

Forest succession and prey availability influence the strength and scale of terrestrial-aquatic linkages in a headwater salamander system

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SUMMARY

1. Trophic linkages between terrestrial and aquatic ecosystems are common and sensitive to disruption. However, there is little information on what causes variation in the strength and spatial scale of these linkages.

2. In the highly aquatic adults of the headwater salamander *Gyrinophilus porphyriticus* (family Plethodontidae), use of terrestrial prey decreases along a gradient from early- to late-successional riparian forests. To understand the cause of this relationship, we tested the predictions that (i) terrestrial prey abundance is lower in late-successional forests, and (ii) *G. porphyriticus* adults cannot move as far from the stream to forage in late-successional forests, thus limiting access to terrestrial prey.

3. We established 100-m long study reaches on six headwater streams in the Hubbard Brook Experimental Forest, New Hampshire. Three reaches were in early-successional forests and three were in late-successional forests. We conducted pitfall trapping for invertebrate prey in June and July of 2005, with three traps at 0, 2, 5 and 10 m from the stream at each reach. In June, July and August of 2004 and 2005, nighttime salamander surveys were conducted at each reach along ten, 10-m long by 2.5-m wide transects perpendicular to the stream.

4. Abundance of terrestrial prey was consistently lower in late-successional forests, suggesting that consumption of terrestrial prey by *G. porphyriticus* is affected by prey abundance. Contrary to our prediction, *G. porphyriticus* adults moved farther from the stream in late-successional forests, suggesting that habitat conditions in late-successional forests do not limit movement away from the stream, and that lower abundances of terrestrial prey in these forests may cause salamanders to move farther from streams.

5. Our results provide novel insight on the extent of terrestrial habitat use by *G. porphyriticus*. More broadly, these results indicate that major habitat gradients, such as forest succession, can affect the strength and scale of terrestrial-aquatic linkages.

Application of this insight to the design of vegetation buffers along headwater streams would have widespread benefits to freshwater ecosystems.

Keywords: amphibian, food webs, *Gyrinophilus porphyriticus*, headwater streams, riparian forest

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Introduction

Interactions between stream and terrestrial ecosystems have long been recognized (Likens & Borrmann, 1974; Hynes, 1975). With the recent emphasis on spatial processes in food-web research (e.g. Polis, Anderson & Holt, 1997; Huxel & McCann, 1998), studies have also begun to elucidate direct interactions between stream and riparian species (e.g. Nakano & Murakami, 2001; Sabo & Power, 2002), reinforcing the need to protect key species and associated pathways of interhabitat exchange. Disrupting these pathways can have cascading effects across both aquatic and terrestrial systems (Baxter *et al.*, 2004; Whiles *et al.*, 2006), but examinations of the spatial scale of interactions between stream and riparian species are rare (Baxter, Fausch & Saunders, 2005; Lowe, Likens & Power, 2006b.). For example, although it is clear that terrestrial invertebrates serve as food for consumers in streams (e.g. Kawaguchi & Nakano, 2001; Nakano & Murakami, 2001) and that consumers in the riparian zone prey on adult stream insects (e.g. Nakano & Murakami, 2001; Sabo & Power, 2002), few studies have quantified the area of the riparian zone contributing terrestrial invertebrates to or receiving aquatic insects from the stream (but see Briers *et al.*, 2005). Consequently, we lack basic information to determine the scale of land protection required to keep stream-riparian food webs intact.

Because of their high edge to area ratio, small, headwater streams are especially prone to interactions with adjacent terrestrial ecosystems. Although the spatial scale of these interactions is poorly resolved, the productivity and structure of headwater communities are clearly dependent on terrestrial resources (Wallace *et al.*, 1997; Nakano, Miyasaka & Kuhara, 1999; England & Rosemond, 2004), more so than in higher-order streams and rivers (Hall, Likens & Malcom, 2001; McCutchan & Lewis, 2002). Paradoxically, however, there are no riparian buffer requirements for low-order streams in most of the U.S.A., and the minimal protection given to headwater streams and watersheds under the U.S. Clean Water Act (33 U.S.C., chapter 26) has been challenged unsuccessfully numerous times in the last decade. Empirical information on the scale of stream-riparian interactions will significantly advance understanding of the ecology of headwaters, and address an urgent

need to resolve the conservation requirements of these ecosystems.

The spring salamander (*Gyrinophilus porphyriticus* Green; family Plethodontidae) is a large salamander [up to 110 mm snout-vent length (SVL)] found in headwater streams along the Appalachian Mountains of eastern North America, from Alabama to southern Quebec (Petranka, 1998). *G. porphyriticus* larvae are strictly aquatic. Adults are highly aquatic and generally restricted to streams, springs and seeps (Grover & Wilbur, 2002; Bruce, 2003), but have been observed in the riparian zones of headwater streams at night (DeGraaf & Rudis, 1990; Grover, 2006). In New Hampshire, larvae feed almost exclusively on aquatic invertebrates (Burton, 1976), but terrestrial invertebrates are a significant component of adult diets (Burton, 1976; Lowe, Nislow & Likens, 2005). The absence of terrestrial prey in larval diets strongly suggests that this species does not use terrestrial prey that fall into the stream, and that adults leave the stream to forage for these prey. However, like other cases where stream and riparian food webs are known to be linked, explicit analyses of the spatial extent of terrestrial habitat use by *G. porphyriticus* adults and of sources of variation in the use of terrestrial prey and terrestrial habitat by this species have not been done.

In a previous study, we found that the relative contributions of terrestrial and aquatic prey to diets of 76 *G. porphyriticus* adults in ten streams throughout New Hampshire were closely related to the structure of riparian forests (Lowe *et al.*, 2005). The mean proportion of terrestrial prey biovolume in salamander gut contents ranged from 0 to 0.74 across streams and was negatively related to the mean diameter at breast height (DBH, cm) of riparian trees, an index of successional stage (Bormann & Likens, 1979; Keeton, Kraft & Warren, 2007). The relative contribution of terrestrial prey to diets of adult *G. porphyriticus* was unrelated to the proportion of coniferous riparian trees, and unrelated to the abundance of aquatic prey and predatory brook trout (*Salvelinus fontinalis* Mitchell), further supporting a direct relationship with forest age. Based on these results, we hypothesized that consumption of terrestrial prey by *G. porphyriticus* adults was regulated by changes in the abundance of these prey, or in their accessibility, with forest succession, and we initiated the current study to test this hypothesis.

The current study quantifies variation in the abundance of terrestrial prey and variation in terrestrial

habitat use by *G. porphyriticus* adults in relatively early- and late-successional riparian forests (50–70 years since disturbance versus >100 years since disturbance, respectively). Specifically, we tested the predictions that (i) abundance of terrestrial prey is lower in late-successional riparian forests than early-successional riparian forests, and (ii) *G. porphyriticus* adults do not move as far into the riparian zone to forage in late-successional forests as they do in early-successional forests. Support for only the first prediction would indicate that variation in the availability of terrestrial prey is an important control on consumption of these prey by *G. porphyriticus* adults. This prediction is consistent with numerous studies showing that aboveground net primary production declines with stand age in mature forests (reviewed in Gower, McMurtrie & Murty, 1996; Pregitzer & Euskirchen, 2004). Leaves are a significant component of aboveground net primary productivity in forests of the northeastern U.S.A. (Bormann & Likens, 1979) and important resources for terrestrial invertebrates (Speight, Hunter & Watt, 1999). Support for only the second prediction would indicate that other habitat conditions affecting access to terrestrial prey are important in controlling their use by *G. porphyriticus* adults. Little is known about how riparian habitats and communities change with succession in the northeastern U.S.A., but it is possible that abiotic or biotic conditions in late-successional forests (e.g. temperature, humidity, abundance of terrestrial predators) prevent *G. porphyriticus* from spatially extended foraging into the riparian zone (e.g. Grover & Wilbur, 2002; Marsh & Beckman, 2004).

This study was not designed to identify predictors of terrestrial habitat use other than prey availability, for which there was *a priori* support (Lowe *et al.*, 2005). However, in addition to testing our *a priori* predictions, our objective was to provide spatially explicit information on the abundance of riparian invertebrates and habitat use by *G. porphyriticus* to improve understanding of the spatial structure of terrestrial-aquatic linkages in headwater ecosystems.

Methods

Study species and site

This study was conducted at the Hubbard Brook Experimental Forest in the White Mountains of central

New Hampshire, U.S.A. We established 100-m long study reaches on six, hydrologically independent first-order streams set in this northern hardwood forest: Zigzag Brook, Canyon Brook, Falls Brook, Bear Brook, Watershed 4 Brook and Paradise Brook. All study reaches were above natural barriers to brook trout, known predators of *G. porphyriticus* (Resetarits, 1991). The downstream ends of all study reaches were between 500 and 600 m in elevation. Typical of headwater streams in New Hampshire, the study 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 midday summer temperatures (13.0–17.0 °C) (Likens & Bormann, 1995; Likens & Buso, 2006). More detailed information on the physical and chemical conditions in these streams is available at the Hubbard Brook website (<http://www.hubbardbrook.org>).

Using available information on logging history, experimental manipulations, and natural disturbances of the forest (Bormann & Likens, 1979; Likens & Bormann, 1995; website) and observations collected during preliminary surveys of the riparian forests (B.T.G., unpubl. data), we situated these reaches within early-successional forest stands (i.e. low mean DBH, 50–70 years since major disturbance; Bormann & Likens, 1979) along Paradise, Watershed 4, and Zigzag Brooks, and within late-successional stands (i.e. high mean DBH, >100 years since disturbance) along Bear, Canyon and Falls Brooks. These successional categories were relative and based on the disturbance history of the Hubbard Brook Experimental Forest, which is similar to that of many forested areas of the northeastern U.S.A. The forest was extensively logged during the early 1900s (Likens & Bormann, 1995), and was damaged by a major hurricane in 1938. These factors created a structurally diverse forest with stands in many different stages of development (Schwarz *et al.*, 2001), but there had been no recent, extensive forest disturbance at the study reaches. The dominant tree species in these stands are *Acer saccharum* Marshall, *Fagus grandifolia* Ehrhart, *Betula alleghaniensis* Britton, *Picea rubens* Sargent, *Abies balsamea* Linnaeus, and *B. papyrifera* Marshall (Bormann & Likens, 1979; Schwarz, Fahey & McCulloch, 2003).

To confirm the relative successional stages of forest stands surrounding the study reaches, we assessed the structure and composition of these stands directly.

In June of 2004, six 25-m long by 1-m wide transects were set perpendicular to the stream channel at random locations along each study reach. Three forest transects were set on each side of the stream, and all began at the bank-full channel edge. We measured the DBH of all trees in transects with DBH \geq 3.0 cm. These data were used to calculate the mean DBH of trees surrounding each study reach, pooling individuals across the six transects. We also identified trees as either deciduous or coniferous to estimate the proportion of coniferous trees in the riparian forest [$1 - (\text{proportion deciduous trees})$], pooling individuals across all transects. We then used analysis of variance (ANOVA) to test the assumptions that (i) mean DBH was lower in the early-successional stands than in the late-successional stands, and that (ii) this difference was unrelated to variation in the composition of the stands, as represented by the proportion of coniferous trees.

Along each study reach, we established ten 'salamander transects' for our examination of terrestrial habitat use by *G. porphyriticus* adults, and three 'prey transects' for our examination of terrestrial prey availability. Salamander transects were 10-m long by 2.5-m wide, beginning at the wetted channel edge of the stream and extending 10 m into the riparian forest at an angle perpendicular to the axis of the stream channel. By setting these transects to begin at the channel edge, and thus allowing them to shift with changes in discharge over the field season, we were able to standardize data on terrestrial habitat use based on distance to the nearest water. Salamander transects were spaced at 10-m intervals along each study reach, and located on alternating sides of the stream. To eliminate potential interference between sampling methods, prey transects were set on the opposite side of the stream from three, randomly selected salamander transects. Prey transects were lines beginning at the bank-full channel edge of the stream and extending 10 m into the riparian forest at an angle perpendicular to axis of the stream channel.

Terrestrial prey sampling

We used pitfall traps to quantify the abundance of terrestrial invertebrates at four locations along the prey transects in the riparian forest. Three sessions of pitfall trapping were conducted at three-week

intervals during the summer of 2005, on June 18, July 7, and July 26. All traps were open for 24 hours, beginning at 1500 h. Along each prey transect, one pitfall trap was placed at 0, 2, 5 and 10 m from the bank-full, channel edge of the stream, resulting in three traps at each distance for each study reach. Pitfall traps were 130-ml plastic specimen jars with mouths 5-cm in diameter, and were half-filled with a 70% ethanol solution.

At the end of each trapping session, traps were sealed with plastic lids and returned to the lab to sort and identify contents. All invertebrates were identified to order. We quantified the total number of prey individuals within each sample, excluding orders that do not occur in *G. porphyriticus* diets (Lowe *et al.*, 2005). Data were pooled from the three samples at each distance to calculate total abundance of prey at that distance within a trapping session. These total abundance values were used to calculate mean abundance of terrestrial prey at each distance over the sampling period (June–July), when *G. porphyriticus* is most surface-active in the northeastern United States (Bishop, 1941; Burton & Likens, 1975). We used mean abundance of terrestrial prey as an index of the availability of these prey to *G. porphyriticus* adults. We acknowledge that pitfall traps are not equally effective at sampling all terrestrial invertebrate taxa (Luff, 1975; Work *et al.*, 2002), and that abundance of terrestrial prey is not necessarily correlated with the biomass of terrestrial prey in riparian forests. However, by restricting our analysis to those taxa (and related size categories) of terrestrial prey that were present in *G. porphyriticus* gut contents, we believe that this is a valid and informative index for testing our prediction on the availability of terrestrial prey in early- and late-successional forests.

With ANOVA, we tested for effects of (i) riparian forest stage (early- and late-successional) and (ii) distance from the bank-full channel edge (0, 2, 5 and 10 m) on mean abundance of terrestrial prey. Study reach nested within forest stage was a random effect in the ANOVA model to account for variability among reaches within forest stage categories. Following Underwood (1981) and Sokal & Rohlf (1995), the interaction of forest stage and distance from the channel was included in the final ANOVA model when $P < 0.5$. To achieve normality, mean prey abundances were square-root transformed.

Nighttime salamander surveys

To test whether the extent of terrestrial habitat use by *G. porphyriticus* adults differed between early- and late-successional riparian forests, multiple, nighttime searches along the salamander transects of each study reach were conducted between early June and early August of 2004 and 2005. Each of the six study reaches was visited 12 times in 2004 and 13 times in 2005, and all transects were searched on each visit. In addition to the salamander transects, the 100-m stream channel was also searched on each visit to estimate the number of *G. porphyriticus* adults in the stream. To standardize these channel surveys, they were limited to 0.5-m wide bands extending from water's edge into the channel, and along both sides of the channel. No more than three study reaches were visited in one night (20:00–05:00 hours), and the orders in which study reaches were visited over the field season and within nights were randomized to prevent sampling bias.

Searches were conducted using a Nite Sport II light (NLC Products Inc, Little Rock, AR, U.S.A.) to scan the 10-m long by 2.5-m wide salamander transects. Cover objects were not disturbed during these searches, but the ground cover and understory vegetation were thoroughly inspected. We recorded the position along the transect (m from the channel edge) of each *G. porphyriticus* individual observed, and measured the size (SVL, mm) and mass (mg) of these individuals at the time of capture. To eliminate bias in this data set caused by multiple observations of the same individual, each salamander was individually marked by subcutaneous injection of a fluorescent elastomer (Northwest Marine Technologies, Shaw Island, WA, U.S.A.). Previously marked individuals were recorded, and these data were not used in subsequent analyses. The same methods were used to search the stream channel. All salamander surveys were conducted by B.T.G.

Nighttime survey data were used to calculate mean distances from the stream channel of *G. porphyriticus* individuals observed along each study reach in each year. Two-way ANOVA was then used to test for direct and interactive effects of (i) riparian forest stage (early and late-successional) and (ii) year (2004 and 2005) on mean distance from the stream channel of *G. porphyriticus* individuals. The interaction was included in the final ANOVA model only when

$P < 0.5$. Mean distance values were square-root transformed to achieve normality.

We also used ANOVA to test for effects of riparian forest stage and year on (i) number of individuals observed along salamander transects, (ii) mean size of observed individuals (SVL, mm), (iii) mean body condition of observed individuals (size-corrected mass, log mg) and (iv) relative frequency of terrestrial habitat use among *G. porphyriticus* adults observed at a study reach [(no. individuals observed along salamander transects)/(total no. individuals observed along salamander transects and in the stream channel)]. Number of individuals observed along salamander transects, mean size of these individuals, and relative frequency of terrestrial habitat use were analysed to assess potentially confounding correlations with terrestrial habitat use. Numbers of individuals observed and mean sizes of observed individuals were square-root transformed to achieve normality. Relative frequencies of terrestrial habitat use were arcsine square-root transformed.

We analysed mean body condition to determine whether differences in terrestrial habitat use were associated with variation in this index of individual fitness (Green, 2001; Schulte-Hostedde *et al.*, 2005). In previous studies, body condition was positively correlated with growth and reproduction in *G. porphyriticus* (e.g. Lowe, Likens & Cosentino, 2006a). Size-corrected mass, the residuals from ordinary least squares linear regression of log-transformed mass and SVL measurements, was used to measure body condition. Use of linear regression was justified by the lack of statistical support for more complex models of the relationship between log mass and log SVL (W.H.L., unpubl. data) and by the lack of correlation between log SVL and residuals from this regression ($r = -0.0001$, $n = 60$, $P = 1.0$). Mean body conditions were square-root transformed to achieve normality.

Results

Forest classification

Consistent with our *a priori* classifications of successional stage, mean DBH values of trees along study reaches on Paradise, Watershed 4, and Zigzag Brooks (mean \pm 1 SE = 12.6 \pm 3.41 cm, 9.53 \pm 0.86 cm, 12.57 \pm 2.86 cm, respectively) were significantly lower than those of trees along Bear, Canyon, and Falls Brooks

(17.75 ± 4.58 cm, 16.71 ± 3.26 cm, 17.59 ± 3.17 cm, respectively) ($F = 29.3$, d.f. = 1, 4, $P < 0.01$). There was no difference between early- and late-successional riparian forests in the proportion of deciduous trees ($F = 0.2$, d.f. = 1, 4, $P = 0.68$), supporting the assumption that variation in successional stage was related to differences in tree size and age, but not forest composition.

Terrestrial prey abundance

Based on the earlier study of the diets of 76 adult *G. porphyriticus* from streams throughout New Hampshire (Lowe *et al.*, 2005), terrestrial invertebrates in the following orders were included in the analysis of terrestrial prey availability: Araneae, Basommatophora, Chordeumida, Coleoptera, Diptera, Hemiptera, Lepidoptera, Oligochaeta, Opiliones, Orthoptera, Psocoptera, Stylommatophora, Thysanoptera. Because they did not appear in adult *G. porphyriticus* gut contents, the orders Acari, Collembola and Hymenoptera were excluded, as well as winged adult insects. A table of the raw invertebrate data is available from W.H.L.

There were significant effects of forest stage and distance from the stream on abundance of terrestrial prey in riparian forests (forest stage effect, $F = 15.94$, d.f. = 1, 15, $P = 0.02$; distance effect, $F = 6.89$, d.f. = 3, 15, $P < 0.01$). There was no interactive effect of forest stage and distance from the stream ($F = 0.36$, d.f. = 3, 12, $P = 0.78$). Abundance of terrestrial prey was higher in early-successional forests than in late-successional forests, and abundance of terrestrial prey increased with distance from the stream in both forest types (Fig. 1). Only one family (Thysanoptera) was present at late-successional sites and not early-successional sites.

Terrestrial habitat use

In nighttime surveys, *G. porphyriticus* adults were observed farther from the stream in late-successional forests than early-successional forests (Fig. 2a), and distance from the stream did not differ between years (forest stage effect, $F = 6.5$, d.f. = 1, 9, $P = 0.03$; year effect, $F = 0.94$, d.f. = 1, 9, $P = 0.36$). The interactive effect of forest stage and year was non-significant ($F = 0.27$, d.f. = 1, 8, $P = 0.62$). In early-successional riparian forests, mean distance from the stream

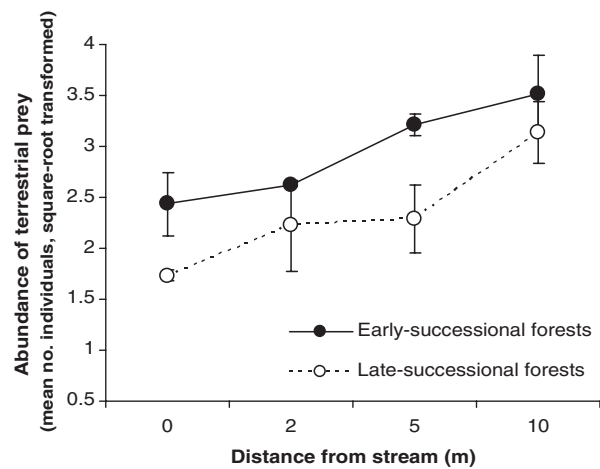


Fig. 1 Relationship between distance from the stream (m) and abundance of terrestrial invertebrate prey of adult *Gyrinophilus porphyriticus* (mean number of individuals \pm 1 SE) at study reaches in early- and late-successional riparian forests. In three 24-h trapping sessions in 2005 (June 18, July 7 and July 26), terrestrial invertebrate prey were sampled with pitfall traps along 10-m long transects perpendicular to the streams. Abundance of terrestrial prey (square-root transformed) was significantly greater in early-successional riparian forests ($P = 0.02$). In both forest types, there was a significant effect of distance from the stream on abundance of terrestrial prey ($P < 0.01$).

(± 1 SE) of all individuals observed along salamander transects ($n = 24$) was 1.76 ± 0.31 m, and maximum distance from the stream was 6.4 m (Fig. 2b). In late-successional riparian forests, mean distance from the stream of all individuals ($n = 36$) was 3.11 ± 0.37 m, and maximum distance from the stream was 9.02 m (Fig. 2b). Two recaptures occurred in the early-successional forests, and four in the late-successional forests.

There was no difference between forest stages or years in the number of individuals observed along salamander transects (forest stage effect, $F = 1.66$, d.f. = 1, 9, $P = 0.23$; year effect, $F = 0.88$, d.f. = 1, 9, $P = 0.37$), the mean size of observed individuals (forest stage effect, $F = 1.47$, d.f. = 1, 9, $P = 0.26$; year effect, $F < 0.001$, d.f. = 1, 9, $P = 0.99$), the mean body condition of observed individuals (forest stage effect, $F = 0.18$, d.f. = 1, 9, $P = 0.68$; year effect, $F = 0.30$, d.f. = 1, 9, $P = 0.6$), or the relative frequency of terrestrial habitat use by *G. porphyriticus* adults (forest stage effect, $F = 2.40$, d.f. = 1, 9, $P = 0.16$; year effect, $F = 0.38$, d.f. = 1, 9, $P = 0.55$). Additionally, in direct correlation analyses, mean distance from the stream was unrelated to number of individuals

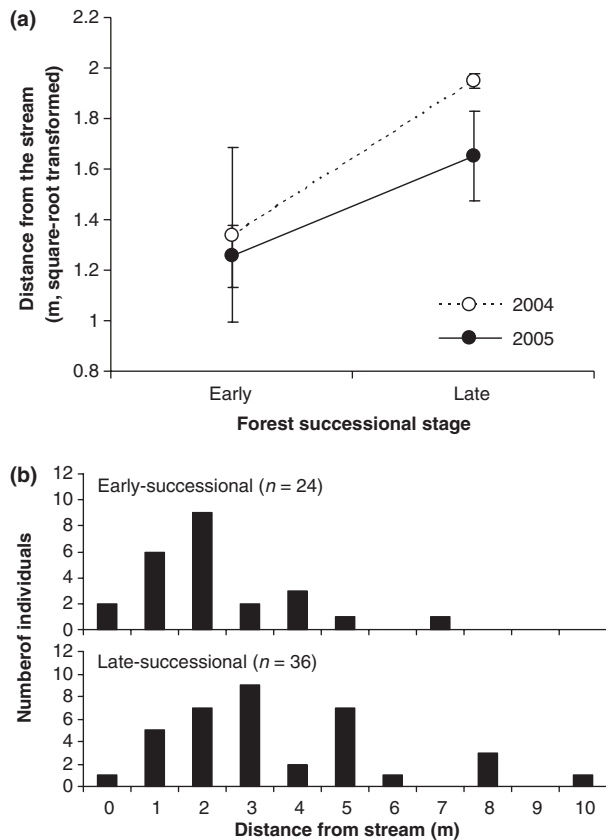


Fig. 2 (a) Relationship between successional stage of riparian forests and distance from the stream (mean of means \pm 1 SE) of adult *Gyrinophilus porphyriticus* observed during nighttime surveys of transects perpendicular to six study reaches in the Hubbard Brook Experimental Forest, New Hampshire, USA. In 2004, 12 surveys were conducted at early- and late-successional study reaches ($n = 3$ and 3 , respectively) between early June and early August. In 2005, 13 surveys were conducted at early- and late-successional study reaches during the same time period. Mean distance from the stream was significantly greater at late-successional study reaches ($P = 0.03$), but did not differ between years ($P = 0.36$). (b) Frequency distributions of distance from the stream (m) of all *Gyrinophilus porphyriticus* individuals observed during nighttime surveys at early- and late-successional study reaches.

observed ($r = 0.06$, $n = 12$, $P = 0.85$), mean size of observed individuals ($r = -0.12$, $n = 12$, $P = 0.71$), mean body condition of observed individuals ($r = -0.39$, $n = 12$, $P = 0.21$), and the relative frequency of terrestrial habitat use by *G. porphyriticus* adults ($r = 0.14$, $n = 12$, $P = 0.67$). Therefore, it is unlikely that the analysis of terrestrial habitat use was confounded by correlates with salamander behaviour or forest stage.

Discussion

Results from six, hydrologically independent study reaches in the Hubbard Brook Experimental Forest indicate that successional stage of riparian forests influences the availability of terrestrial prey to *G. porphyriticus* adults and terrestrial habitat use in this species. Data from riparian pitfall traps supported our prediction that late-successional riparian forests have lower abundances of terrestrial prey than early-successional riparian forests, suggesting that changes in the abundance of terrestrial prey with forest succession underlie variation in use of these prey by *G. porphyriticus* adults (Lowe *et al.*, 2005). The observed difference in abundance of terrestrial prey is likely related to reductions in aboveground net primary production and leaf production with succession in relatively mature forests like those where this work was conducted (Gower *et al.*, 1996; Pregitzer & Euskirchen, 2004). Studies at the Hubbard Brook Experimental Forest and other forests in the region indicate that leaf production is highest approximately 30–70 years following disturbance (e.g. our early-successional sites) and declines 100–200 years following disturbance (e.g. our late-successional sites) (Bormann & Likens, 1979; Covington & Aber, 1980). Both new leaves and leaf litter are important resource pools for terrestrial invertebrate taxa that contribute to the diet of *G. porphyriticus* adults (Scheu & Schulz, 1996; Speight *et al.*, 1999). Because there was no difference between forest stages in the number of *G. porphyriticus* adults observed, it is unlikely that predation by these salamanders accounted for the difference between forest stages in terrestrial prey abundance.

Nighttime survey results highlight the value of direct data on animal movement for understanding ecological processes in complex landscapes (Lima & Zollner, 1996; Bélisle, 2005). For example, our prediction that *G. porphyriticus* adults do not move as far into the riparian zone in late-successional forests was not supported by data from nighttime surveys. Surprisingly, the trend was in the opposite direction from what we predicted: *G. porphyriticus* adults moved farther into the riparian zone in late-successional forests than in early-successional forests. Terrestrial prey abundance increased with distance from the stream in both early- and late-successional forests and 64% of the salamanders observed in late-successional

forests were greater than or equal to 3 m from the stream, where prey abundances were similar to those found nearer to the stream in early-successional forests. This pattern strongly suggest that the difference in *G. porphyriticus* foraging behaviour was driven primarily by the availability of terrestrial prey resources, and not by abiotic or biotic conditions in late-successional forests (e.g. temperature, humidity, abundance of terrestrial predators) that prevent *G. porphyriticus* adults from moving as far from the stream to forage as they do in early-successional forests. Although salamanders were, on average, only 1.35 m farther from the stream in late-successional forests than early-successional forests, this represents a relative increase of 77%. For *G. porphyriticus* adults, which are highly aquatic and exhibit low overall vagility (Lowe *et al.*, 2006a), we interpret this as a significant difference in behaviour.

Our results provide new insight into the role of stream amphibians as links between terrestrial and aquatic components of headwater ecosystems, and on important sources of variation in the strength of this link. *G. porphyriticus* used more of the riparian zone in late-successional riparian forests than they did in early-successional forests. However, previous data on diet composition (Lowe *et al.*, 2005) and variation in terrestrial prey availability shown in this study indicate that this pattern of habitat use is not related to increased contribution of terrestrial resources to *G. porphyriticus* populations. Likewise, although the scale of riparian habitat use in early-successional forests was reduced relative to late-successional forests, the prey resources found in these early-successional forests are clearly important to *G. porphyriticus* populations (Burton, 1976; Lowe *et al.*, 2005). Interactions between *G. porphyriticus* adults and specific terrestrial prey taxa may affect ecosystem process within the riparian zone (e.g. nitrogen cycling, litter decomposition) or nutrient fluxes between the riparian forest and the stream (Johnson *et al.*, 2006; Whiles *et al.*, 2006; Peterman, Crawford & Semlitsch, 2008). We will explore these interactions in future studies.

As understanding of amphibians' dual reliance on aquatic and terrestrial resources increases (e.g. Regosin *et al.*, 2005; Trenham & Shaffer, 2005; Perkins & Hunter, 2006), regulations that protect upland habitat surrounding wetlands and streams are likely to become more common (Semlitsch, 2002; Semlitsch & Bodie, 2003; Crawford & Semlitsch, 2007). At the same

time, managers will need to provide more detailed justifications for these regulations, and build in flexibility to accommodate other uses of the land, or the requirements of other species (Hunter, 1999). Direct data on intraspecific variation in terrestrial habitat use by amphibians, like those in this study, will be critical in meeting these needs. With these data, managers can justify the specific scale of upland habitat protection necessary for a focal species. Perhaps more importantly, these data allow managers to adjust upland habitat regulations according to local habitat conditions that vary in both space and time (e.g. forest successional stage), thus creating opportunities for other land uses.

More broadly, this study expands understanding of the spatial dynamics and structure of food webs spanning multiple habitats. Previous studies have shown that terrestrial-aquatic food webs are dependent on the transfer of aquatic prey to terrestrial consumers, and the transfer of terrestrial prey to aquatic consumers (e.g. Nakano & Murakami, 2001; Sabo & Power, 2002; Baxter *et al.*, 2004). Our results show that the integrity of these food webs may be equally dependent on the movement of the consumers themselves between aquatic and terrestrial habitats, and on the relative availability of prey in those habitats. Also, although we examined only one of the many, complex connections between terrestrial and aquatic food webs (Likens & Bormann, 1974; Wallace *et al.*, 1997; Baxter *et al.*, 2005), our results provide novel insight on variation in the spatial scale of this connection critical to translating the science of spatially structured food webs into management strategy (e.g. buffer-zone regulations) that is effective and responsive to competing land uses.

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