Does dispersal influence the strength of intraspecific competition in a stream salamander?

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Abstract

Metacommunity ecology emphasizes the role of dispersal in linking local processes across space. Competition is one such local process that can be affected by dispersal. Dispersal can influence intraspecific trait variation, thereby affecting the strength of intraspecific competition and, consequently, the relative importance of intra- versus interspecific interactions. Prior research has shown that spring salamanders, *Gyrinophilus porphyriticus*, self-organize within streams by a common trait (body condition) and that dispersal and gene flow along streams vary with slope. Building on this prior work, we tested how dispersal influences the strength of intraspecific competition via one of two spatial mechanisms: (1) spatial sorting of individuals by traits that affect competitive performance or (2) variation in gene flow resulting in evolutionary divergence of traits affecting competitive performance. To test these alternative mechanisms, we conducted a mesocosm experiment with spring salamanders from downstream and upstream sites of streams with low and high rates of dispersal and gene flow. Spatial patterns of intraspecific competitive performance differed significantly in the low- and high-dispersal streams. In the low-dispersal stream, downstream individuals were better intraspecific competitors than upstream individuals, whereas the opposite was true in the high-dispersal stream. These differences support the spatial sorting mechanism, reinforcing direct dispersal data showing that high-performance individuals are more likely to move upstream in the high-dispersal stream and to remain downstream in the low-dispersal stream. To our knowledge, this is the first time that spatial sorting has been explicitly identified as contributing to the strength of intraspecific interactions. Our study underscores the importance of integrating natural rates of dispersal into mechanistic experiments to understand spatial variability in the strength of intra- and interspecific species interactions.

Introduction

Dispersal is a fundamental ecological and evolutionary process (McPeek & Holt, 1992); however, most empirical studies lack direct data on dispersal (Logue *et al.*, 2011). This lack of direct data is not surprising because dispersal can be difficult to measure directly, especially when dispersers are a small fraction of the population (Johnson & Gaines, 1990). Nevertheless, this discrepancy impedes our understanding of how natural patterns of dispersal affect ecological and evolutionary dynamics. To address this empirical gap in understanding of the community-level effects of dispersal, direct data on dispersal should be integrated with information on species interactions. A logical place to begin is with the effects of dispersal on the strength of intraspecific interactions, an aspect of metacommunity ecology that is often overlooked in favor of interspecific interactions (Post *et al.*, 2008). Intraspecific interactions are often strong (Svanbäck &

Bolnick, 2007), and classic theory shows the importance of these interactions in determining the strength and outcome of interspecific interactions (Volterra, 1926; Lotka, 1932). Furthermore, recent work has expanded understanding of how ecological differences among conspecifics influence the strength of intra- and interspecific interactions, as well as overall biodiversity (Svanbäck & Bolnick, 2007; Post *et al.*, 2008).

One-way dispersal could influence the strength and spatial structure of intraspecific competition is by spatial sorting. Spatial sorting is the organization of individuals in space by similar traits (Shine, Brown & Phillips, 2011). This can occur when dispersers have traits in common (Roff & Fairburn, 2001; Cote *et al.*, 2010) and will influence intraspecific interactions when the same traits influence competitive ability (Booth & Beretta, 2004). For example, individual traits that influence variation in dispersal can also be good predictors of competitive ability (Stamps, 2006). In these cases, there is no

trade-off between dispersal and competitive ability within a species (Yu & Wilson, 2001) and individuals that are better intraspecific competitors and dispersers will be concentrated spatially, excluding poor intraspecific competitors.

Evolutionary divergence is another way dispersal can influence the strength of intraspecific competition. Low rates of dispersal and gene flow between sampling sites (e.g. local communities) allow for intraspecific evolutionary divergence, whether by adaptive or non-adaptive processes (Garant *et al.*, 2005). Generally, individuals from sites that are genetically divergent because of low dispersal and gene flow are more likely to be phenotypically divergent, particularly relative to individuals from sites with high dispersal and gene flow (Postma & van Noordwijk, 2005). These spatial patterns of evolutionary divergence can produce spatial variation in intraspecific competitive performance. For example, intraspecific competition between individuals from high-divergence populations may be weaker than between individuals from low-divergence populations because of differences in traits affecting resource use (Svanbäck & Bolnick, 2007). Likewise, individuals from low-divergence populations are more likely to be phenotypically similar (Slatkin, 1987), thus increasing the strength of intraspecific competition. Differences in divergence can affect the strength of interspecific interactions (e.g. Storfer & Sih, 1998), but less is known about the effects on intraspecific competition (but see Nadell & Basslet, 2011).

Our previous work suggests that these mechanisms – spatial sorting or evolutionary divergence – could influence the strength and spatial structure of intraspecific competition in a headwater salamander system. Based on capture-mark-capture data from multiple populations and >10 years of sampling, we know that dispersal by the northern spring salamander, *Gyrinophilus porphyriticus*, is strongly biased upstream and occurs mainly along stream corridors (Lowe, 2003). Individuals of higher body condition are more likely to disperse upstream and contribute to population stability at upstream sites, suggesting that spatial sorting along streams may influence the strength and spatial structure of intraspecific competition (Lowe, 2003; Lowe, Likens & Cosentino, 2006a). Individuals dispersing the farthest also have relatively long forelimbs and short hindlimbs in comparison with non-dispersing individuals (Lowe & McPeek, 2012), and survival probability increases with dispersal distance, reinforcing the process of spatial sorting. In the same system, patterns of evolutionary divergence along streams were consistent with a reduction in upstream dispersal and gene flow with stream slope (Lowe *et al.*, 2006b, 2012; Lowe & McPeek, 2012). Specifically, genetic distance increases with slope between downstream and upstream sampling sites separated by 1 km (Lowe *et al.*, 2006b, 2008), suggesting that intraspecific evolutionary divergence could also influence the strength and spatial structure of intraspecific competition.

To test whether spatial sorting or evolutionary divergence affect the strength and spatial structure of intraspecific competition in *G. porphyriticus*, we conducted a mesocosm experiment. We took advantage of two streams in the Hubbard Brook watershed, New Hampshire, USA, where rates of upstream dispersal and gene flow differ (Lowe *et al.*, 2006b, 2008). Rates of dispersal and gene flow along Kineo Brook are low because of the stream's steep slope, potentially allowing for evolutionary divergence between downstream and upstream sampling sites, but preventing spatial sorting. In contrast, dispersal along Bagley Trail Brook is high because of the stream's shallow slope, potentially preventing evolutionary divergence between downstream and upstream sampling sites, but allowing for spatial sorting (Lowe *et al.*, 2006b, 2008).

If spatial sorting influences the strength and spatial structure of intraspecific competition, then we predict downstream individuals to be superior competitors relative to upstream individuals in the low-dispersal stream (Kineo) because previous work shows they have higher body condition (Lowe *et al.*, 2006a), whereas upstream individuals have higher body condition in the high-dispersal stream (Bagley Trail) and will be superior competitors relative to downstream individuals (Table 1). Conversely, if evolutionary divergence influences the strength and spatial structure of intraspecific competition, then we expected to find weak intraspecific competition between downstream and upstream individuals in the low-dispersal stream (Kineo) because of differences in co-varying traits that affect both dispersal and resource use (Slatkin, 1987; Table 1). In contrast, we expected to find strong intraspecific competition between downstream and upstream individuals in the high-dispersal stream (Bagley Trail) because of a lack of evolutionary divergence in traits affecting resource use (Table 1). It is important to note that, for the evolutionary divergence hypothesis, our goal was not to identify the traits mediating the strength of intraspecific competition, which could be numerous and complex (Schluter, 2000), but to assess the overall effect of this mechanism on the strength and spatial structure of intraspecific competition. However, if we were to find evidence of this mechanism, identifying these traits would clearly be a priority.

Table 1 Predicted outcomes of intraspecific competition in streams that differ in dispersal, based on either the spatial sorting mechanism or the evolutionary divergence mechanism

Dispersal within stream	Mechanisms	
	Spatial sorting	Evolutionary divergence
Low dispersal	Downstream ⇐ upstream	Downstream ⇎ upstream
High dispersal	Downstream ⇒ upstream	Downstream ⇔ upstream

Symbols indicate the net pathway of competitive effects resulting from differences in the competitive performance of individuals from downstream and upstream sampling sites. For example, the spatial sorting mechanism predicts that upstream individuals should be better competitors than downstream individuals in a high-dispersal stream. This is indicated by a ⇒ pointing toward the hypothesized superior competitors, upstream individuals. A ⇎ indicates that intraspecific competition should be weak; ⇔ indicates that individuals from both sampling sites should experience equally strong negative competitive effects.

Materials and methods

Study system and background

Gyrinophilus porphyriticus, a lungless salamander in the family Plethodontidae, is found in small, cool, well-oxygenated streams along the Appalachian uplift, from central Alabama, USA to southern Quebec, Canada (Petranka, 1998). Adult *G. porphyriticus* are highly aquatic but can forage terrestrially at night (Greene, Lowe & Likens, 2008). Both adults and larvae are generalist predators with diets that consist mainly of aquatic invertebrates (Greene *et al.*, 2008), which comprise up to 78% of diets in some Hubbard Brook streams (Mondelli, Davenport & Lowe, 2014). Adults, however, also engage in cannibalism and intraguild predation (Bruce, 1979; Davenport & Lowe, unpubl. data) and can have strong interactions with other species in stream food webs (Resetarits, 1991, 1995).

Our work was conducted within the Hubbard Brook watershed of the White Mountains in central New Hampshire, USA (43°56′ N, 71°45′ W). Hubbard Brook streams have low conductivity (12.0–15.0 µS), slight acidity (pH of 5.0–6.0), high dissolved oxygen content (80–90% saturation) and moderate mid-day summer temperatures (13.0–17.0°C; Likens & Buso, 2006). The dominant tree species in the watershed are *Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis*, *Picea rubens*, *Abies balsamea* and *B. papyrifera*.

Experimental methods

To test if spatial sorting or evolutionary divergence influences the strength and spatial structure of intraspecific competition in *G. porphyriticus*, we conducted a mesocosm experiment. Mesocosms were constructed from 189-L polyethylene tubs that were modified to allow water to flow. Each mesocosm was 1-m-long by 0.54-m-wide by 0.46-m-tall. The holes that allowed flow in each mesocosm also maintained water levels at a depth of 0.32 m. Mesocosms were situated in eight spatial blocks, with three mesocosms per block (24 total experimental units) along the bank of Norris Brook in the Hubbard Brook watershed. Mesocosms were gravity fed from Norris Brook and flow was maintained at approximately 5 L min⁻¹. Substrate composition of each mesocosm was standardized with untreated playground sand topped with a single layer of gravel. Each mesocosm was then randomly assigned four cobble-sized rocks (150–340 mm in diameter) collected from the main stem of Hubbard Brook. Mesocosms were open to colonization by stream invertebrates and input from falling terrestrial litter and invertebrates. Mesocosms were constructed on 21–22 June 2012 and water flow from Norris Brook to the mesocosms began on 23 June 2012.

To test how the strength of intraspecific competition varied within streams, we applied three treatments for each of the two study streams in each of four spatial blocks. For each stream, we applied the following three treatments: (1) one upstream individual versus one upstream individual, (2) one upstream individual versus one downstream individual, and (3) one downstream individual versus one downstream individual. Therefore, we could evaluate how intraspecific competition varied as a function of which site an individual came from (upstream or downstream) and whether salamanders were competing with a neighbor (e.g. upstream vs. upstream) or non-neighbor (e.g. upstream vs. downstream). All treatments were randomly assigned within each block, which was nested by stream. The density of salamanders for the experiment was kept constant at the minimum number of individuals needed to test for intraspecific competition: two individuals per meter of mesocosm length. Natural densities at Hubbard Brook can vary from 0.16 individuals per meter to 0.46 individuals per meter of stream length (Davenport & Lowe, unpubl. data), but these densities are likely, in part, a consequence of intraspecific competitive interactions. Both authors have observed higher localized salamander densities at Hubbard Brook during periods of concentrated resources (e.g. low water flow conditions of the summer and mating opportunities of the fall).

The experiment was a randomized block design using individuals from downstream and upstream sampling sites along two study streams (Kineo Brook and Bagley Trail Brook) within the Hubbard Brook watershed. These two study streams were chosen for several reasons. First, these two streams are at opposing ends of the dispersal/gene flow and morphological divergence gradients documented in the Hubbard Brook watershed (Lowe *et al.*, 2006a,b, 2008). It is also important to note that experimental animals came from the same sampling sites used in these previous studies. Second, both streams harbor robust populations of *G. porphyriticus*, which are notoriously hard to detect in nature (Beachy, 2005), leading to low replication and sample sizes in ecological experiments. Third, the remaining streams with background information in the Hubbard Brook watershed are being used for long-term mark-recapture studies and we did not want to remove animals.

We acknowledge that our experiment had low spatial replication (i.e. one low-dispersal stream and one high-dispersal stream), which limits our scope of inference. However, adding one additional stream would require 24 more *G. porphyriticus* adults and 12 more mesocosms. The rarity of *G. porphyriticus* adults in other streams and the challenges of maintaining flow in 36 stream-fed mesocosms throughout the field season made this infeasible. We believe that this limitation is offset, however, by the extensive background data on dispersal and gene flow in the study streams, which greatly increases our strength of inference about the specific mechanism underlying experimental results. In addition to salamander dispersal and gene flow data, we also know that aquatic conditions do not differ significantly between the downstream and upstream sampling sites of the two study streams (Likens & Buso, 2006). Preliminary analyses indicate that total prey abundance does not differ between downstream sampling sites of the two study streams (K. Yurewicz, pers. comm.). Therefore, we believe that our experimental design will still be informative and applicable to other ecological systems.

Salamanders were collected from the sampling sites (downstream: 0–250 m from Hubbard Brook confluence; upstream: 750–1000 m from Hubbard Brook confluence) on 26–30 June

2012. Salamanders were weighed, measured, photographed and marked before being randomly assigned to a mesocosm. All salamanders were uniquely marked by a dorsal subcutaneous injection of a fluorescent elastomer (Northwest Marine Technologies, Shaw Island, WA, USA). To prevent bias, all salamanders were matched for size and then randomly assigned to mesocosms (Resetarits, 1991, 1995). The sex of salamanders was not able to be determined for this study. Initial mean body condition across all experimental salamanders did not differ between upstream and downstream sampling sites within streams (Bagley Trail Brook: $t_{17} = 0.026$, $P = 0.980$, Kineo Brook: $t_{15} = 0.874$, $P = 0.396$). The experiment began on 1 July 2012 and ran for 65 days. Upon termination, all large cover objects in mesocosms were overturned until both experimental salamanders were recovered. All experimental salamanders were weighed, measured and photographed before release back to their collection site. We also used ImageJ (Schneider, Rasband & Eliceiri, 2012) to verify salamander length measurements on all photographs.

Data analysis

The response variable calculated for our analysis was mean proportional change in body condition. Mean proportional change was calculated from initial measurements as follows: Final – Initial/Initial. Body condition was calculated using the scaled mass index procedure outlined in Peig & Green (2009) for each individual at the beginning and end of the experiment. Body condition is often used as an index to measure the energy stores, fitness and reproductive potential of vertebrates (MacDonald et al., 2002; Lowe et al., 2006a). Changes in mass and snout-vent length are traditional response variables in these types of experiments (Resetarits, 1995); however, both are also components of scaled mass calculations. Therefore, we did not include them as separate response variables.

Relative Interaction Intensity Indices (RII) was calculated for the proportional change in body condition. In our study, RII is a statistical measure of an individual's competitive ability toward a non-neighbor relative to a neighbor, where positive values indicate a competitive advantage and negative values indicate a disadvantage of an individual when challenged with a non-neighbor relative to a neighbor (e.g. upstream vs. downstream relative to upstream vs. upstream; Armas, Ordiales & Pugnaire, 2004). Interaction values are centered on zero with positive interactions (values between 0 and +1) indicating less intense intraspecific competition with a non-neighbor relative to a neighbor, and negative interactions (values between 0 and −1) indicating more intense intraspecific competition with a non-neighbor relative to a neighbor. RII calculations were based on Armas et al. (2004), where RII is calculated by dividing the difference between mean proportional change in a response variable of the treatment (B_w) and the control (B_o) by the sum of those mean proportional changes in that response variable (B_w-B_o/B_w + B_o). The standard error was calculated with the formula provided in Armas et al. (2004).

In our experiment, B_w was the mean proportional change in inter-site treatments (e.g. upstream vs. downstream) and B_o was the mean proportional change in intra-site treatments (e.g. upstream vs. upstream). Each numerator and denominator would change depending on the RII comparison. For example, to calculate the RII for Kineo Brook upstream individuals, B_w was the mean proportional change in body condition of the upstream individuals in the upstream vs. downstream treatments. B_o was the mean proportional change in body condition of individuals in the upstream vs. upstream treatments. In this example, a RII value less than zero would indicate that upstream individuals do better with other upstream individuals than with downstream individuals, an RII value around zero would indicate that upstream individuals do just as well with other upstream individuals as with downstream individuals, and an RII greater than zero would indicate that upstream individuals do better with downstream individuals than with other upstream individuals.

Our RII calculations were based on experimental replicates for each stream (Kineo Brook and Bagley Trail Brook). Replicates with escaped salamanders were excluded from RII calculations and statistical analyses ($n = 3$ for all treatments except Bagley upstream vs. downstream and Kineo upstream vs. upstream where $n = 2$). To determine if neighbor individuals were superior competitors against non-neighbor individuals than against other neighbor individuals, we compared the RII calculations for mean proportional change in body condition to zero for both upstream and downstream sampling sites of each stream with a one-sample t-tests (Aschehoug et al., 2012). All statistical analyses were conducted using Sigmaplot software 11.0 (Systat Software, San Jose, CA, USA).

Results

For Kineo Brook, the low-dispersal stream, salamanders from the downstream site had positive RII values for body condition that were significantly different from zero ($t_2 = 35.01$, $P < 0.001$; Fig. 1). In contrast, salamanders from the upstream site had negative RII values for body condition that were significantly different from zero ($t_3 = 4.14$, $P = 0.026$; Fig. 1). These results indicate that salamanders from the downstream site had better performance (i.e. positive RII values = gain in body condition) with a non-neighbor than with a neighbor. Conversely, salamanders from the upstream site had poorer performance (i.e. negative RII values = reduction in body condition) with a non-neighbor than with a neighbor.

For Bagley Trail Brook, the high-dispersal stream, salamanders from the upstream site had positive RII values for body condition, but these positive RII values were not significantly different from zero ($t_2 = 2.97$, $P = 0.097$; Fig. 1). Downstream individuals had negative RII values for mean proportional change in body condition that were significantly different from zero ($t_3 = 43.99$, $P < 0.001$; Fig. 1). These results indicate that individuals from the upstream site performed just as well (i.e. RII values near zero = no difference in body condition) with a neighbor as with a non-neighbor. Individuals from downstream sampling sites, however, had poorer performance (i.e. negative RII values = reduction in body condition) with a non-neighbor than with a neighbor.
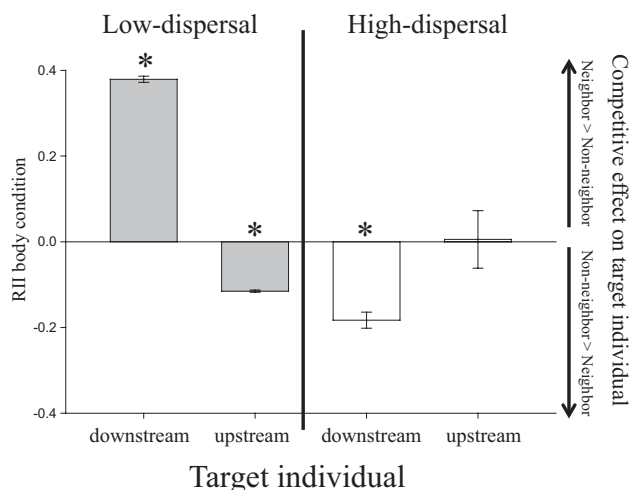
Figure 1 Intraspecific competitive effects on mean proportional change in body condition of *Gyrinophilus porphyriticus* caused by competition between target individuals from upstream and downstream sampling sites in a low-dispersal stream (Kineo Brook) and a high-dispersal stream (Bagley Trail Brook). The strength of intraspecific competition is measured by the Relative Interaction Intensity Index (RII) in which the effect of a non-neighbor individual on a focal individual is determined relative to the effect of a neighbor individual. Positive values indicate less intense intraspecific competition with a non-neighbor individual and negative values indicate more intense intraspecific competition with a non-neighbor individual. Asterisks above bars indicate a significant difference from zero ($P < 0.05$). Error bars indicate ± 1 SE.

Discussion

Our data support the hypothesis that spatial sorting influences the strength and spatial structure of intraspecific competition in *G. porphyriticus*. Based on the spatial sorting hypothesis, we predicted that in a low-dispersal stream, downstream individuals would be better intraspecific competitors than upstream individuals because of the aggregation of high-performance individuals downstream (Lowe *et al.*, 2006b; Table 1). In the stream with low-dispersal (Kineo Brook), downstream individuals were significantly better competitors against non-neighbor, upstream individuals (positive RII; Fig. 1) than were upstream individuals against non-neighbor, downstream individuals (negative RII). Because dispersal is upstream-biased in *G. porphyriticus* (Lowe, 2003), and high-performance animals are more likely to move upstream than low-performance animals (Lowe *et al.*, 2006b), we predicted that individuals from upstream sampling sites would be better competitors in a high-dispersal stream (Table 1). Consistent with this prediction, we found that in the high-dispersal stream (Bagley Trail Brook), downstream individuals were weak competitors against non-neighbor, upstream individuals (negative RII; Fig. 1). Upstream individuals, however, were affected similarly by both a non-neighbor, downstream individual and a neighbor, upstream individual (RII $\approx$ 0). These

results likely reflect the ongoing upstream-biased dispersal of high-performance individuals. To our knowledge, this is the first time that spatial sorting has been explicitly identified as a potential mechanism contributing to the strength of intraspecific interactions.

Traditionally, traits associated with colonization (i.e. dispersal) were thought to negatively co-vary with traits associated with competitive performance, promoting species coexistence (Hastings, 1980). However, competitive traits and performance can also influence rates of emigration and immigration (Stamps, 2006), leading to positive covariation in competitive and dispersal traits (e.g. aggression, Duckworth, 2008; endurance, Llewelyn *et al.*, 2010) and, ultimately, spatial variation in competitive performance (Nadell & Basslet, 2011). This appears to be the case in our study system, where individuals that are more likely to disperse are also more likely to be superior competitors, leading to spatial variation in intraspecific competitive performance that is predicted by rates of dispersal along streams. The process of spatial sorting in stream salamanders is thereby reinforced by traits that not only enhance dispersal ability, but also appear to have indirect effects on competitive traits. We found support for the spatial sorting hypothesis by explicitly testing the strength of intraspecific competition between neighbor and non-neighbor salamanders in streams that differ in dispersal and gene flow.

Originally, we hypothesized that spatial sorting or evolutionary divergence could be responsible for spatial variation in the strength of intraspecific competition, based on dispersal and gene flow data that could support either mechanism (Lowe *et al.*, 2006b, 2008). The specific pattern that we found matches the spatial sorting mechanism; however, we cannot eliminate evolutionary divergence as a mechanism contributing to differences in intraspecific competitive performance. Evolutionary processes or non-random mating based on performance traits could still be reinforcing the patterns created by spatial sorting (Garant *et al.*, 2005). For instance, if assortative mating occurs based on location within the low-dispersal stream (i.e. upstream vs. downstream sampling sites), then traits underlying competitive performance could diverge over time between sampling sites. In this case, however, spatial sorting would still be the initial cause of the observed variation in intraspecific competitive performance. We do not believe that local abiotic conditions (i.e. habitat quality) are responsible for the results of our study. Prior analyses showed no association between gene flow in *G. porphyriticus* and elevational variation of 17 aquatic conditions (e.g. water temperature, dissolved oxygen, acidity; Likens & Buso, 2006).

Our results revealed an exciting pattern in the spatial variation of intraspecific competitive ability of *G. porphyriticus* and suggest that the traits associated with dispersal may also be important for competitive performance. Previous work on other plethodontid salamanders has linked variation of head morphology to relative competitive ability (Adams, 2010). *G porphyriticus* can exhibit morphological variation (Adams & Beachy, 2001; Lowe *et al.*, 2008), and dispersal ability has been linked to limb morphology in this species (Lowe & McPeek, 2012). However, we are unaware of studies testing

the competitive effects of morphological traits known to vary in *G. porphyriticus*. Nevertheless, this prior work provides a foundation for developing hypotheses for the specific traits responsible for our experimental results. We did not expect to find morphological differences in our experimental salamanders because of the low sample size ($n = 48$ individuals); past studies that have linked differences in salamander morphology to species interactions have used hundreds of museum specimens (Adams, 2010). In *a posteriori* comparisons, the limb phenotypes of all individuals across the four sampling sites were analyzed with a PCA analysis (Lowe *et al.*, 2008; Lowe & McPeek, 2012) and were not significantly different from one another ($F_{3, 33} = 1.25$, $P = 0.306$). We are currently conducting long-term, capture-mark-recapture studies of *G. porphyriticus* populations in five streams in the Hubbard Brook valley to assess divergence in competition-related traits across an in-stream dispersal gradient.

Our study is novel by using direct data on dispersal to predict variation in the strength and spatial structure of intraspecific competition. Traditional approaches to experimental ecology have relied on indirect indices of dispersal (Lowe & Allendorf, 2010) that treat dispersal as random process with respect to individual traits (Matthiessen, Mielke & Sommer, 2010). This approach likely misses the importance of variation in dispersal traits of individuals and populations, and could lead to different conclusions in metacommunity ecology studies if dispersing individuals are not random (Edelaar & Bolnick, 2012). For example, by randomly drawing individuals from a source population for metacommunity experiments, researchers may miss the causal link between dispersal-related traits and relative competitive performance, leading to erroneous conclusions on mechanisms controlling patterns of species coexistence and community assembly (Bélisle, 2005). Direct data on dispersal of *G. porphyriticus* indicate that dispersal is not random – dispersing individuals have higher body condition and longer forelimbs relative to hindlimbs than non-dispersing individuals (Lowe *et al.*, 2006a; Lowe & McPeek, 2012). Based on our results, it appears that these dispersal-related traits may either directly affect competitive performance, or be coupled to traits affecting competitive performance. Without these direct data on dispersal, we would have assumed that dispersal within streams was random, which could have led to a misinterpretation of the mechanism responsible for our experimental results.

A substantial amount of recent research has been devoted to understanding the consequences of dispersal at the community level, especially in regard to community assembly (Resetarits, Binckley & Chalcraft, 2005). Many of these studies, however, do not consider how the traits of dispersing individuals may affect species interactions and community assembly. This is surprising because differential dispersal has been linked to intraspecific trait variation (Phillips *et al.*, 2006; Lowe & McPeek, 2012), and intraspecific trait variation can affect the strength of species interactions (Bolnick *et al.*, 2011). Our study demonstrates that intraspecific variation in traits related to dispersal may be coupled with competitive performance, producing variation in intraspecific competitive

ability at relatively small spatial scales (<1 km). This work fills an important gap in the literature by showing the importance of understanding dispersal from an individual perspective, and its role in structuring the strength of intraspecific interactions. This first step focused on intraspecific competitive ability, but the intraspecific effects of differential dispersal shown here likely cascade up to influence interspecific interactions and the outcome of evolution in metacommunities (Urban & Skelly, 2006). Future studies should elucidate the link between intraspecific trait variation, differential dispersal and spatial patterns of metacommunity assembly.

Acknowledgments

References

Adams, D.C. (2010). Parallel evolution of character displacement driven by competitive selection in terrestrial salamanders. *BMC Evol. Biol.* **10**, 1–10.

Adams, D.C. & Beachy, C.K. (2001). Historical explanations of phenotypic variation in the plethodontid salamander *Gyrinophilus porphyriticus*. *Herpetologica* **57**, 353–364.

Armas, C., Ordiales, R. & Pugnaire, F.I. (2004). Measuring plant interactions: a new comparative index. *Ecology* **85**, 2682–2686.

Aschehoug, E.T., Metlen, K.L., Callaway, R.M. & Newcombe, G. (2012). Fungal endophytes directly increase the competitive effects of an invasive forb. *Ecology* **93**, 3–8.

Bélisle, M. (2005). Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* **86**, 1988–1995.

Beachy, C.K. (2005). Gyrinophilus porphyriticus Green, 1827. Spring salamander. In *Amphibian declines: the conservation status of United States Species*: 590–593. Lannoo, M. (Ed.). Berkeley and Los Angeles: University of California Press.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C. & Vasseur, D.A. (2011). Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* **28**, 183–192.

Booth, D.J. & Beretta, G.A. (2004). Influence of recruit condition on food competition and predation risk in a coral reef fish. *Oecologia* **140**, 289–294.

Bruce, R.C. (1979). Evolution of paedogenesis in salamanders of the genus *Gyrinophilus*. *Evolution* **33**, 998–1000.

Cote, J., Fogarty, S., Weinersmith, K., Bodin, T. & Sih, A. (2010). Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proc. Roy Soc. Lond. Ser. B.* **277**, 1571–1579.

Duckworth, R.A. (2008). Adaptive dispersal strategies and the dynamics of a range expansion. *Am. Nat.* **172**, S4–S17.

Edelaar, P. & Bolnick, D. (2012). Non-random gene flow: an underappreciated force in evolution and ecology. *Trends Ecol. Evol.* **27**, 659–665.

Garant, D., Kruuk, L.E.B., Wilkin, T.A., McCleery, R.H. & Sheldon, B.C. (2005). Evolution driven by differential dispersal within a wild bird population. *Nature* **433**, 60–65.

Greene, B.T., Lowe, W.H. & Likens, G.E. (2008). Forest succession and prey availability influence the strength and scale of terrestrial-aquatic linkages in a headwater salamander system. *Freshwater Biol.* **53**, 2234–2243.

Hastings, A. (1980). Disturbance, coexistence, history and competition for space. *Theor. Popul. Biol.* **22**, 323–338.

Johnson, M.L. & Gaines, M.S. (1990). Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annu. Rev. Ecol. Syst.* **21**, 449–480.

Likens, G.E. & Buso, D.C. (2006). Variation in streamwater chemistry throughout the Hubbard Brook Valley. *Biogeochemistry* **78**, 1–30.

Llewelyn, J., Phillips, B.L., Alford, R.A., Schwarzkopf, L. & Shine, R. (2010). Locomotor performance in an invasive species, Cane toads from the invasion front have greater endurance, but not speed, compared to conspecifics from a long-colonised area. *Oecologia* **162**, 343–348.

Logue, J.B., Mouquet, N., Peter, H. & Hillebrand, H., the Metacommunty Working Group (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol. Evol.* **26**, 482–491.

Lotka, A.J. (1932). The growth of mixed populations: two species competing for a common food supply. *J. Wash. Acad. Sci.* **22**, 461–469.

Lowe, W.H. (2003). Linking dispersal to local population dynamics: a case study using a headwater salamander system. *Ecology* **84**, 2145–2154.

Lowe, W.H. & Allendorf, F.W. (2010). What can genetics tell us about population connectivity? *Mol. Ecol.* **19**, 3038–3051.

Lowe, W.H. & McPeek, M.A. (2012). Can natural selection maintain long-distance dispersal? Insight from a stream salamander system. *Evol. Ecol.* **26**, 11–24.

Lowe, W.H., Likens, G.E. & Cosentino, B.J. (2006a). Self-organization in streams: the relationship between movement behavior and body condition in a headwater salamander. *Freshwater Biol.* **51**, 2052–2062.

Lowe, W.H., Likens, G.E., McPeek, M.A. & Buso, D.C. (2006b). Linking direct and indirect data on dispersal, isolation by slope in a headwater stream salamander. *Ecology* **87**, 334–339.

Lowe, W.H., McPeek, M.A., Likens, G.E. & Cosentino, B.J. (2008). Linking movement behaviour to dispersal and divergence in plethodontid salamanders. *Mol. Ecol.* **17**, 4459–4469.

Lowe, W.H., McPeek, M.A., Likens, G.E. & Cosentino, B.J. (2012). Decoupling of genetic and phenotypic divergence in a headwater landscape. *Mol. Ecol.* **21**, 2399–2409.

MacDonald, D.W., Newman, C., Stewart, P.D., Domingo-Roura, X. & Johnson, P.J. (2002). Density-dependent regulation of body mass and condition in Badgers (*Meles meles*) from Wytham Woods. *Ecology* **83**, 2056–2061.

Matthiessen, B., Mielke, E. & Sommer, U. (2010). Dispersal decreases diversity in heterogeneous metacommunities by enhancing regional competition. *Ecology* **91**, 2022–2033.

McPeek, M.A. & Holt, R.D. (1992). The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.* **140**, 1010–1027.

Mondelli, M.J., Davenport, J.M. & Lowe, W.H. (2014). *Gyrinophilus porphyticus* Diet: fish versus fishless streams. *Herpetol. Rev.* **45**, 109–110.

Nadell, C.D. & Basslet, B.L. (2011). A fitness trade-off between local competition and dispersal in Vibrio cholerae biofilms. *Proc. Natl. Acad. Sci. USA* **108**, 14181–14185.

Peig, J. & Green, A.J. (2009). New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* **118**, 1883–1891.

Petranka, J.W. (1998). *Salamanders of the United States and Canada*. Washington, DC: Smithsonian Institution Press.

Phillips, B.L., Brown, G.P., Webb, J.K. & Shine, R. (2006). Invasion and the evolution of speed in toads. *Nature* **439**, 803.

Post, D.M., Palkovacs, E.P., Schielke, E.G. & Dodson, S.I. (2008). Intraspecific phenotypic variation in a predator affects zooplankton community structure and cascading trophic interactions. *Ecology* **89**, 2019–2032.

Postma, E. & van Noordwijk, A.J. (2005). Gene flow maintains a large genetic difference in clutch size at a small spatial scale. *Nature* **433**, 65–68.

Resetarits, W.J.J. (1991). Ecological interactions among predators in experimental stream communities. *Ecology* **72**, 1782–1793.

Resetarits, W.J.J. (1995). Competitive asymmetry and coexistence in size-structured populations of brook trout and spring salamanders. *Oikos* **73**, 188–198.

Resetarits, W.J.J., Binckley, C.A. & Chalcraft, D.R. (2005). Habitat selection, species interactions, and processes of community assembly in complex landscapes: a metacommunity perspective. In *Metacommunities: spatial*

dynamics and ecological communities: 374–398. Holyoak, M., Leibold, M.A. & Holt, R.D. (Eds). Chicago: University of Chicago Press.

Roff, D.A. & Fairburn, D.J. (2001). The genetic basis of dispersal and migration, and its consequences for the evolution of correlated traits. In *Dispersal*: 191–202. Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (Eds). Oxford: Oxford University Press.

Schluter, D. (2000). *The ecology of adaptive radation*. Oxford: Oxford Univ Press.

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012). NIH Image to ImageJ, 25 years of image analysis. *Nat. Methods* **9**, 671–675.

Shine, R., Brown, G.P. & Phillips, B.L. (2011). An evolutionary process that assembles phenotypes through space rather than through time. *Proc. Natl. Acad. Sci. USA* **108**, 5708–5711.

Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science* **236**, 787–792.

Stamps, J.A. (2006). The silver spoon effect and habitat selection by natal dispersers. *Ecol. Lett.* **9**, 1179–1185.

Storfer, A. & Sih, A. (1998). Gene flow and ineffective antipredator behavior in a stream-breeding salamander. *Evolution* **52**, 558–565.

Svanbäck, R. & Bolnick, D.I. (2007). Intraspecific competition drives increased resource use diversity within a natural population. *Proc. Roy. Soc. Lond. Ser. B.* **274**, 839–844.

Urban, M.C. & Skelly, D.K. (2006). Evolving metacommunities: toward an evolutionary perspective on metacommunities. *Ecology* **87**, 1616–1626.

Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. *Nature* **118**, 558–560.

Yu, D.W. & Wilson, H.B. (2001). The competition-colonization trade-off is dead; long live the competition-colonization trade-off. *Am. Nat.* **158**, 49–63.