned with the direction of arrows show positive associations with those explanatory variables (solid lines). The bottom and left-hand scales are for the taxa and sites, whereas the top and right-hand scales are for the explanatory variables. In panels (c) and (d), the locations of *Enallagma* and *Ischnura* in the ordination overlap with one another completely because these genera co-occur in almost every lake.

that respond similarly to this underlying environmental variation (i.e. ecological filters; Chase *et al.*, 2011). Surprisingly, though, variance partitioning of β_{RC} into environmental and spatial components revealed that for genera only spatial variation was an important factor, whereas for *Enallagma* both spatial and environmental variation were important factors explaining differences in β_{RC} among lakes.

The canonical ordination models based on Hellinger distances from genera and *Enallagma* species' presence/absence and abundances also found signatures of spatial variation in assemblage composition being shaped by pure spatial and environmental components, but two exceptions to the models discussed previously were apparent. First, we found that a significant fraction of variation in generic assemblage composition was explained by pure environmental variation. Second, we found that pure spatial effects were not important for explaining turnover in *Enallagma* species composition, but pure spatial effects from this model explained more variation for turnover in genera composition than the distance-based approach. A number of possibilities could

explain these seemingly conflicting patterns between models (see reviews in Legendre, Borcard & Peres-Neto, 2008; Gilbert & Bennett, 2010; Smith & Lundholm, 2010). For example, simulation studies have shown that the two different types of models employed here often perform differently in capturing the importance of environmental and spatial components of community composition. Gilbert & Bennett (2010) recently showed that multiple regression of distance matrices often under-fit spatial components, whereas RDA models under-fit environmental components (see also Smith & Lundholm, 2010). Not surprisingly, the merit of these different approaches is under much debate (Anderson *et al.*, 2011; Gilbert & Bennett, 2010). Nevertheless, both models clearly show that some combination of spatial and environmental variation explains spatial variation in assemblage composition at both genera and *Enallagma* species levels of organisation.

Identifying specifically what a pure spatial component of assemblage composition reveals in the kind of observational study employed here is difficult. While a number of authors have discussed the importance of pure spatial

effects as evidence for neutrality (specifically, a decline in community similarity within increasing distance; Chave & Leigh, 2002; Condit *et al.*, 2002), even after accounting for measured environmental variation, this is recognised as far too simple an argument (e.g. Chase & Myers, 2011; Smith & Lundholm, 2010). Clearly, dispersal limitation can be an important feature affecting the spatial composition of communities across the landscape (Partel *et al.*, 2011). Indeed, studies of the damselflies studied here and other odonates have suggested that they may frequently be dispersal limited (McPeek, 1989; McCauley, 2006; McCauley *et al.*, 2008). Surprisingly, however, we found limited evidence for dispersal limitation among *Enallagma* species, which is what we would expect to be the dominant driver of *Enallagma* assemblage composition for strictly ecologically equivalent species (Hubbell, 2001). One possibility is that the spatial scale of this analysis is too limited; however, previous mark–recapture studies have found that *Enallagma* exhibit dispersal limitation at scales <1 km (McPeek, 1989). Regardless, unless a carefully controlled study (e.g. Gilbert & Lechowicz, 2004; Myers & Harms, 2009; Pinto & MacDougall, 2010) is conducted to disentangle the roles of spatially autocorrelated environmental variation, such analyses can lead to erroneous results because any evidence of a spatial signature even once decoupled from any measured environmental variation may simply be picking up some unmeasured environmental factor that varies through space.

We fully anticipated that generic assemblage composition across the landscape would be explained by environmental variation because genera are ecologically quite different (e.g. McPeek, 1990, 1998; Stoks & McPeek, 2003, 2006; Siepielski *et al.*, 2011), but based on our previous studies that showed their ecological similarity, we did not expect that variation in *Enallagma* species composition would be explained by environmental variation (Siepielski *et al.*, 2010). These contrasting predictions were made based on experimental studies showing that each genus is clearly ecologically differentiated in ways that allow for niche differences to promote their coexistence within a given lake, which would necessarily result in differences in community composition across the landscape, whereas *Enallagma* species in lakes with fish are essentially ecologically equivalent. The finding that turnover, as captured by β_{RC} and the RDA of both presence/absence and abundances of *Enallagma* species, was related to environmental variation, albeit weakly, is inconsistent with these previous experimental results.

One explanation for these results is that the factors which determine variation in species distributions among communities are not necessarily the same sets of factors that determine a species demographic performance and thus its ability to persist once established within a given location. Our analyses found several factors were important for explaining *Enallagma* species turnover and that these factors tended to differ depending on whether the presence/absence or abundance data were analysed. Interestingly, several of the factors explaining *Enallagma* turnover were also important for explaining turnover among genera. Given the observational nature of this study, we cannot ascribe a specific role for these factors and why they appear important in segregating *Enallagma* species (or different genera) into different assemblages. Each of these factors could very well be important, or be correlated with different unmeasured factors. Other studies have also found environmental factors to be important for explaining spatial variation in *Enallagma* species composition. For instance, *Enallagma* adults appear to have oviposition preferences for certain macrophytes, and so turnover in their abundances is often correlated across lakes with differences in the abundance of different macrophytes (Gibbons *et al.*, 2002; Butler & deMaynadier, 2008).

Similarly, some *Enallagma* species are found only in lakes with fish as top predators, and some only in lakes where fish are absent and large dragonflies are the top predator (McPeek, 1998). *Enallagma* species in lakes with fish have adaptations for deterring predation by fish, whereas *Enallagma* species in fishless lakes have adaptations allowing them to escape predation from dragonflies (the top predator where fish are absent) (McPeek, 1997, 1998). These different adaptations cause considerable trade-offs in performance, which prevent the two groups of *Enallagma* species from co-occurring, and result in a distinct checkerboard pattern across the landscape (McPeek, 1990). However, once in their respective fish or dragonfly-lake habitats, this strong ecological filter has no bearing on the species composition of individual lakes. The latter arises because the ecological differences segregating fish and dragonfly-lake *Enallagma* species are unlikely to affect their demographic performance differentially within lakes and thus maintain within lake diversity (e.g. McPeek, 1998; Siepielski *et al.*, 2010). We also know that some *Lestes* species segregate across the landscape both in response to the permanence of ponds and different predator assemblages (Stoks & McPeek, 2006). Thus, we suspect that ecological filters (probably along with some dispersal limitation; see McPeek, 1989) may drive some spatial variation in *Enallagma* species composition, but once these smaller subsets of the regional species pools are created, ecological drift still

operates within a lake for a given set of species (e.g. Siepielski *et al.*, 2010). Identifying the regional species pool is therefore clearly essential for evaluating the importance of stochastic and deterministic community assembly because ecological differences may be more apparent at larger spatial scales (Ricklefs, 1987, 2004; Steinitz *et al.*, 2006; Chase & Myers, 2011).

These results provide an important piece of the puzzle towards disentangling the myriad processes that structure communities. Consistent with previous studies that have integrated niche and neutral arguments, we find that a combination of dispersal limitation combined with ecological segregation likely explains damselfly community turnover. Such patterns are especially likely in systems of relatively weak dispersers like damselflies (Thompson & Townsend, 2006). In combination with previous studies, we have now shown two ways in which niche and neutral process are likely to act within the damselfly system. First, within a given community, our previous experimental studies have shown that niche differences maintain damselfly genera within this system (McPeek, 1998; Siepielski *et al.*, 2011), whereas neutral-based ecological drift operates among species within a given genus (Siepielski *et al.*, 2010). Second, the present analysis focussing on among-community diversity suggests that weak ecological filters acting on the regional pool of *Enallagma* species of lakes with fish appears to result in assemblages of ecologically similar species which are probably undergoing ecological drift within a give lake. The latter results highlight the importance of distinguishing between mechanisms that regulate between- versus within-community species composition.

Acknowledgments

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Supporting Information

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

Appendix S1. Abundance data of damselflies from sampling 40 lakes and ponds in NH and VT during 2008 and 2009.

Figure S1. Variance partitioning of the Hellinger-transformed distance abundance matrix for damselfly genera and species of *Enallagma* among lakes.

Figure S2. Ordination plots from the partial RDA of damselfly genera and *Enallagma* species composition of Hellinger-transformed abundances among lakes.

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