

## LETTER

# Top predators determine how biodiversity is partitioned across time and space

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### Abstract

Natural ecosystems are shaped along two fundamental axes, space and time, but how biodiversity is partitioned along both axes is not well understood. Here, we show that the relationship between temporal and spatial biodiversity patterns can vary predictably according to habitat characteristics. By quantifying seasonal and annual changes in larval dragonfly communities across a natural predation gradient we demonstrate that variation in the identity of top predator species is associated with systematic differences in spatio-temporal  $\beta$ -diversity patterns, leading to consistent differences in relative partitioning of biodiversity between time and space across habitats. As the size of top predators increased (from invertebrates to fish) habitats showed lower species turnover across sites and years, but relatively larger seasonal turnover within a site, which ultimately shifted the relative partitioning of biodiversity across time and space. These results extend community assembly theory by identifying common mechanisms that link spatial and temporal patterns of  $\beta$ -diversity.

### Keywords

Beta-diversity, deterministic, meta-community, Odonata, phenology, spatial, stochastic, temporal.

*Ecology Letters* (2017) 20: 1004–1013

## INTRODUCTION

Natural communities are not constant. Instead, community structure can change substantially over short- and long-time scales (White *et al.* 2006; Magurran & Dornelas 2010; Hatosy *et al.* 2013; Shimadzu *et al.* 2013). For instance, species may occupy the same site but at different times because of differences in phenologies, leading to seasonal turnover in community composition (Winemiller 1990; Guo *et al.* 2002; Woodward *et al.* 2005; Shimadzu *et al.* 2013; Grøtan *et al.* 2014). Similarly, local extinction and recolonisation events or temporal variation in abiotic conditions (e.g. temperature, precipitation) can lead to changes in community composition across seasons and years, especially when species respond differentially to environmental changes (Chesson 2000; Amarasekare 2003; Angert *et al.* 2009; Gotelli *et al.* 2010; Angeler & Drakare 2013; Grøtan *et al.* 2014). While these studies emphasise the temporal dimension of biodiversity, we still have a limited understanding of how consistent these temporal patterns are across different environments and how they are related to spatial patterns (Magurran & Dornelas 2010; Wolfovich *et al.* 2014).

Theory predicts that diversity patterns should depend on the relative strength of deterministic vs. stochastic processes driving community assembly and stability (Paine 1969; Chase 2003, 2007, 2010; Fukami 2004; Farnon Ellwood *et al.* 2009; Fukami & Nakajima 2011). Spatial biodiversity can be partitioned into local species richness ( $\alpha$ -diversity), regional

species richness ( $\gamma$ -diversity), and variation in community composition across sites (spatial  $\beta$ -diversity) (Jost 2007). As deterministic processes (e.g. trait–environment matching, niche partitioning, keystone species) increase in relative importance, site-to-site variation in species composition (i.e. spatial  $\beta$ -diversity) should decrease among sites sharing similar characteristics (Paine 1969; Chase 2007, 2010). In contrast, when stochastic processes dominate (e.g. priority effects, colonisation/competition trade-offs) community assembly occurs relatively idiosyncratically and habitats should show large site-to-site variation in community structure (spatial  $\beta$ -diversity) at any given time point, even when environmental conditions are otherwise very similar (Amarasekare 2003; Chase 2003, 2007; Kneitel & Chase 2004; Leibold *et al.* 2004; Fukami & Nakajima 2011; Van Allen & Rudolf 2016). Thus, differences in factors such as habitat size and complexity (Geange & Stier 2010; Orrock & Watling 2010) or predation that alter the relative strength of stochastic vs. deterministic processes can alter biodiversity patterns (Chase 2007; Stegen *et al.* 2013). For example, high-altitude plant communities, with relatively harsh temperature, nutrient and rainfall conditions, often contain a more consistent and characteristic subset of species than lowland communities in the same region (Mori *et al.* 2013). Thus, theory predicts clear differences in spatial biodiversity patterns across habitats with strong vs. weak environmental filters, but do these patterns extend to stable and predictable dynamics over time?

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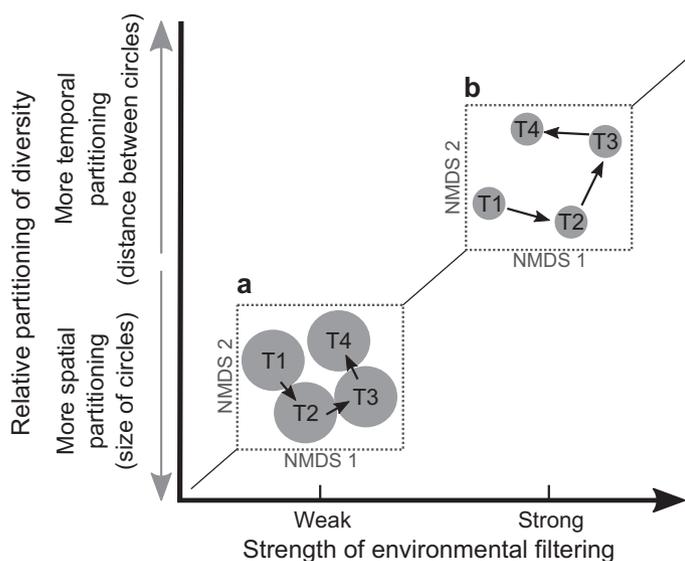
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Temporal changes in environmental conditions (e.g. temperature, precipitation) and differences in species phenologies can alter species composition within a site over time. This change in community composition over time at a given site is often referred to as temporal  $\beta$ -diversity. Extending the predictions on spatial  $\beta$ -diversity, habitats sharing the same strong environmental filter are expected to have a similar composition of species at all points in time because deterministic processes continuously dominate community assembly (Chase 2007; Chase *et al.* 2009). Consequently, we might also expect that temporal changes in species composition will be largely consistent across similar habitats (e.g. synchronised changes in community structure, Fig. 1). Conversely, communities lacking such strong environmental filters will be structured more stochastically and differ considerably from one another in community structure across both time and space. Given these differences in species composition, communities likely will show different patterns of phenologies and respond differentially to environmental change (Fig. 1). These communities should therefore exhibit less consistent temporal changes in species turnover compared to habitats with strong environmental filters.



**Figure 1** Hypothesised relationship between relative partitioning of  $\beta$ -diversity and strength of environmental filters. Habitats lacking strong environmental filters (a) are expected to be dominated by stochastic community assembly processes, resulting in a relatively larger proportion of dissimilarity across sites (large circle area) compared to across time (less space between circles, leading to lower temporal/spatial ratio of biodiversity partitioning). In contrast, in habitats with strong environmental filters (b), communities are dominated more by deterministic processes resulting in higher similarity of sites (small circle area) at any given time point and synchronised temporal species turnover. Thus, these habitats should partition relatively more of their overall biodiversity over time rather than between sites (space). Circles represent communities transitioning across times (T1–T4) in hypothetical NMDS space (mean  $\pm$  SE ellipse), with circle colour and location depicting differences in community composition. Circle size denotes the amount of  $\beta$ -diversity across sites within a time point (i.e. spatial dissimilarity), and distance among circles (arrows) shows  $\beta$ -diversity within sites across time points (i.e. temporal dissimilarity). However, this hypothetical pattern is untested and could be modified by a range of other factors.

Current theory thus suggests that there could be a systematic change in the relative partitioning of biodiversity across time and space (i.e. how much  $\beta$ -diversity within a single patch of habitat varies across time vs. how much it varies between different patches at a given point in time) with changes in the strength of environmental filters (Fig. 1), but this prediction relies on several largely untested assumptions. First, for temporal patterns of biodiversity to be consistent within a habitat, there must be an ‘intrinsic’ environmental filter that consistently determines the relative strength of stochastic vs. deterministic dynamics. This filter could be a continuous process, such as the presence of certain predator species, or a reoccurring process, such as a fire regime, as long as it selects for species with specific traits and thus leads to deterministic community structure. Second, there must be consistency in how the communities in different habitats respond to changing environmental conditions. In nature, environmental conditions can change substantially even over short time periods. For instance, abiotic (e.g. weather) or biotic (e.g. primary productivity) conditions change dramatically among seasons. These environmental changes can either modify an existing environmental filter over time or impose additional filters and thereby modify the relative strength of deterministic vs. stochastic processes within a given habitat and concordant spatial ( $\beta$ ) diversity patterns over time. Furthermore, they can lead to changes in community composition within a given habitat over time, but whether these changes are consistent across habitats remains unknown. To improve our understanding of the relationship between spatial and temporal patterns of biodiversity, we therefore need to determine how consistent differences in spatial  $\beta$ -diversity are across habitat types over time, whether habitats differ predictably in their temporal  $\beta$ -diversity and how these two patterns are related.

To fill this conceptual gap, we analysed the spatio-temporal patterns of biodiversity in habitats spanning a stochastic to deterministic gradient of drivers of community assembly. Specifically we used time series of natural larval odonate (dragonfly and damselfly) communities in freshwater ponds representing a diversity of environmental conditions to determine (1) what environmental factors are key drivers of spatio-temporal patterns of species composition, (2) whether there are consistent differences in the partitioning of spatio-temporal  $\beta$ -diversity across habitats that vary in the strength of habitat filtering (and thus deterministic vs. stochastic processes) as predicted by theory (Fig. 1), and (3) do these differences in spatio-temporal  $\beta$ -diversity vary predictably through time? We show that top predators were a key driver of spatio-temporal biodiversity patterns in our system. Importantly, habitats with different top predators differed substantially and predictably in how they partitioned biodiversity across time and space, indicating that differences in top predators led to concurrent differences in the relative strength of stochastic vs. deterministic processes.

## METHODS

To test our hypotheses, we sampled 45 freshwater ponds for the immature stages of dragonflies and damselflies. We sampled each pond four times per year (spring, summer, fall and

winter) over a 4-year period starting in summer 2008 (45 ponds  $\times$  14 dates = 630 samples). We also collected data on biotic and abiotic characteristics of ponds. Across all samples, we collected and identified 18 874 individual odonates from 36 species (see SI Methods for details, Table S1 for species list, Fig. S1 for  $\alpha$  diversity and Fig. S2 for individual abundances in different pond types). To measure  $\beta$ -diversity for the following statistical tests we used incidence-based Sørensen dissimilarity. We choose this metric for simplicity and consistency, but a number of other abundance- and incidence-based metrics produces very similar results (see SI, Figs S3 and S4, and Tables S3–S6).

### Predictors of biodiversity patterns

We employed distance-based linear models (DISTLM) to identify the factors that best explained variation in odonate community structure, using the software program PRIMER 6 & PERMANOVA+ (McArdle & Anderson 2001). Through comparison of a series of conditional tests, this analysis also allowed us to determine how much of the variation in community structure is explained by each predictor alone as well as the amount of overlap in variation explained by multiple predictors (see Anderson & Gribble 1998 for calculation methods). To perform the test, we generated an  $n \times p$  matrix of response variables (i.e. odonate abundances) and an  $n \times r$  matrix of predictor variables (i.e. pond characteristics), where  $n$  = pond identity by survey date combination,  $p$  = odonate species identity, and  $r$  = pond characteristic identity. Top predator, season and year were included in analyses as categorical predictors, while canopy cover, spatial position (latitude, longitude), pond area, pond depth and aquatic vegetation cover were included as continuous predictors. These analyses require exclusion of empty samples (i.e. pond-date combinations with no odonates) because (dis)similarity is undefined for any pairwise comparison of communities in which at least one of the two values is zero (McArdle & Anderson 2001). Fifty-one of 630 samples were empty (8.1%), with 25 due to dry pond conditions and 26 due to no odonates found during sampling. Empty ponds and comparisons involving empty ponds were excluded from all other analyses as well. All predictors were normalised, and AIC was used for model selection. Model selection did not eliminate any of the predictors from the model, so we only eliminated predictors that increased the variation explained by  $< 1\%$  (i.e. pond depth and surface area) (McArdle & Anderson 2001). These analyses indicated that top predator type explained more variation in odonate community structure than any other predictor, followed by season of the year, informing our decision to focus on these predictors.

Based on results from this analysis, we categorised ponds into four groups based on top predator type: largemouth bass (*Micropterus salmoides*), green sunfish (*Lepomis cyanellus*), salamander (multiple species) and invertebrate (multiple species) (see SI methods for details). Bass and green sunfish are both generalist predators, but bass grow larger in size and become piscivorous (including consumption of green sunfish). Therefore, bass ponds exhibit an additional trophic level compared to green sunfish ponds.

Assuming that the strength of filtering processes generally increases with predator body size and foraging efficiency (Wellborn *et al.* 1996), we followed previous studies (Chase *et al.* 2009) by categorising ponds with only invertebrate predators as most stochastic (weakest predation filter) ( $N = 5$ ), and assumed that deterministic processes increase in relative importance from habitats dominated by salamanders (multiple species,  $N = 13$ ), to green sunfish ( $N = 13$ ) and finally largemouth bass ( $N = 15$ ) respectively. Many species of fish are voracious predators of smaller aquatic animals. As a consequence many aquatic organisms, including odonates, have developed the ability to detect which predator species are present before selecting a habitat (Binckley & Resetarits 2005; McCauley & Rowe 2010; Resetarits & Silberbush 2016) and only odonates that have certain anti-predator traits (e.g. spines, reduced activity) can reliably recruit successfully in ponds with fish (McPeck 1990; Johansson & Samuelsson 1994; Wellborn *et al.* 1996). Salamanders are also generalist predators and can have strong impacts on community structure but not to the extent of fish (Morin 1981; Fauth 1999). Some salamander ponds did not always contain salamanders, however, due to their complex life cycles. Except for the odonates, all major invertebrate predators are present in ponds throughout the hydroperiod (see supplementary methods for additional salamander and invertebrate species lists and other details). Note that top predator classification simply indicates that no predators from a higher trophic level were ever present in the community, although all ponds contained a diverse group of predators in addition to the named species (see SI methods S1 and Table S2). Categorising habitats by top predator type has proven useful for describing and predicting the composition of communities of a variety of aquatic taxa, particularly crustaceans, amphibians and insects such as odonates (Wellborn *et al.* 1996; Binckley & Resetarits 2005; Werner *et al.* 2007; McCauley *et al.* 2008; Resetarits & Silberbush 2016). This natural predation gradient thus provided an excellent opportunity to test our hypothesis that differences in strength of environmental filters lead to systematic differences in the partitioning of biodiversity along the time-space axis.

### Spatial and temporal $\beta$ -diversity

To explore how both spatial and temporal  $\beta$ -diversity changed over time for the odonate communities in our four top predator pond types, we used general linear mixed effects models. For spatial dissimilarity we examined whether top predator type, seasonal transition (i.e. spring to summer), year and their interactions affected pairwise  $\beta$ -diversity among ponds. This model included a random effect of both ponds (e.g. pond A and pond B) used in each of the pairwise diversity values. For temporal  $\beta$ -diversity, we also examined whether top predator type, seasonal transition (i.e. spring to summer), year and their interactions affected temporal dissimilarity (i.e.  $\beta$ -diversity within a site from one season to the next), treating site identity as a random effect. These tests are designed to determine whether ponds with different levels of predation differ from one another in spatial or temporal  $\beta$ -diversity patterns of odonates.

### Ordinations of community structure across years and seasons

We used ordination to visually examine how community structure transitions across seasons and years for pond communities with each of the four top predators. Specifically, we used non-metric multidimensional scaling (nMDS) with Sørensen dissimilarities based on square root transformed abundances of species using the ‘vegan’ package in R (Oksanen *et al.* 2015). In addition, we calculated centroids of every predator type  $\times$  season  $\times$  year combination using the same software. This examination of community structure over time allows us to visualise how odonate communities in ponds with different top predators changed differently over the seasons and year of our sampling.

### Partitioning of $\beta$ -diversity in time and space

To test how ponds in our different predator groups partitioned biodiversity (i.e.  $\beta$ -diversity) between time and space, we examined the natural log-transformed ratio of the temporal and spatial  $\beta$ -diversity for each top predator group using a general linear model. We quantified temporal  $\beta$ -diversity between a site and itself one season in the future and spatial biodiversity as the mean pairwise dissimilarity between all sites with a common predator type, within a single season. This compares changes in temporal and spatial diversity across seasons by examining how ponds in a predator group at specific times differ from one another, and then how ponds differ from themselves across time. We included the season used for the spatial  $\beta$ -diversity measurement as a covariate as well as the interaction between season and top predator status. This approach satisfied the assumptions of the tests and fit our data well.

This approach gives four ‘spatial’  $\beta$ -diversity values for each seasonal sample, one for each top predator group, and four corresponding temporal  $\beta$ -diversity points for a total of 52 values across 4 years. As the number of samples is one higher than the number of transitions between samples, we chose to compare the  $\beta$ -diversity of first spatial sample to each temporal transition (e.g. the fall to winter temporal comparison paired with the fall sample spatial comparisons for the regression and so on). As a result, we appended the final spatial sample of our data set. This test is designed to determine whether the relative strength of temporal or spatial  $\beta$ -diversity is significantly different between communities structured by different top predators. We obtained the same general result when we repeated the analysis using the second spatial sample instead of the first or the mean of the first and second spatial sample. We additionally repeated all tests using Bray–Curtis, Jaccard, Gower, AltGower and Euclidean  $\beta$ -diversity (Oksanen *et al.* 2015; Stier *et al.* 2016) to control for differences in metric sensitivity to incidence and relative abundance as well as using repeated subsampling to control for variation caused by differences in pond number or individual abundance between top predator groups (see SI). All additional analyses resulted in qualitatively identical results with the same significant effects.

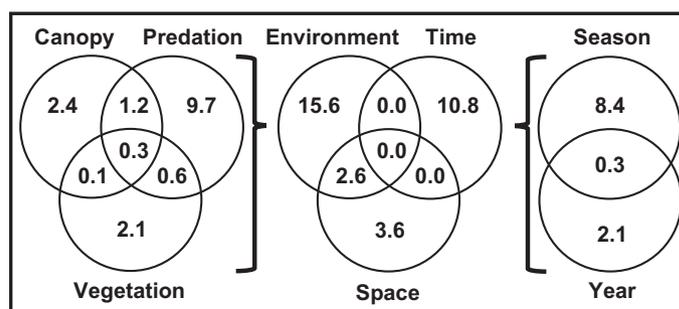
## RESULTS

### DISTLM analysis

Results for incidence- and abundance-based analyses were highly similar. Therefore, we describe here only the results for the incidence-based analyses (but see Tables S3–S6 for results of additional analyses). The predictors included in the final model explained 32.6% of the variation in odonate community structure (Fig. 2, Tables S4). The environmental predictor group explained 1.7 $\times$  and 2.9 $\times$  the variation explained by the temporal and spatial groups, respectively (Fig. 2). Variation explained by the environmental and spatial groups overlapped by 2.6%, but that which was explained by the temporal group did not overlap with either of the other groups. The environmental group predicted more variation than the other two groups, in part, because top predator type explained more variation than any other predictor in the model, at least 3 $\times$  more variation than any other environmental predictor (Fig. 2, Table S6). Season (Winter, Spring, Summer and Fall) explained 3.6 $\times$  more variation than year, the other temporal predictor and explained 74% as much variation in community structure as top predator type (Fig. 2). The strong effect of top predator on aquatic community structure is consistent with previous work in similar systems (Werner *et al.* 2007; McCauley *et al.* 2008; Chase *et al.* 2009). The importance of season is expected given the differences in phenologies of species (Abbot 2006) and indicates that odonate communities vary significantly over time.

### Temporal consistency of spatial $\beta$ -diversity

We found striking differences in how odonate diversity was spatially structured in different habitat types. Spatial  $\beta$ -diversity was significantly influenced by the three-way interaction between top predator type, season and year (Wald  $\chi^2 = 59.604$ , d.f. = 9,  $P < 0.0001$ , Fig. 3a). Generally, salamander and invertebrate ponds showed higher spatial dissimilarity



**Figure 2** Percent of variation in odonate community structure explained by predictors as determined by distance-based linear models. Centre: Predictors grouped into three general categories of environment, space and time. Left: The environmental predictor category decomposed into its three primary components (top predator, canopy cover and aquatic vegetation). Right: The temporal predictor category decomposed into its two components (season and year). Space has no underlying predictors. Predictors that increased the explained variation by  $< 1\%$  are excluded. Note that 2.6% of the variation explained by the environmental predictors overlaps with that explained by the spatial predictor category.

than green sunfish and bass ponds, although this difference varied by season and year (Fig. 3a). The large increase in spatial dissimilarity in all habitat types in the spring of 2010 was associated with lower abundances of many species that season (Fig. S2). In general, the higher spatial  $\beta$ -diversity (and thus larger variation across habitats) in invertebrate and salamander ponds is consistent with the hypothesis that they are consistently more dominated by stochastic processes compared to fish ponds which showed much more similar community compositions indicating that deterministic processes were more important in these habitat types (Fig. 3a).

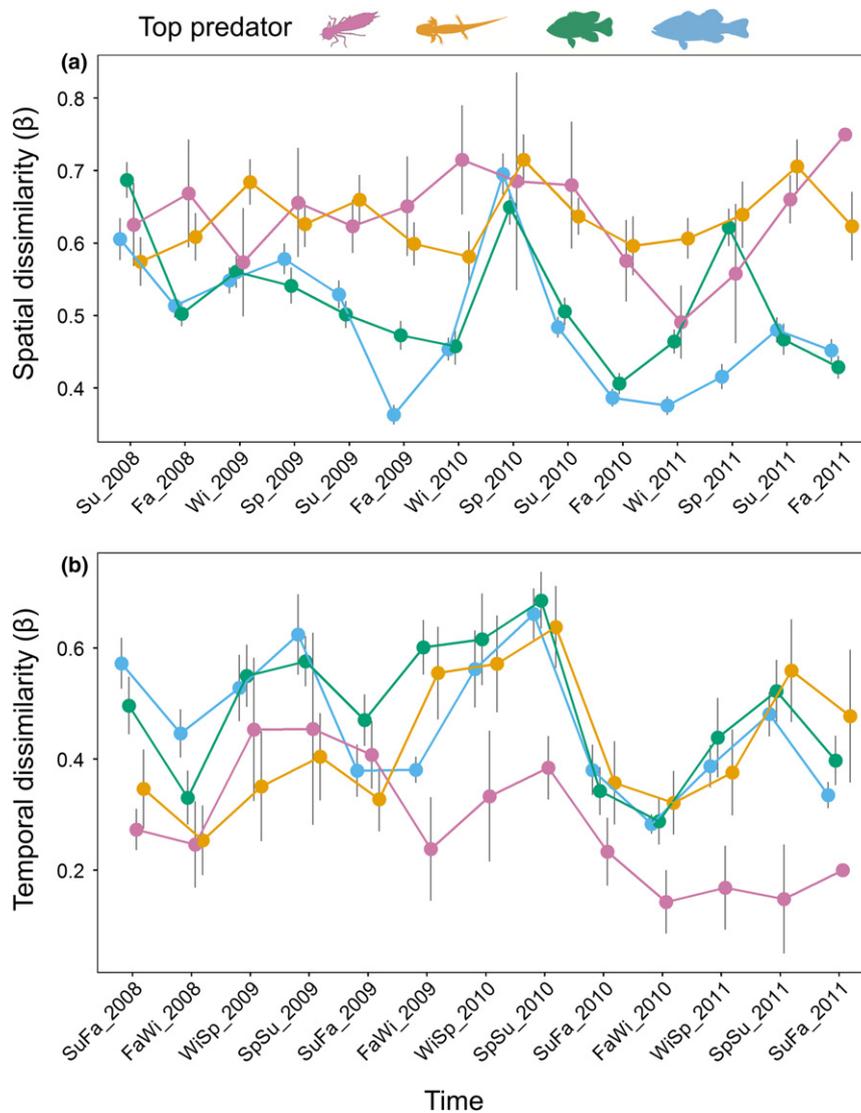
#### Temporal consistency of season-to-season $\beta$ -diversity

Analysis of temporal (season to season) trends of  $\beta$ -diversity in our pond communities revealed that bass and green sunfish

ponds (i.e. more deterministic communities) had higher temporal dissimilarity in all years except 2011 (salamander ponds had highest temporal dissimilarity), resulting in a significant interaction between top predator type and year (Wald  $\chi^2 = 24.41$ , d.f. = 9,  $P = 0.0037$ , Fig. 3b). The amount of dissimilarity generated by all transitions varied from year to year, although the spring–summer transition consistently led to the most change across all top predator pond types (significant transition by year interaction; Wald  $\chi^2 = 56.12$ , d.f. = 6,  $P < 0.0001$ , Fig. 3b).

#### Ordinations of community structure across years and seasons

Ordinations revealed that habitat types clearly differed in their temporal variation in species composition over seasons and years. Bass (Fig. 4a) and green sunfish (Fig. 4b) communities



**Figure 3** Patterns of spatial and temporal  $\beta$ -diversity over time among communities with different top predators. Panel (a) depicts patterns in spatial dissimilarity, quantified as the mean pairwise Sørensen dissimilarity among all sites of a top predator type.  $X$  axis represents season and year (Su = Summer, Fa = Fall, Wi = Winter, Sp = Spring). Panel (b) shows patterns in temporal dissimilarity, quantified as the Sørensen  $\beta$ -diversity between a site at a given time ( $t_x$ ) and itself one season later ( $t_{x+1}$ ).  $X$  axis denotes time as Season1Season2\_year (e.g. SuFa is the transition from summer to fall, WiSp is the transition from winter to spring). For both panels,  $Y$  axis is mean Sørensen diversity  $\pm 1$  SE, and colours represent the top predator in each site.

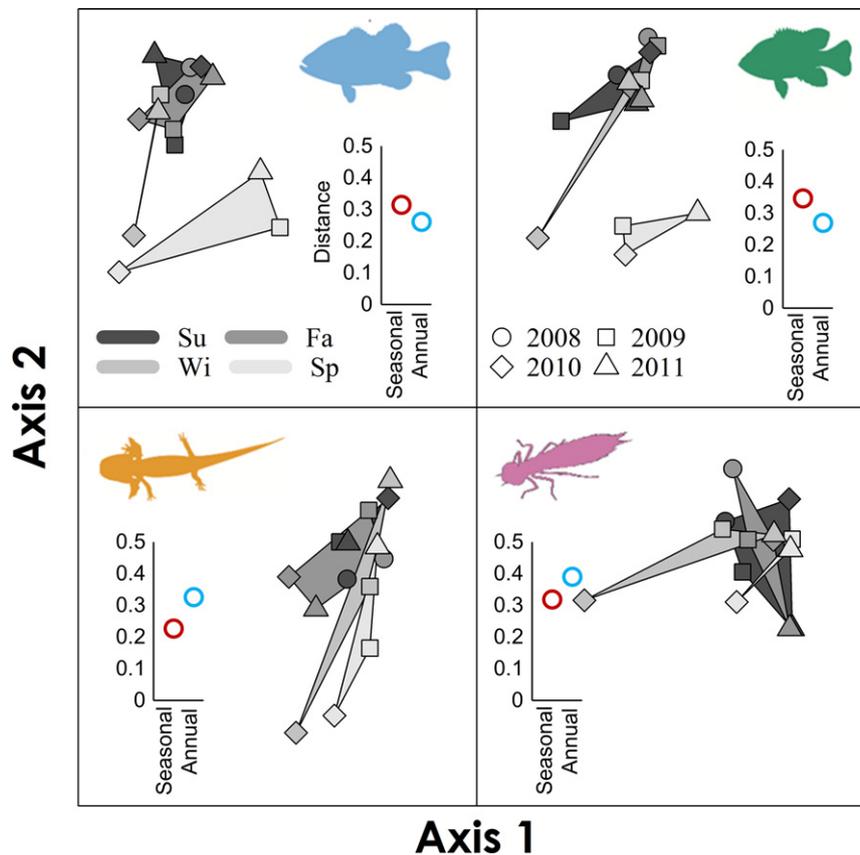
transitioned through distinct shifts in species composition across seasons but returned to similar compositions each year (Fig. 4). In contrast, seasonal changes in community composition were generally smaller in both salamander and invertebrate ponds and much less predictable across years and within seasons (Fig. 4c,d).

### Partitioning of $\beta$ -diversity in time and space

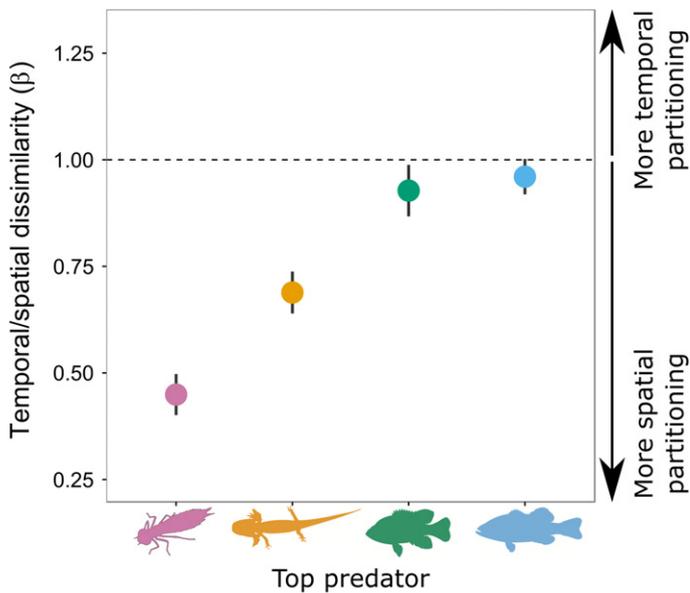
Examining the seasonal dynamics of our odonate ponds, we found that habitats with stronger environmental filters (i.e. those with large and active fish predators) harboured a significantly larger proportion of their  $\beta$ -diversity across time (i.e. seasons) relative to space (Fig. 5, top predator identity effect,  $\chi^2 = 18.08$ ,  $P < 0.001$ ). Specifically,  $\beta$ -diversity in fish ponds was almost equal across time and space. Conversely, salamander and invertebrate ponds harboured increasingly more  $\beta$ -diversity across space than time (Fig. 5). Neither seasonal transition ( $\chi^2 = 2.48$ ,  $P = 0.479$ ) nor the interactions

between top predator identity and season ( $\chi^2 = 3.19$ ,  $P = 0.956$ ) were significant predictors of the partitioning of temporal and spatial  $\beta$ -diversity, indicating that each of the communities in ponds with different top predator types still responded to seasonal variation in similar ways (also see Figs 3 and 4).

The striking difference in the spatio-temporal partitioning of biodiversity of fish vs. salamander and invertebrate habitats was driven by both higher spatial  $\beta$ -diversity and lower temporal  $\beta$ -diversity for the latter two habitat types (see Fig. 3). Interestingly, despite clear differences in odonate species composition (Table S1) and environmental characteristics (Table S2) between green sunfish habitats and bass habitats, both habitat types showed almost identical spatio-temporal biodiversity partitioning patterns. This indicates that results are not simply driven by differences in community composition across habitat types and suggests that habitats with similar filters likely show similar biodiversity partitioning across time and space. Extensive simulations based on



**Figure 4** Top predator type drives differences among habitats in seasonal and annual shifts in community structure. Points represent centroids of year × season × predator combinations in NMDs plots. Hulls connect centroids of a given season (abbreviated in the figure caption, different shades) in different years (shapes in the caption) and their size represents annual variation in community structure within a season for habitats with a given top predator type. The mean Euclidean distance between the same seasons across years (light blue circles in plot insets) vs. between subsequent seasons across years (dark red circles) is 1.29 times shorter for green sunfish, 1.21 times shorter for bass, 1.44 times longer for salamanders and 1.22 times longer for invertebrates. The patterns made by fish communities over time indicate that deterministic communities vary more across seasonal transitions than they do from 1 year to the next. In contrast, salamander and invertebrate communities vary less across seasons, but much more from 1 year to the next. This indicates that deterministic communities undergo seasonal shifts that return to their previous state, while stochastic communities 'drift' in composition more slowly, but do not necessarily return to the previous state. Axes (NMDs scores) are equivalent for each panel. Stress = 0.22. Horizontal axis explains 52% of community variation. Vertical axis explains 20% of community variation.



**Figure 5** Differences in partitioning of biodiversity in time vs. space in natural habitats with different top predators. Odonate communities with fish predators, which represent more deterministic environmental filtering of community assembly, partition  $\beta$ -diversity nearly evenly between time and space (i.e. the same community one season later is roughly as different as two different communities at the same time). In contrast, salamander and invertebrate ponds differ more from each other at any given time than they do over time, indicating a clear difference in partitioning of biodiversity across predator categories.

different null models also confirmed that these patterns are robust and were not driven by potential differences among habitat types in sample size, species diversity or size of habitats (Figs S3–S6).

## DISCUSSION

Natural ecosystems are shaped along two fundamental axes, space and time, but how biodiversity is partitioned along both axes is not well understood. Our results demonstrate that biodiversity partitioning along space and time can differ systematically across a natural predation gradient, but the relationship between spatial and temporal diversity along this gradient depended upon the temporal scale examined. As the size of top predators increased (from invertebrates to fish) habitats showed lower species turnover across sites and years, but larger seasonal turnover within a site, which ultimately shifted the relative partitioning of biodiversity across time and space (Figs 4 and 5). Overall, the systematic differences in temporal-spatial patterns of biodiversity suggest that similar processes shape both temporal and spatial dimension of biodiversity.

### Differences in temporal biodiversity patterns

Ecologists have long recognised that all habitats go through temporal changes in community composition, but predicting which habitats should change more than others and how these changes are related to spatial variation remained elusive. We

found a positive relationship between top predator body size and seasonal turnover in community composition, but a negative relationship between predator size and annual turnover. The reversal of seasonal and annual patterns of temporal change in our communities can be explained by the strength of environmental filtering present in more deterministic communities. The vast majority of odonates in our system complete their larval stages in a few months and different species have different breeding phenologies (Abbot 2006). This leads to different seasonal guilds of odonate larvae, and the shift between these guilds was most likely a major driver of temporal change in all habitats. However, fish-dominated communities had much smaller spatial  $\beta$ -diversity, suggesting that fish acted as strong environmental filters (Fig. 3a) (Chase 2007; Chase *et al.* 2009). This is consistent with previous field and experimental studies, which indicate that fish select for certain traits of species that reduce risk of fish predation (e.g. defensive spines, reduced activity) (Benke & Benke 1975; McPeck 1990; Johansson & Samuelsson 1994; Wellborn *et al.* 1996). Similar odonate species composition across habitats also implies similar patterns of phenologies. Thus, when seasons changed and species abundance and presence changed with them, a similar set of species tended to colonise and emerge from fish ponds, leading to a clear seasonal signal of temporal  $\beta$ -diversity. However, because of the strong environmental filter, the seasonal dynamics of odonate community assembly were highly similar among years (i.e. low interannual variation).

Habitats dominated by salamanders and invertebrates (i.e. stochastic communities) contained many species that rarely, if ever, persist in fish ponds. However, the high spatial  $\beta$ -diversity we observed between communities supports our hypothesis that they formed based on more idiosyncratic colonisation events. The lack of a characteristic suite of species changing in abundance across all ponds without fish predators could then explain the weaker seasonal  $\beta$ -diversity we observed within ponds. Furthermore, because a relatively 'random' set of species would colonise each pond every year for a given season, odonate communities in habitats without fish would change more with time (i.e. greater change over one year than over one season), as we also observed. This stochastic drift in community structure is consistent with theory and is expected in the absence of strong environmental filters (Chase *et al.* 2009; Stegen *et al.* 2013). Thus, differences in the relative strength of deterministic vs. stochastic processes across the predation gradient can explain variation in spatial, seasonal and annual  $\beta$ -diversity patterns.

The life histories and meta-community dynamics in pond odonate systems help explain why both incidence- and abundance-based dissimilarity metrics show nearly identical results. Different odonate species vary markedly in their dispersal behaviour (Wellborn *et al.* 1996; McCauley *et al.* 2008), in their ability to persist under the threat of different predator regimes and how they affect other odonates (Benke & Benke 1975; McPeck 1990; Wellborn *et al.* 1996). Thus, habitat selection and individual performance are driven by similar factors, likely leading to correlated variation in both the incidence of species and their abundance along the predation gradient, depending on adult oviposition choices and the

growth and survival of larvae hatching from their eggs. In other systems where different sets of factors determine patterns of community dynamics, abundance and presence patterns may not be correlated. Consequently, dissimilarity metrics which capture only incidence or relative abundance may not be able to identify differences between stochastic and deterministic dynamics in these systems. For example, in communities with stable sets of species that vary in abundance but not incidence, incidence-based metrics of temporal dissimilarity would not detect effects that abundance-based metrics would. It is important to pick appropriate metrics which can capture the way in which the communities being studied actually change over time and space.

While our study focused on a freshwater pond system with well-known environmental filter mechanisms, similar patterns are likely to occur in many other systems. Seasonal changes in community composition are ubiquitous in nature, and there is ample evidence that strong gradients in predation pressure exist in marine, freshwater and terrestrial systems for both animal and plant taxa (Crooks & Soulé 1999; Meyers & Worm 2003; Kolb *et al.* 2007; Shimadzu *et al.* 2013). Furthermore, predation pressure is only one type of environmental filter, and similar patterns are expected along other gradients of environmental filters such as drought, extreme temperatures or productivity (Chase 2007, 2010; Chase *et al.* 2009; Mori *et al.* 2013; Stegen *et al.* 2013; Grøtan *et al.* 2014; Huttunen *et al.* 2014). Importantly the magnitude of the temporal turnover will likely depend on the sampling interval relative to the length of the generation cycle or developmental periods of species within a community. For instance, microbial communities can turn over in minutes while tree communities turn over in decades. Thus, the patterns we have identified should apply to a large range of systems, although the time scale at which they manifest can vary among systems.

### Systematic variation in spatio-temporal biodiversity patterns

Our results suggest that we can improve our ability to sample and understand community dynamics in two ways. Ecologists often sample biodiversity by visiting many sites a single time because human or capital resources are often limited (Joseph *et al.* 2009; Lindenmayer *et al.* 2012). However, our results indicate that this may not be sufficient to quantify biodiversity patterns and that the most efficient sampling regime may differ depending on the habitat type. If deterministic processes are known to dominate (e.g. our fish ponds), repeated observations of a few sites could provide the most efficient way to quantify diversity because sites are very similar and change consistently over time. In contrast, more sites must be sampled when stochastic processes dominate (e.g. invertebrate ponds), but it may not be necessary to sample as heavily across time. As a result, repeated sampling on the correct scale of temporal cycling for a community is critically important to adequately quantify species diversity or variation in community structure. When time-series data are available, our results also suggest that it may be possible to infer the relative strength of stochastic and deterministic process structuring community assembly by using similar methods to our own.

Understanding more about the interplay between temporal and spatial variation in community structure and turnover is important for enhancing our ability to monitor and understand species and communities.

### CONCLUSIONS

The incidence and abundance of species varies over both short and long time scales in virtually every ecosystem. Understanding how these dynamics vary across habitats with different characteristics gives us an important window into the organisation of natural biodiversity. For instance, invasive species, pollution, extinction of top predators, desertification and climate change can either remove or add a strong environmental filter (Estes *et al.* 2011; Harley 2011; Wardle *et al.* 2011; Garcia *et al.* 2014). Our results indicate that such changes can shift how biodiversity is partitioned across time and space. They also shed new light onto the fundamental processes that drive biodiversity patterns and suggest that we need to revise existing strategies to take a multidimensional approach that account for both spatial and temporal scales when assessing and protecting biodiversity.

### ACKNOWLEDGEMENTS

We thank the wildlife biologists of the U.S.D.A. Forest Service Wildlife and Silviculture Southern Research Laboratory, particularly D. Saenz, for locating the study ponds and conducting preliminary surveys of the predator communities. We also thank A. Roman and G. Ross for help collecting samples and P. Delclos for help with keying odonates. This work was supported by NSF DEB-1256860 and DEB-0841686 to V.H.W. Rudolf.

### AUTHORSHIP

VHWR, NLR, CJD and BGV conceived of and designed the study, conducted field work and processed samples, VHWR, NLR, CJD, BGV and PAC analysed data, VHWR and BGV wrote the manuscript with significant input from all authors.

### DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: doi:10.5061/dryad.c553k.

### REFERENCES

- Abbot, J. (2006). *Dragonflies and Damselflies (Odonata) of Texas, Volume I*. The Odonata Survey of Texas, Austin, Texas.
- Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a synthesis: Spatial coexistence mechanisms. *Ecol. Lett.*, 6, 1109–1122.
- Anderson, M.J. & Gribble, N.A. (1998). Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. *Aust. J. Ecol.*, 23, 158–167.
- Angeler, D.G. & Drakare, S. (2013). Tracing alpha, beta, and gamma diversity responses to environmental change in boreal lakes. *Oecologia*, 172, 1191–1202.

- Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009). Functional tradeoffs determine species coexistence via the storage effect. *Proc. Natl Acad. Sci.*, 106, 11641–11645.
- Benke, A.C. & Benke, S.S. (1975). Comparative dynamics and life histories of coexisting dragonfly populations. *Ecology*, 56, 302–317.
- Binkley, C.A. & Reseritis, W.J. (2005). Habitat selection determines abundance, richness and species composition of beetles in aquatic communities. *Biol. Lett.*, 1, 370–374.
- Chase, J.M. (2003). Community assembly: when should history matter? *Oecologia*, 136, 489–498.
- Chase, J.M. (2007). Drought mediates the importance of stochastic community assembly. *Proc. Natl Acad. Sci.*, 104, 17430–17434.
- Chase, J.M. (2010). Stochastic community assembly causes higher biodiversity in more productive environments. *Science*, 328, 1388–1391.
- Chase, J.M., Biro, E.G., Ryberg, W.A. & Smith, K.G. (2009). Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. *Ecol. Lett.*, 12, 1210–1218.
- Chesson, P. (2000). General theory of competitive coexistence in spatially-varying environments. *Theor. Popul. Biol.*, 58, 211–237.
- Crooks, K.R. & Soulé, M.E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, 400, 563–566.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. *et al.* (2011). Trophic downgrading of planet earth. *Science*, 333, 301–306.
- Farnon Ellwood, M.D., Manica, A. & Foster, W.A. (2009). Stochastic and deterministic processes jointly structure tropical arthropod communities. *Ecol. Lett.*, 12, 277–284.
- Fauth, J. (1999). Identifying potential keystone species from field data – an example from temporary ponds. *Ecol. Lett.*, 2, 36–43.
- Fukami, T. (2004). Assembly history interacts with ecosystem size to influence species diversity. *Ecology*, 85, 3234–3242.
- Fukami, T. & Nakajima, M. (2011). Community assembly: alternative stable states or alternative transient states? *Ecol. Lett.*, 14, 973–984.
- Garcia, R.A., Cabeza, M., Rahbek, C. & Araujo, M.B. (2014). Multiple dimensions of climate change and their implications for biodiversity. *Science*, 344, 1247579.
- Geange, S.W. & Stier, A.C. (2010). Priority effects and habitat complexity affect the strength of competition. *Oecologia*, 163, 111–118.
- Gotelli, N.J., Dorazio, R.M., Ellison, A.M. & Grossman, G.D. (2010). Detecting temporal trends in species assemblages with bootstrapping procedures and hierarchical models. *Philos. Trans. R. Soc. B Biol. Sci.*, 365, 3621–3631.
- Grøtan, V., Lande, R., Chacon, I.A. & DeVries, P.J. (2014). Seasonal cycles of diversity and similarity in a Central American rainforest butterfly community. *Ecography*, 37, 509–516.
- Guo, Q., Brown, J.H. & Valone, T.J. (2002). Long-term dynamics of winter and summer annual communities in the Chihuahuan Desert. *J. Veg. Sci.*, 13, 575–584.
- Harley, C.D.G. (2011). Climate change, keystone predation, and biodiversity loss. *Science*, 334, 1124–1127.
- Hatosy, S.M., Martiny, J.B., Sachdeva, R., Steele, J., Fuhrman, J.A. & Martiny, A.C. (2013). Beta diversity of marine bacteria depends on temporal scale. *Ecology*, 94, 1898–1904.
- Huttunen, K.-L., Mykrä, H., Huusko, A., Mäki-Petäys, A., Vehanen, T. & Muotka, T. (2014). Testing for temporal coherence across spatial extents: the roles of climate and local factors in regulating stream macroinvertebrate community dynamics. *Ecography*, 37, 599–608.
- Johansson, F. & Samuelsson, L. (1994). Fish-induced variation in abdominal spine length of *Leucorrhinia dubia* (Odonata) larvae? *Oecologia*, 100, 74–79.
- Joseph, L.N., Maloney, R.F. & Possingham, H.P. (2009). Optimal allocation of resources among threatened species: a project prioritization protocol. *Conserv. Biol.*, 23, 328–338.
- Jost, L. (2007). Partitioning diversity in independent alpha and beta components. *Ecology*, 88, 2427–2439.
- Kneitel, J.M. & Chase, J.M. (2004). Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecol. Lett.*, 7, 69–80.
- Kolb, A., Ehrlen, J. & Eriksson, O. (2007). Ecological and evolutionary consequences of spatial and temporal variation in pre-dispersal seed predation. *Perspect. Plant Ecol. Evol. Syst.*, 9, 79–100.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F. *et al.* (2004). The metacommunity concept: a framework for multi-scale community ecology: The metacommunity concept. *Ecol. Lett.*, 7, 601–613.
- Lindenmayer, D.B., Gibbons, P., Bourke, M., Burgman, M., Dickman, C.R., Ferrier, S. *et al.* (2012). Improving biodiversity monitoring. *Austral Ecol.*, 37, 285–294.
- Magurran, A.E. & Dornelas, M. (2010). Biological diversity in a changing world. *Philos. Trans. R. Soc. B Biol. Sci.*, 365, 3593–3597.
- McArdle, B.H. & Anderson, M.J. (2001). Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, 82, 290–297.
- McCaughey, S.J. & Rowe, L. (2010). Notonecta exhibit threat-sensitive, predator-induced dispersal. *Biol. Lett.*, 6, 449–452.
- McCaughey, S.J., Davis, C.J., Relyea, R.A., Yurewicz, K.L., Skelly, D.K. & Werner, E.E. (2008). Metacommunity patterns in larval odonates. *Oecologia*, 158, 329–342.
- McPeck, M.A. (1990). Determination of species composition in the enallagma damselfly assemblages of permanent lakes. *Ecology*, 71, 83–98.
- Meyers, R.A. & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, 423, 280–283.
- Mori, A.S., Shiono, T., Koide, D., Kitagawa, R., Ota, A.T. & Mizumachi, E. (2013). Community assembly processes shape an altitudinal gradient of forest biodiversity: Altitudinal changes in community assembly processes. *Glob. Ecol. Biogeogr.*, 22, 878–888.
- Morin, P.J. (1981). Predatory salamanders reverse the outcome of competition among three species of Anuran Tadpoles. *Science*, 212, 1284–1286.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B. *et al.* (2015). *vegan: Community Ecology Package*. R package version 2.4-2. <https://CRAN.R-project.org/package=vegan>.
- Orrock, J.L. & Watling, J.I. (2010). Local community size mediates ecological drift and competition in metacommunities. *Proc. R. Soc. B Biol. Sci.*, 277, 2185–2191.
- Paine, R.T. (1969). A note on trophic complexity and community stability. *Am. Nat.*, 103, 91–93.
- Reseritis, W.J. & Silberbush, A. (2016). Local contagion and regional compression: habitat selection drives spatially explicit, multiscale dynamics of colonisation in experimental metacommunities. *Ecol. Lett.*, 19, 191–200.
- Shimadzu, H., Dornelas, M., Henderson, P.A. & Magurran, A.E. (2013). Diversity is maintained by seasonal variation in species abundance. *BMC Biol.*, 11, 1–9.
- Stegen, J.C., Freestone, A.L., Crist, T.O., Anderson, M.J., Chase, J.M., Comita, L.S. *et al.* (2013). Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities: drivers of spatial and temporal turnover. *Glob. Ecol. Biogeogr.*, 22, 202–212.
- Stier, A.C., Bolker, B.M. & Osenberg, C.W. (2016). Using rarefaction to isolate the effects of patch size and sampling effort on beta diversity. *Ecosphere*, 7, e01612.
- Van Allen, B.G. & Rudolf, V.H. (2016). Carryover effects drive competitive dominance in spatially structured environments. *Proc. Natl Acad. Sci.*, 113(25), 6939–6944.
- Wardle, D.A., Bardgett, R.D., Callaway, R.M. & Van der Putten, W.H. (2011). Terrestrial ecosystem responses to species gains and losses. *Science*, 332, 1273–1277.
- Wellborn, G.A., Skelly, D.K. & Werner, E.E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annu. Rev. Ecol. Syst.*, 337–363.

- Werner, E.E., Skelly, D.K., Relyea, R.A. & Yurewicz, K.L. (2007). Amphibian species richness across environmental gradients. *Oikos*, 116, 1697–1712.
- White, E.P., Adler, P.B., Lauenroth, W.K., Gill, R.A., Greenberg, D., Kaufman, D.M. *et al.* (2006). A comparison of the species-time relationship across taxonomic groups. *Oikos*, 185–195.
- Winemiller, K.O. (1990). Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.*, 60, 331–367.
- Wolkovich, E.M., Cook, B.I., McLauchlan, K.K. & Davies, T.J. (2014). Temporal ecology in the Anthropocene. *Ecol. Lett.*, 17, 1365–1379.
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. *et al.* (2005). Body size in ecological networks. *Trends Ecol. Evol.*, 20, 402–409.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Editor, Jonathan Chase

Manuscript received 25 January 2017

First decision made 2 March 2017

Manuscript accepted 18 May 2017

**Supplementary Material For:**

**Top predators determine how biodiversity is partitioned across time and space**

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**This file includes:**

Materials and Methods

Figs. S1 to S6

Tables S1 to S6

## **Materials and Methods**

### **Data collection**

#### *Study system*

We studied communities of pond-dwelling nymphs of dragonflies and damselflies (Order Odonata) to determine how diversity is partitioned across space (i.e., among ponds) versus time (i.e., across seasons and years) as well as whether this relative partitioning differs predictably across pond habitat types (i.e., different top predators). These ponds were located within two neighboring national forests (as little as 33 km apart) in the Piney Woods ecoregion of eastern Texas. We sampled 36 ponds in the Davy Crockett National Forest (DCNF; Houston and Trinity Counties) and nine ponds in the Angelina National Forest (ANF; Angelina, Nacogdoches, San Augustine, and Jasper Counties). These ponds were constructed between 1988 and 1995 for wildlife habitat improvement and are distributed throughout the two forests. Despite their anthropogenic origins, these ponds vary substantially in abiotic and biotic characteristics (see ‘Habitat characteristics’ below).

#### *Specimen collection and identification*

To determine how community structure changed over space and time, we sampled odonates in the 45 ponds four times per year (generally February, April, July, and October) for three consecutive years (July 2008 to October 2011; 14 samples per pond). Four full days were generally required to sample all ponds. Depending on weather conditions, these days were usually consecutive and were never spread over more than nine days. Samples were collected by making standardized sweeps with dip nets (net:

40.6 cm × 22.9 cm; mesh diameter: 0.48 cm) through sediment, vegetation, and leaf litter. The contents of each sweep were emptied into a white sorting tray, and odonates were hand-picked from debris. Nymphs were preserved in 70% ethanol immediately after collection. Using this sampling approach, we could access areas of ponds ≤ 1 m in depth, meaning we sampled the entirety of small and/or shallow ponds and the littoral zone of deeper ponds. Previous work on odonate communities has demonstrated that the abundance and diversity of odonates declines sharply at depths greater > 1 m (Benke & Benke 1975; Wissinger 1992). Even species that prefer deep water habitats, such as *Perithemis tenera*, are still detectable by our methods because they remain common at shallower depths (Wissinger 1992) and must migrate to the littoral zone to emerge from the water and eclose as adults. Sampling effort per pond was usually 24 person-minutes but varied somewhat across dates due to logistical constraints ( $22.22 \pm 7.64$  *SD* person-minutes).

To estimate how much of the richness we detected with this amount of effort, we sampled four ponds on May 15-17, 2011 for 60 person-minutes each. These ponds spanned a range of sizes (564-1393 m<sup>2</sup> surface area). These surveys indicated that 86% ( $\pm 10\%$  *SD*) of the species collected in 60 person-minutes were detected within the first 24 person-minutes. There was no correlation between pond size and proportion of species detected in the first 24 person-minutes ( $t = -0.8044$ , d. f. = 2,  $p = 0.5056$ ). This sampling approach is standard for this taxonomic group and should provide a robust means of detection and quantification of species (McCauley *et al.* 2008).

The 18,891 specimens collected during this study were identified using taxonomic keys (Needham *et al.* 2000; Westfall & May 2006), in the vast majority of cases, to the

species level. A few specimens were excluded from the data set because they were too small for positive identification (n = 10, 0.05% of specimens). Nymphs of *Celithemis ornata* and *C. verna* were included in the data set as one taxon because they cannot be distinguished with existing keys. Nymphs of the genus *Libellula* were included as a genus-level taxon because the species present in our region could not be identified to species reliably. We identified 41 taxa belonging to five families: Aeshnidae (6 species), Coenagrionidae (11 species), Gomphidae (3 species), Lestidae (3 species), and Libellulidae (Corduliinae: 3 species; Libellulinae: 12 species, *Celithemis ornata* / *C. verna*, and *Libellula*; Macromiinae: 1 species). Five species were excluded from the final data set because they were exceedingly rare: *Arigomphus lentulus*, *Didymops transversa*, *Enallagma basidens*, *Ishnura ramburii*, and *Sympetrum ambiguum* (each appeared in < 3 samples or 0.3% of samples, n = 7 specimens total across all five species). Ultimately, 18,874 specimens belonging to 36 taxa were included in the data set used for analyses (Table S1).

### *Habitat characteristics*

We collected data on a series of abiotic and biotic pond characteristics that we identified as potential predictors of odonate community structure based on previous work in similar systems (Werner *et al.* 2007; McCauley *et al.* 2008; Siepielski & McPeck 2013) and our own observations. This included top predator type, distances among ponds, pond size, canopy cover, and aquatic vegetation cover. To determine the top predator in each pond, we conducted predator surveys using methods similar to those employed for surveying odonates (see ‘Specimen collection and identification’ above), except that

predator surveys were always 60 person-minutes, and predators were identified in the field and released rather than preserved. These predator dip net surveys were conducted four times per year for three years (February 2007 – March 2010) in collaboration with the Wildlife Habitat and Silviculture Laboratory of the Southern Research Station of the United States Department of Agriculture Forest Service. We supplemented the predator dip net surveys with hook and line surveys to facilitate detection of large predatory fish species. These supplemental surveys were conducted March 13 – June 13, 2007 and generally consisted of two person-hours per pond. All fish species detected with hook and line surveys were also detected with dip net surveys, except for two cases (i.e., hook and line surveys detected largemouth bass in two ponds where dip net surveys did not). All the predatory fish species in our system occupy the littoral zone of ponds as juveniles, so it is reasonable that the extensive dip net surveys (13-person hours per pond across all survey dates) generally would provide robust predator detection.

Both across and within ponds, a great diversity of predators existed capable of consuming odonates and/or structuring the community of species that do. A predator was considered a member of a given pond's community if it was detected during at least two of the 13 predator surveys. Top predator status was assigned to the taxon present with the largest average body size, which we presumed would have the largest overall effect on pond community structure. Aquatic taxa, including odonates, typically exhibit habitat sorting based on top predator due, in large part, to tradeoffs associated with species traits (e.g., anti-predator defenses, body size, foraging strategies) (Wellborn *et al.* 1996). Traits that increase survival with one type of predator often decrease survival with another (McPeck 1990a, b; Stoks & McPeck 2003; McCauley 2008). Many aquatic organisms

have developed the ability to detect which predator species are present before selecting a habitat (Resetarits & Wilbur 1989; Binckley & Resetarits 2005; McCauley & Rowe 2010). Consequently, categorizing habitats by top predator type has proven useful for describing and predicted the composition of communities of a variety of aquatic taxa, particularly crustaceans, amphibians, and insects such as odonates (reviewed by Wellborn *et al.* 1996; Werner *et al.* 2007; McCauley *et al.* 2008).

We identified four types of ponds based on top predator: largemouth bass, green sunfish, salamander, and invertebrate (Table S2). Largemouth bass (*Micropterus salmoides*) are large, aggressive predators (to 97 cm in length) (Page *et al.* 1991) that feed on odonates and other invertebrates as juveniles and shift to piscivory as they increase in size (Post 2003). Therefore, bass (1) can only persist in ponds containing other fish species (up to seven other species in our system, Table S2), (2) affect odonates directly when young/small, and (3) affect odonates indirectly by structuring communities of smaller-bodied, insectivorous fishes when mature/large. Green sunfish (*Lepomis cyanellus*) are moderate-sized predatory fish (to 31cm in length) (Page *et al.* 1991), which feed largely upon odonates (Sadzikowski & Wallace 1976). This species most commonly occurs as the sole fish species within a habitat (80% of green sunfish ponds in our study, Table S2), and in such habitats, they can achieve high population densities, often developing a stunted morphology (Chizinski *et al.* 2010). We analyzed the community dynamics of odonates in ponds dominated by these two fish predators separately, rather than combining them into a single fish predator category, largely because of the differences in fish community structure that generally exist between ponds containing these two species (Table S2).

Ponds dominated by salamanders were primarily inhabited by the mole salamander (*Ambystoma talpoideum*) (75% of salamander ponds in our study). This species generally occupies ponds throughout the entire hydroperiod in the form of slow-developing larvae (Semlitsch *et al.* 1988) and paedomorphic individuals (fully aquatic and sexually mature; Semlitsch 1987). These ponds also frequently supported other salamander species, including the larvae of other ambystomatids (spotted salamanders, *A. maculatum*; marbled salamanders, *A. opacum*) as well as eastern newts (*Notophthalmus viridescens*) and lesser sirens (*Siren intermedia*). Newts are present in ponds spring to fall in the form of larvae and/or adults. Sirens are fully aquatic and occur in ponds all year. The 25% of ponds without mole salamanders were dominated by sirens. Therefore, all salamander ponds were occupied by one or more salamander species through the annual hydroperiod.

We categorized ponds devoid of vertebrate predators as invertebrate ponds. These ponds were dominated by crayfishes (*Procambarus* spp., *Fallicambarus* spp.), predatory hemipterans (e.g., *Belostoma* spp., *Lethocerus* spp., *Notonecta* spp., *Pelocoris* spp.), predatory beetles (e.g., *Cybister fimbriolatus*, *Tropisternus* spp.), and/or the odonates themselves (Table S1). All the invertebrate predators, except for the odonates, complete their entire life cycle within ponds and are present as long as ponds remain hydrated. Differences in traits among these four predator categories, including body size, gape width, prey detection mode, and mobility, likely have a variety of consequences for odonate community structure and how it varies across space and time.

In addition to top predator type, we quantified four other habitat characteristics. We hypothesized that ponds in closer proximity would exhibit more similar communities

due to forces such as spatial autocorrelation in environmental conditions and mass effects (Holyoak *et al.* 2005). For identifying the spatial position of ponds and calculating the distances among them, we used a GPS unit (Garmin PSMAP 60CSx) to determine the latitude and longitude of each pond and used these coordinates to generate a matrix of pairwise Euclidian distances among ponds (Geographic Distance Matrix Generator, v 1.2.3). Mean pairwise distances among ponds within DCNF and ANF were 23.20 km  $\pm$  13.16 km SD (range: 0.24–52.20 km) and 22.72 km  $\pm$  14.01 km SD (range: 0.59–44.65 km), respectively. We quantified the remaining pond characteristics December 8–11, 2009 (pond size, canopy cover, vegetation cover). We quantified aspects of pond size because we anticipated that size would affect a variety of important habitat traits such as temperature and hydroperiod (Wellborn *et al.* 1996; Werner *et al.* 2007; McCauley *et al.* 2008). We determined pond surface area by tracing the perimeter of each pond on foot with the GPS unit, which then generated surface area values, and we measured maximum depth using a fishing pole with flagging attached at 30 cm increments along the line. Means for surface area and maximum depth were 598 m<sup>2</sup>  $\pm$  557 m<sup>2</sup> SD (range: 25–2324 m<sup>2</sup>) and 135 cm  $\pm$  58 cm SD (range: 18–285 cm), respectively. Ponds did fluctuate somewhat in size during the study period, but these fluctuations were due to seasonal changes in temperature and precipitation at a regional level. Therefore, sizes of ponds relative to one another should have remained fairly similar through time. The extent of canopy cover is likely important because it determines visibility of ponds to ovipositing females. The canopy also produces shade, which affects temperature and primary productivity, and leaf litter (Binckley & Resetarits 2007, 2009), which affects the benthic habitat structure where many odonates forage. We visually estimated canopy cover and

sorted ponds into five ordinal categories: < 15% (3 ponds), 15–35% (8 ponds), 36–64% (18 ponds), 65–85% (16 ponds), >85% (0 ponds). The canopy of these forests is dominated by pines, so seasonal variation in canopy cover is very low compared to that of deciduous forests. Finally, we quantified the extent of aquatic vegetation cover, including both submerged and emergent vegetation, because it determines the availability of microhabitats for oviposition and nymph foraging (Siepielski & McPeck 2013). We visually estimated aquatic vegetation cover and sorted ponds into five ordinal categories: < 15% (10 ponds), 15–35% (9 ponds), 36–64% (10 ponds), 65–85% (12 ponds), >85% (4 ponds). The mild, subtropical climate of the Gulf Coast of eastern Texas promotes fairly consistent aquatic vegetation cover during most of the year, except for a short period in mid-winter, a time period when none of the odonate species in our system are ovipositing (Abbott 2008). We used this set of pond characteristics as predictors in a variety of analyses to determine their relative importance in explaining variation in odonate diversity across space and time.

Species richness and individual abundances of odonates varied considerably with time and across ponds, but showed some consistent patterns. On average, bass ponds tended to contain the greatest number of species and individuals (Figs. S1 and S2). Invertebrate and salamander ponds tended to contain the fewest species, but invertebrate ponds contained nearly as many individuals on average as bass ponds, while salamander and green sunfish ponds contained similar numbers of individuals on average (Figs. S1 and S2). Richness and abundance both tended to be lowest for a particular group in the spring (Figs. S1 and S2).

## **S2. Checking robustness to differences in site area, pond sample size, and individual abundance.**

### *Rarefying individual abundances*

In addition to patterns driven by area or unequal sample sizes of pond types, our results could be affected by differences in individual abundance (Ricklefs & Lau 1980; Stier *et al.* 2016). To account for this, we rarefied individual abundances in our dissimilarity calculations in two different ways. First, we limited total abundance to 5 individuals across all sites and sample dates, assigning these individuals randomly to species that were present at the site, using the `rrarefy` function in the `vegan` package (vegan citation). Our calculations of  $\beta$ -diversity for temporal dissimilarity = (site A at time 1 vs. site A at time 2), and for spatial dissimilarity = (average dissimilarity of all pairwise site comparisons at time 1), following the approach we outline in the methods. This procedure generates comparisons with identical abundance in each pairwise diversity calculation, but also severely restricts species richness in each site compared to our observed values (because limiting abundance necessarily drops some species out of each comparison). Thus, these rarefied dissimilarities were almost always higher than observed values (Fig. S3). We repeated this procedure 100 times to obtain means and standard errors.

Second, we rarefied abundances by simply reducing the total abundance of the higher-abundance site in each comparison to that of the lower. For instance, if site A had 25 individuals and site B had 21, we randomly assigned 21 individuals to site A (leaving B alone) using the `rrarefy` function, constrained to the species actually observed in site A. This procedure is less severe than the first, and provides diversity estimates much closer

to what we actually observed (Fig. S3). Again, we repeated the procedure 100 times to obtain means and standard errors.

For each of the rarefaction procedures, we re-calculated the ratio of spatial:temporal biodiversity partitioning as presented in the main text (Fig. S3, compare to Fig. 5), for each of three dissimilarity metrics: Sørensen (presence/absence), Bray-Curtis (abundance), and AltGower (abundance).

#### *Other Metrics*

To further examine the effect of using different metrics for  $\beta$ -diversity on our results, we additionally calculated the ratios of spatial:temporal  $\beta$ -diversity using Jaccard, Euclidian and Gower metrics using our full data set. In total, we calculated spatial:temporal  $\beta$ -diversity with six metrics: Sorensen, Bray-Curtis, AltGower, Gower, Jaccard, and Euclidean. While these metrics vary in how they calculate dissimilarity using incidence or relative abundance and in other ways, they all produce qualitatively similar results including the same rank order of top predator classes (Fig. S4). This indicates that variation in our Odonate communities occurred similarly in terms of both species incidence and relative abundance.

#### *Area*

Our main result is a significant difference in the relative spatial/temporal partitioning of  $\beta$ -diversity by top predator type. While this is consistent with previous research which has also identified predators as a major environmental filter and driver of spatial  $\beta$ -diversity in aquatic communities (Wellborn *et al.* 1996; Chase *et al.* 2009), an alternative explanation is that some other factor is driving our harshness gradient, and that top predator type is similarly responding to that factor. Habitat area has long been

known to affect expected levels of dissimilarity among habitats, stemming from the island biogeographic principle that larger sites harbor a greater proportion of the overall species pool, and thus two large sites should (on average) be more similar to each other than two small sites (Preston 1960). In our ponds, top predator type is partially correlated with pond area (invertebrate ponds are the smallest, on average, followed by salamander ponds, green sunfish ponds, and bass ponds), and thus area could also explain our results. To test whether area, independent of top predator type, could generate the differences in spatial and temporal partitioning we observed, we used a null-model randomization approach.

We compared our data to two different null models each testing a different aspect of our data. First, we randomized the presence/absence matrix, keeping the row sums (species richness) and column sums (species frequencies) identical. This approach conserves the empirical patterns of species richness we observed in our data, but asks what the spatial/temporal partitioning of dissimilarity would look like with randomly selected species. In other words, this null model provides a baseline ratio of temporal/spatial dissimilarity, assuming no differences in community structure. If our observed ratios fell in the middle of these null distributions, we may conclude that the effects of top predator on biodiversity partitioning had nothing to do with actual species composition.

However, as our observed species richness could be due to both area and top predator, this randomization procedure could still reflect the effects of top predator. Our second approach therefore replaced our observed species richness values with draws from

an underlying species-area-relationship (SAR), rather than the observed species richness. In brief, we fitted a nonlinear model of the form:

$$S = c(A^z) \quad (\text{eq. 1})$$

to all of our observed richnesses (i.e. across all sites and sample dates), where  $S$  is our observed species richness,  $c$  is the 1-unit-area intercept, and  $z$  represents the slope of the species-area relationship on a log-log scale. We bootstrapped the model 9,999 times, and stored each estimated  $c$  and  $z$  value. Next, we simulated species richness for each site by randomly selecting each of  $c$  and  $z$  from their bootstrapped distributions and estimating  $S$  based on the pond's actual area. Note that we allowed both  $c$  and  $z$  to vary independently for each simulation; this is slightly unrealistic, in the sense that the best-fit estimate of  $z$  for a particular iteration of our model relies on the best-fit estimate of  $c$ , but it provides a much broader range of simulated richness values, and thus a more robust null comparison. Finally, we generated 500 random communities based on these simulated richnesses, and calculated  $\beta$ -diversity as before. Note also that sites could have different simulated species richness in separate replicates of this procedure (row sums not identical), though we kept the species frequencies (column sums) throughout.

This approach breaks any associations between top predator and area. Using this approach, significant differences in randomized community dissimilarity between large and small ponds would indicate that area alone was enough to generate substantial differences in spatial/temporal partitioning of  $\beta$ -diversity. Similar ratios would suggest that area alone cannot explain our results and some other factor (i.e. predator) was generating the significant differences we report in the main text.

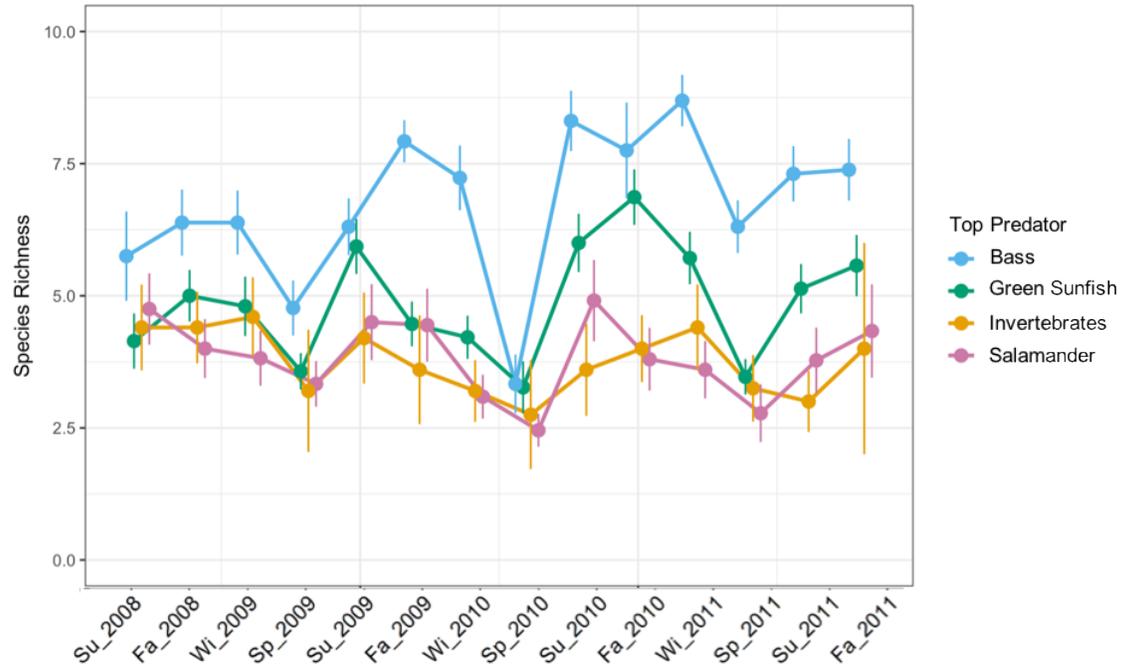
For each procedure, we created 500 random communities. Then, we calculated the ratio of temporal/spatial  $\beta$  diversity for each random community, generating a distribution of null values. We then plotted the distributions of the mean ratio (across all sites and samples, as in Fig. 5) for each top predator type, alongside our observed ratio (Fig. S5).

Figure S5 shows that our results, specifically the higher relative spatial partitioning of odonate communities in salamander- and invertebrate-dominated ponds cannot be explained by pond area. Instead, some other factor was driving differences in biodiversity partitioning. Based on previous work characterizing freshwater communities (Wellborn *et al.* 1996; Chase *et al.* 2009), and results from our distlm analysis (which showed top predator and not pond area to be the main determinant of community structure), we conclude that top predator type presents the strongest gradient of environmental filter across ponds in our study. Interestingly, this randomization approach helps to explain part of our overall results. Fish-dominated ponds (bass and green sunfish) appear closer to the null expectation of temporal/spatial partitioning, based on their area. Invertebrate and salamander ponds, however, show significantly more spatial dissimilarity (relative to temporal dissimilarity) than expected by area alone.

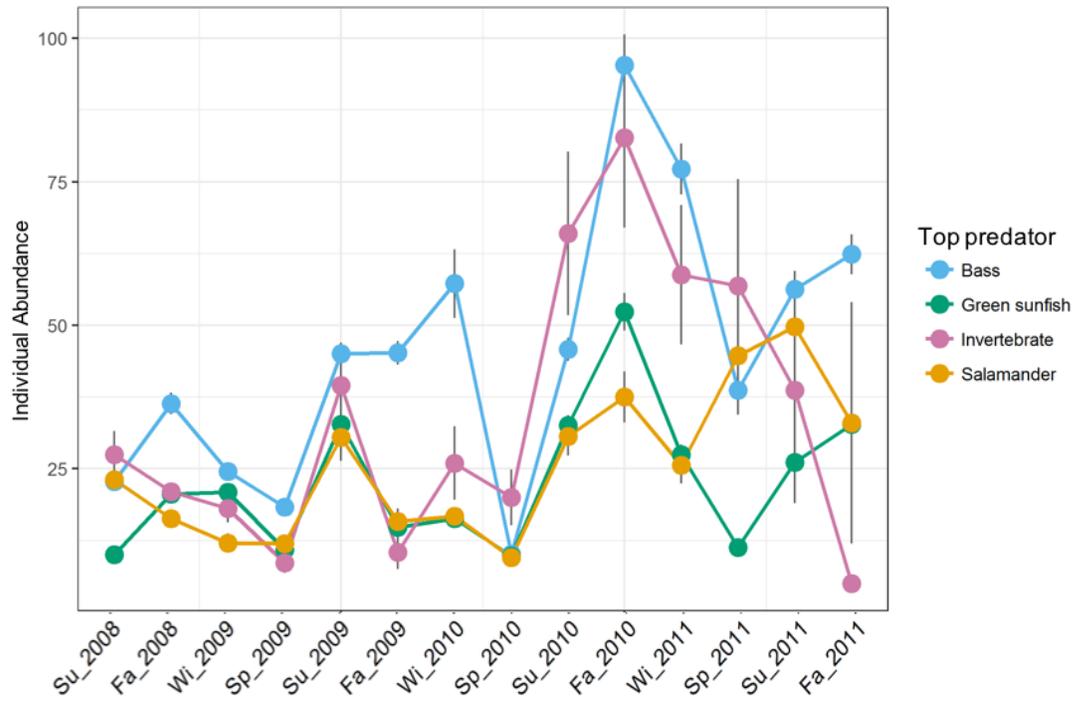
#### *Unequal sample size*

In addition to checking the robustness of results with regard to area, we also ran simulations to determine the influence of sample size. Our set of ponds contains different numbers of bass (13), green sunfish (15), salamander (12), and invertebrate (5) dominated ponds. It is possible that such differences in sample size could affect our results by altering the mean dissimilarity ( $\beta$ -diversity) of our sites. To address this, we

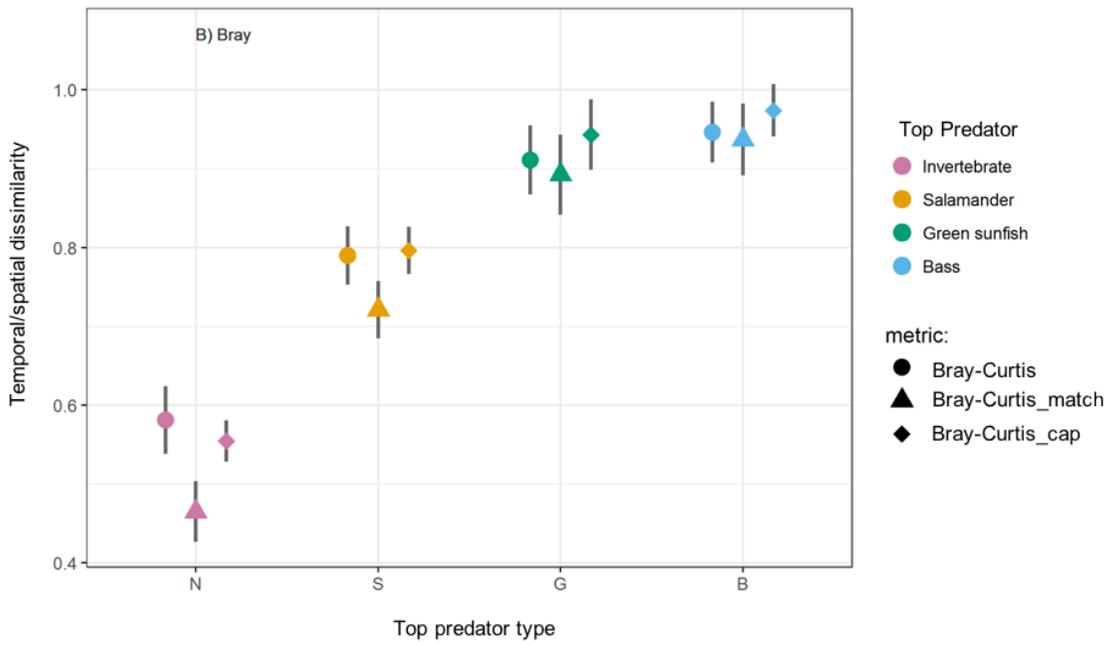
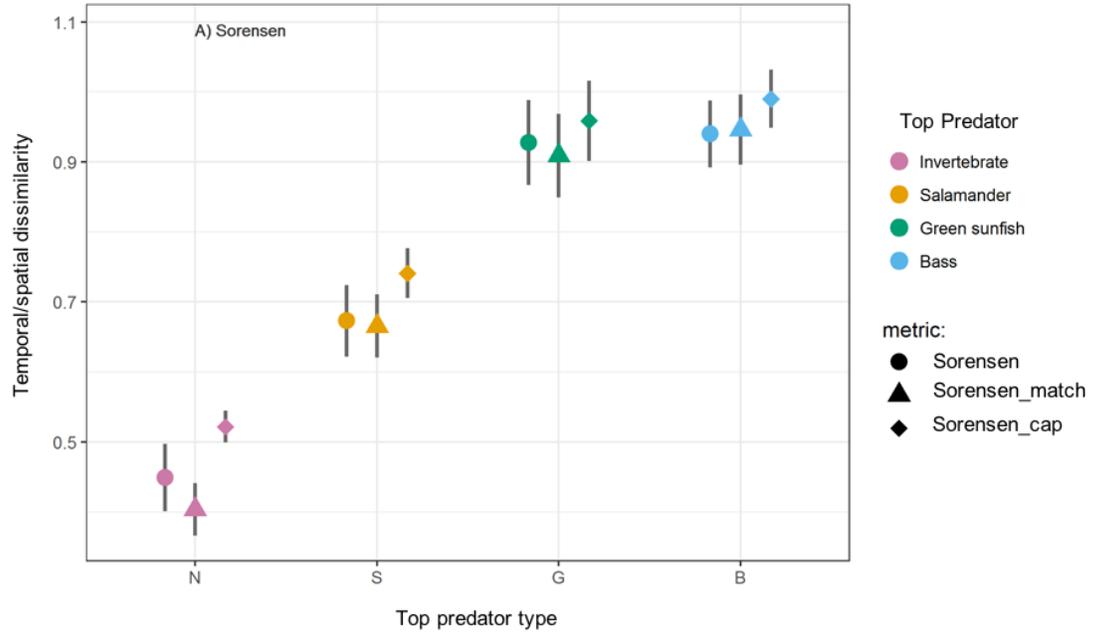
randomly selected 3 ponds from each group, and re-calculated  $\beta$ -diversity ratios for 500 random draws of 3 ponds (e.g. Fig. S6). The distribution of resulting temporal/spatial  $\beta$ -diversity ratios for each pond type shows how often we would expect to get a particular result by sampling only three of each pond type. Overall, we find that this resampling approach shows the same general patterns as our main results (main text Fig. 5 vs. Fig. S6) indicating that our results are robust and not driven by potential sampling biases.

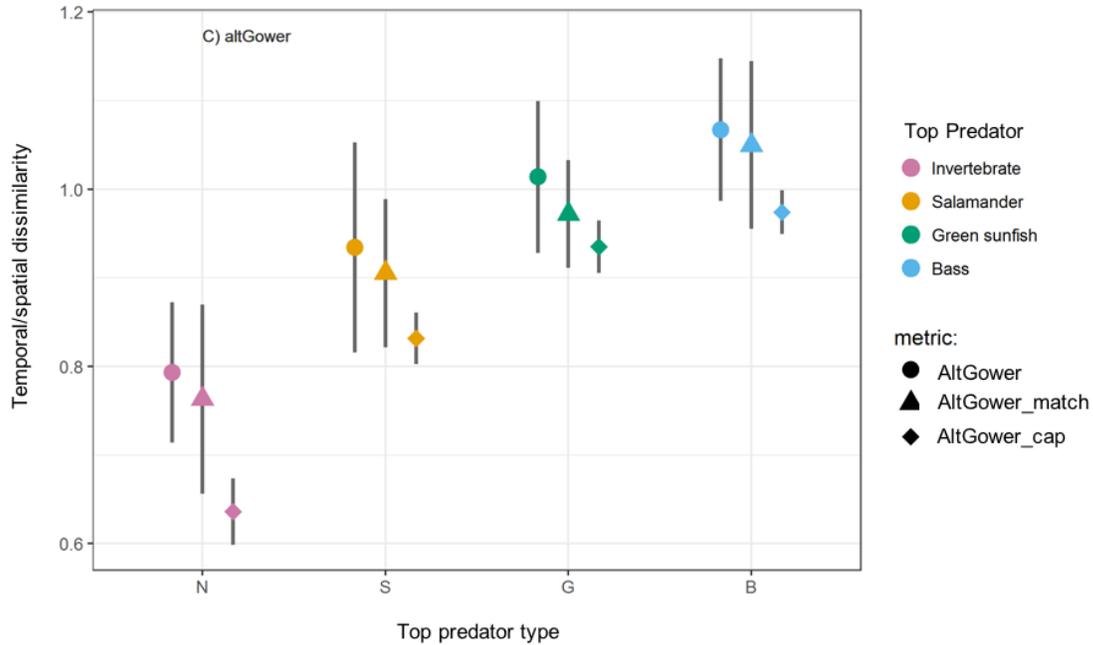


**Figure S1.** Species richness for an average pond (mean  $\pm$  1 SE) from each top predator group across 14 seasonal samples. X-axis indicates season (Su = Summer etc.) and year of sample.

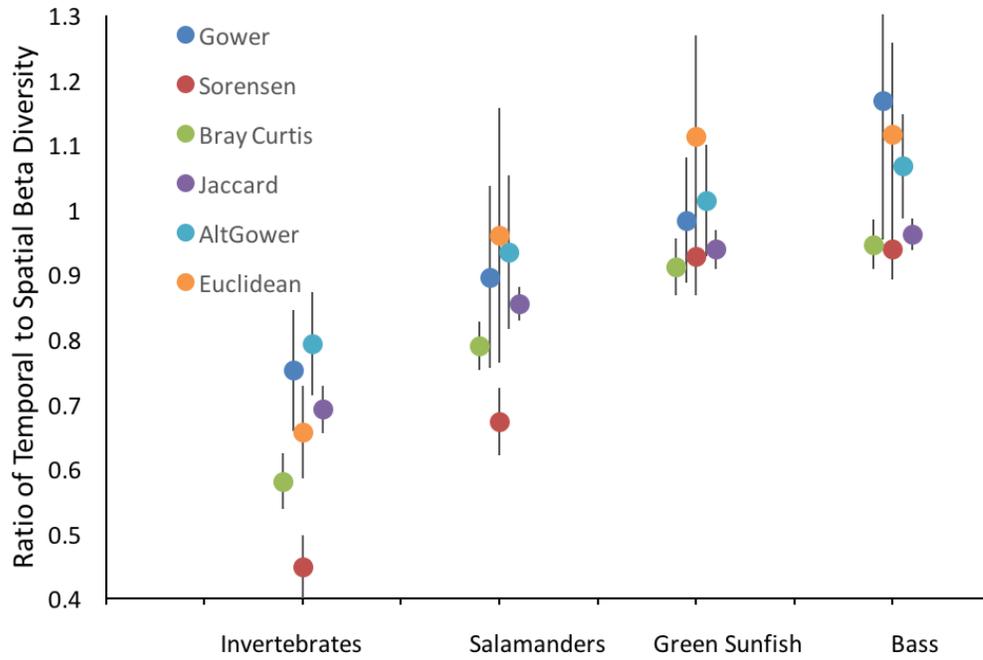


**Figure S2.** Mean ( $\pm 1$  SE) individual abundance of odonate larvae in ponds of each top predator group across 14 seasonal samples.

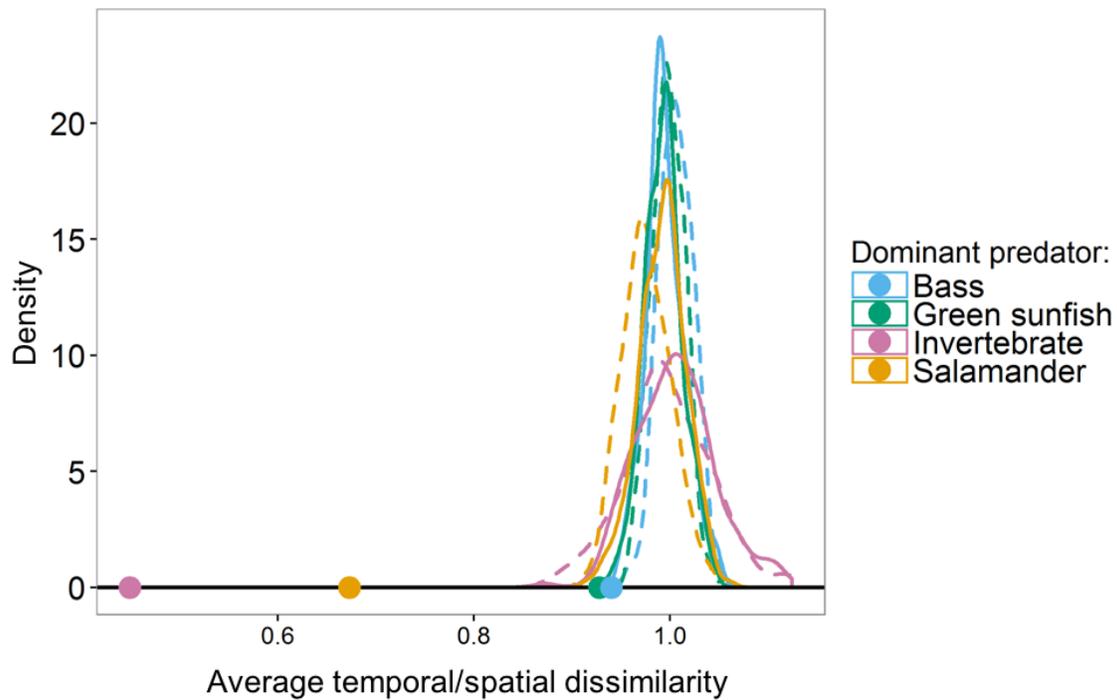




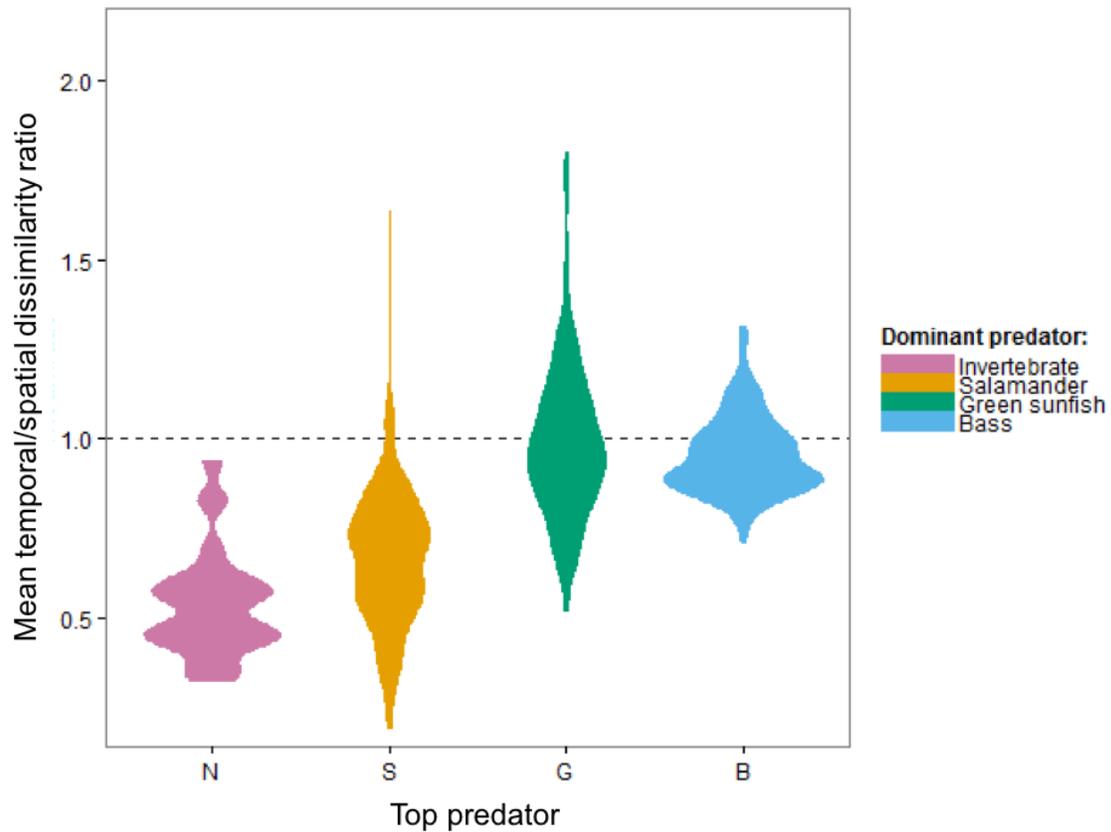
**Figure S3.** Results of rarefying Odonate community data for our observed temporal:spatial dissimilarity ratios using A) Sørensen, B) Bray-Curtis and C) AltGower metrics for dissimilarity. Results using the raw data set are shown as circles, results using rarefaction matched to the abundance of whichever compared community had the lower abundance is shown as triangles and results using rarefaction with a cap of five species for each community is shown as squares. Error bars are one standard error in each direction. Rarefaction of our data has a limited relative effect which is similar for all top predator groups. This indicates that our results did not depend on differences in abundances between community types.



**Figure S4.** Mean and standard errors of the ratio of temporal:spatial  $\beta$ -diversity using six common metrics of dissimilarity.



**Figure S5.** Randomized communities, with species richness drawn either from our observed species richness values (dashed lines), or a nonlinear species-area relationship (SAR), show that the low temporal/spatial dissimilarity of invertebrate and salamander ponds was not dominated by area alone. Solid lines represent density plots of the mean temporal/spatial dissimilarity ratio (Sorenen's  $\beta$ -diversity) for each of 500 randomizations from null models assuming that area alone drives empirical patterns in our study. Points along the x-axis represent mean ratios for each group in our empirical data (main text Fig. 5).



**Figure S6.** Accounting for differences in sample size does not alter our main result. Constricting our analyses to  $N = 3$  ponds of each top predator type reveals the same pattern of diversity partitioning, with more deterministic sites (Bass, Green sunfish) showing a larger ratio of temporal:spatial dissimilarity (Y-axis) across 150 randomizations our spatial and temporal data.

**Table S1.** Proportion of ponds of each top predator type in which each odonate taxa was collected during any of the 14 samples over four years. Bass = 13 ponds, Green sunfish = 15 ponds, Invertebrate = 5 ponds, Salamander = 12 ponds.

<b>Species</b>	<b>Family</b>	<b>Bass</b>	<b>Green Sunfish</b>	<b>Invertebrate</b>	<b>Salamander</b>
<i>Anax junius</i>	Aeshnidae	0.77	0.33	1.00	0.75
<i>Anax longipes</i>	Aeshnidae	0.00	0.00	0.20	0.08
<i>Basiaeschna janata</i>	Aeshnidae	0.15	0.00	0.00	0.08
<i>Coryphaeschna ingens</i>	Aeshnidae	0.31	0.13	0.20	0.00
<i>Epiaeschna heros</i>	Aeshnidae	0.00	0.00	0.00	0.33
<i>Nasiaeschna pentacantha</i>	Aeshnidae	0.31	0.07	0.20	0.00
<i>Enallagma aspersum</i>	Coenagrionidae	0.00	0.00	0.20	0.25
<i>Enallagma divagans</i>	Coenagrionidae	0.92	0.73	0.00	0.08
<i>Enallagma dubium</i>	Coenagrionidae	1.00	0.33	0.20	0.25
<i>Enallagma geminatum</i>	Coenagrionidae	0.69	0.27	0.40	0.00
<i>Enallagma signatum</i>	Coenagrionidae	0.92	0.53	0.20	0.08
<i>Enallagma vesperum</i>	Coenagrionidae	0.46	0.27	0.00	0.00
<i>Ischnura posita</i>	Coenagrionidae	1.00	1.00	0.80	0.92
<i>Nehalennia integricollis</i>	Coenagrionidae	0.08	0.13	0.00	0.00
<i>Telebasis byersi</i>	Coenagrionidae	0.08	0.00	0.20	0.17
<i>Epitheca princeps</i>	Corduliidae	0.15	0.27	0.00	0.00
<i>Epitheca semiaquea</i>	Corduliidae	1.00	1.00	0.80	0.50
<i>Epitheca cynosura</i>	Corduliidae	0.38	0.13	0.00	0.00
<i>Arigomphus maxwelli</i>	Gomphidae	0.00	0.07	0.00	0.00
<i>Gomphus lividus</i>	Gomphidae	0.62	0.60	0.00	0.25
<i>Lestes australis</i>	Lestidae	0.08	0.07	0.00	0.33
<i>Lestes inaequalis</i>	Lestidae	0.54	0.00	0.00	0.08
<i>Lestes vigilax</i>	Lestidae	0.23	0.00	0.00	0.00
<i>Celithemis amanda</i>	Libellulidae	0.23	0.47	0.00	0.00
<i>Celithemis elisa</i>	Libellulidae	0.15	0.07	0.00	0.00
<i>Celithemis fasciata</i>	Libellulidae	0.92	0.93	0.20	0.08
<i>Celithemis ornata/verna</i>	Libellulidae	0.54	0.20	0.00	0.08
<i>Erythemis simplicicollis</i>	Libellulidae	1.00	1.00	0.40	0.50
<i>Erythrodiplax minuscula</i>	Libellulidae	0.23	0.20	0.20	0.08
<i>Ladona deplanata</i>	Libellulidae	1.00	0.80	0.20	0.42
<i>Libellula spp.</i>	Libellulidae	1.00	1.00	1.00	0.92

<i>Pachydiplax longipennis</i>	Libellulidae	1.00	1.00	1.00	1.00
<i>Pantala flavescens</i>	Libellulidae	0.08	0.00	0.40	0.58
<i>Perithemis tenera</i>	Libellulidae	0.62	0.27	0.20	0.08
<i>Plathemis lydia</i>	Libellulidae	0.77	0.27	0.60	0.83
<i>Tramea carolina</i>	Libellulidae	0.92	0.73	0.60	0.58

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**Table S2.** Summary of pond characteristics by top predator type, including the number of fish and salamander predator species present (includes the top predator where relevant), pond area and depth, and ordinal categories for aquatic vegetation and canopy cover (see 'Materials and Methods: Habitat characteristics' for details). Values represent means  $\pm$  standard deviations. n = number of ponds per top predator category.

	<b>n</b>	<b>Fish Species</b>		<b>Salamander Species</b>		<b>Pond Area (m<sup>2</sup>)</b>		<b>Pond Depth (m)</b>		<b>Vegetation Cover</b>		<b>Canopy Cover</b>	
Invertebrate	5	0.00	$\pm$ 0.00	0.00	$\pm$ 0.00	260.60	$\pm$ 193.96	109.00	$\pm$ 61.28	2.60	$\pm$ 1.82	3.80	$\pm$ 0.45
Salamander	12	0.00	$\pm$ 0.00	1.75	$\pm$ 0.75	246.21	$\pm$ 241.73	88.83	$\pm$ 51.65	2.58	$\pm$ 1.56	3.00	$\pm$ 1.04
Green Sunfish	15	1.47	$\pm$ 1.13	0.40	$\pm$ 0.63	598.15	$\pm$ 597.96	145.73	$\pm$ 34.47	2.80	$\pm$ 1.21	2.87	$\pm$ 1.13
Bass	13	3.31	$\pm$ 2.29	0.46	$\pm$ 0.52	1052.38	$\pm$ 509.03	174.62	$\pm$ 56.36	2.85	$\pm$ 1.52	3.00	$\pm$ 0.41

**Table S3.** Distance-based linear model for odonate community structure (Bray-Curtis dissimilarity based on abundance data) against categories of predictors. Prop. is the proportion of additional variation explained by adding each predictor category; Cumul. is the cumulative proportion of variation explained by multiple predictors; res. df is the residual degrees of freedom.

<b>Predictor</b>	<b>AIC</b>	<b>SS (trace)</b>	<b>Pseudo-<i>F</i></b>	<b><i>P</i></b>	<b>Prop.</b>	<b>Cumul.</b>	<b>res. df</b>
Environment	4533.1	2.56E+05	14.781	0.001	0.153	0.153	571
Time	4468.9	1.75E+05	13.263	0.001	0.105	0.258	565
Space	4449.2	53715	8.4776	0.001	0.032	0.290	562

**Table S4.** Distance-based linear model for odonate community structure (Sørensen's similarity based on presence-absence data) against categories of predictors. Prop. is the proportion of additional variation explained by adding each predictor category; Cumul. is the cumulative proportion of variation explained by multiple predictors; res. df is the residual degrees of freedom.

<b>Predictor</b>	<b>AIC</b>	<b>SS (trace)</b>	<b>Pseudo-<i>F</i></b>	<b><i>P</i></b>	<b>Prop.</b>	<b>Cumul.</b>	<b>res. df</b>
Environment	4383.7	2.43E+05	18.162	0.001	0.182	0.182	571
Time	4313.8	1.44E+05	14.309	0.001	0.108	0.290	565
Space	4289.2	48931	10.182	0.001	0.037	0.327	562

**Table S5.** Distance-based linear model for odonate community structure (Bray-Curtis dissimilarities based on abundance data) against individual predictors. Prop. is the proportion of additional variance explained by adding each predictor; Cumul. is the cumulative proportion of variation explained by multiple predictors; res. df is the residual degrees of freedom.

<b>Predictor</b>	<b>AIC</b>	<b>SS (trace)</b>	<b>Pseudo-<i>F</i></b>	<b><i>P</i></b>	<b>Prop.</b>	<b>Cumul.</b>	<b>res. df</b>
Predator	4559.7	1.69E+05	21.598	0.001	0.101	0.101	575
Season	4511.2	1.35E+05	18.83	0.001	0.081	0.182	572
Space	4486.5	6.61E+04	14.479	0.001	0.040	0.222	570
Canopy	4473.4	33573	15.067	0.001	0.020	0.242	569
Year	4461	39548	6.0746	0.001	0.024	0.265	566
Vegetation	4452	23105	10.832	0.001	0.014	0.279	565
Pond area	4450.1	8239.1	3.8823	0.001	0.005	0.284	564
Pond depth	4448.9	6521.7	3.0844	0.003	0.004	0.288	563

**Table S6.** Distance-based linear model for odonate community structure (Sørensen's similarity based on presence-absence data) against individual predictors. Prop. is the proportion of additional variance explained by adding each predictor; Cumul. is the cumulative proportion of variation explained by multiple predictors; res. df is the residual degrees of freedom.

<b>Predictor</b>	<b>AIC</b>	<b>SS (trace)</b>	<b>Pseudo-<i>F</i></b>	<b><i>P</i></b>	<b>Prop.</b>	<b>Cumul.</b>	<b>res. df</b>
Predator	4419.5	1.58E+05	25.61	0.001	0.118	0.118	575
Season	4365.5	1.16E+05	20.812	0.001	0.087	0.205	572
Space	4333.0	64969	18.548	0.001	0.049	0.253	570
Vegetation	4314.2	35239	20.82	0.001	0.026	0.280	569
Year	4303.3	27704	5.5879	0.001	0.021	0.300	566
Canopy	4292.7	20144	12.435	0.001	0.015	0.315	565
Pond area	4289.8	7639.6	4.7475	0.001	0.006	0.321	564
Pond depth	4288.8	4820.4	3.0062	0.014	0.004	0.325	563

## Supplement Literature cited

1. Abbott, J. (2008). *Dragonflies and Damselflies (Odonata) of Texas*. 3rd edn. Odonata Survey of Texas
2. Benke, A.C. & Benke, S.S. (1975). Comparative Dynamics and Life Histories of Coexisting Dragonfly Populations. *Ecology*, 56, 302–317
3. Binckley, C.A. & Resetarits, W.J. (2005). Habitat selection determines abundance, richness and species composition of beetles in aquatic communities. *Biol. Lett.*, 1, 370–374
4. Binckley, C.A. & Resetarits, W.J. (2007). Effects of forest canopy on habitat selection in treefrogs and aquatic insects: implications for communities and metacommunities. *Oecologia*, 153, 951–958
5. Binckley, C.A. & Resetarits, W.J. (2009). Spatial and temporal dynamics of habitat selection across canopy gradients generates patterns of species richness and composition in aquatic beetles. *Ecol. Entomol.*, 34, 457–465
6. Chase, J.M., Biro, E.G., Ryberg, W.A. & Smith, K.G. (2009). Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. *Ecol. Lett.*, 12, 1210–1218
7. Chizinski, C.J., Pope, K.L., Wilde, G.R. & Strauss, R.E. (2010). Implications of stunting on morphology of freshwater fishes. *J. Fish Biol.*, 76, 564–579
8. Holyoak, M., Leibold, M.A. & Holt, R.D. (Eds.). (2005). *Metacommunities: Spatial Dynamics and Ecological Communities*. University Of Chicago Press, Chicago
9. McArdle, B.H. & Anderson, M.J. (2001). Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, 82, 290–297
10. McCauley, S.J. (2008). Slow, fast and in between: habitat distribution and behaviour of larvae in nine species of libellulid dragonfly. *Freshw. Biol.*, 53, 253–263
11. McCauley, S.J., Davis, C.J., Relyea, R.A., Yurewicz, K.L., Skelly, D.K. & Werner, E.E. (2008). Metacommunity patterns in larval odonates. *Oecologia*, 158, 329–342
12. McCauley, S.J. & Rowe, L. (2010). *Notonecta* exhibit threat-sensitive, predator-induced dispersal. *Biol. Lett.*, 6, 449–452
13. McPeck, M.A. (1990a). Behavioral Differences between *Enallagma* Species (Odonata) Influencing Differential Vulnerability to Predators. *Ecol. Wash. C*, 71, 1714–1726

14. McPeck, M.A. (1990b). Determination of Species Composition in the *Enallagma* Damselfly Assemblages of Permanent Lakes. *Ecol. Wash. C*, 71, 83–98
15. Needham, J.G., Westfall, M.J., Jr & May, M.L. (2000). *Dragonflies of North America*. Revised edition. Scientific Publishers, Gainesville, FL
16. Page, L.M., Beckham, E.C. & Peterson, R.T. (1991). *Peterson Field Guide to Freshwater Fishes: North America North of Mexico*. Houghton Mifflin, Boston
17. Post, D.M. (2003). Individual variation in the timing of ontogenetic niche shifts in largemouth bass. *Ecology*, 84, 1298–1310
18. Preston, F.W. (1960). Time and space and the variation of species. *Ecology*, 41, 611–627
19. Resetarits, W.J. & Wilbur, H.M. (1989). Choice of Oviposition Site by *Hyla chrysoscelis*: Role of Predators and Competitors. *Ecology*, 70, 220–228
20. Ricklefs, R.E. & Lau, M. (1980). Bias and dispersion of overlap indices: results of some Monte Carlo simulations. *Ecology*, 61, 1019 – 1024.
21. Sadzikowski, M.R. & Wallace, D.C. (1976). A Comparison of the Food Habits of Size Classes of Three Sunfishes (*Lepomis macrochirus* Rafinesque, *L. gibbosus* (Linnaeus) and *L. cyanellus* Rafinesque). *Am. Midl. Nat.*, 95, 220–225
22. Semlitsch, R.D. (1987). Paedomorphosis in *Ambystoma talpoideum*: Effects of Density, Food, and Pond Drying. *Ecology*, 68, 994–1002
23. Semlitsch, R.D., Scott, D.E. & Pechmann, J.H.K. (1988). Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. *Ecology*, 69, 184–192
24. Siepielski, A.M. & McPeck, M.A. (2013). Niche versus neutrality in structuring the beta diversity of damselfly assemblages. *Freshw. Biol.*, 58, 758–768
25. Stoks, R. & McPeck, M.A. (2003). Antipredator behavior and physiology determine *Lestes* species turnover along the pond-permanence gradient. *Ecology*, 84, 3327–3338
26. Stier, A.C., Bolker, B.M. & Osenberg, C.W. (2016). Using rarefactions to isolate the effects of patch size and sampling effort on beta diversity. *Ecosphere*, 7, e01612
27. Wellborn, G.A., Skelly, D.K. & Werner, E.E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annu. Rev. Ecol. Syst.*, 337–363

28. Werner, E.E., Skelly, D.K., Relyea, R.A. & Yurewicz, K.L. (2007). Amphibian species richness across environmental gradients. *Oikos*, 116, 1697–1712
29. Westfall, M.J., Jr & May, M.L. (2006). *Damselflies of North America*. 2nd edition. Scientific Publishers, Gainesville, FL
30. Wissinger, S.A. (1992). Niche overlap and the potential for competition and intraguild predation between size-structured populations. *Ecology*, 73, 1431–1444