

Local adaptation of stream communities to intraspecific variation in a terrestrial ecosystem subsidy

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Abstract. Cross-ecosystem fluxes can intertwine otherwise disparate food webs, but the effects of biodiversity at the genotypic level on fluxes across ecosystem boundaries is not known. Fresh leaves, which vary in traits such as defensive compounds against terrestrial herbivores, drop off trees and enter streams, providing a vital resource for riverine organisms. We demonstrate substantial variation in decomposition rates among individual trees in four different rivers in the Olympic Peninsula of Washington State, USA. We show that locally derived red alder leaf litter decomposes on average 24% faster than red alder leaf litter introduced from other riparian zones. Within rivers, leaves downstream of their parent trees decompose nearly as quickly as leaves from local trees. Leaves upstream of the parent tree decomposed as slowly as leaves from trees growing alongside different rivers. Over time, aquatic decomposer communities have locally adapted to the specific trees supplying the riparian subsidies. In energy-limited environments, such as small shaded streams, consumers must be efficient foragers. Our results indicate that this pressure for efficiency has led to adaptation at a particularly fine scale. More broadly, these results illustrate how genetic diversity and the effects of selection in one ecosystem can indirectly shape the structure of other ecosystems through ecological fluxes across boundaries.

Key words: *ecosystem subsidies; indirect effects; intraspecific variation; local adaptation; trophic interactions.*

INTRODUCTION

Biodiversity is essential for preserving ecosystem function and maintaining ecosystem resistance and resilience to disturbance. Biodiversity includes both intraspecific and interspecific variation, but with few exceptions (Whitham et al., 2006), most attention has focused on diversity at the species level (Tilman et al., 2001, Downing and Leibold 2002, Cardinale et al., 2006). The community-level consequences of variability between individuals within a species are not well known, despite being an essential element in understanding evolution and ecological function (Valen 1965, Lomnicki 1988, Whitham et al., 2006).

Intraspecific biodiversity can affect interspecific interactions. Interspecific trophic interactions are essential energy conduits for the survival of individuals. Therefore, natural selection, which in this paper we define in the broadest sense as the preferential survival and reproduction of organisms (both within and among species) better suited to their environment, can direct a consumer species toward different diets in different regions. Even an interaction in which a consumer feeds on a single species throughout its range may still vary spatially due to geographical variation in prey attributes

and changing environmental context. Spatial variation in prey and predators can lead to a geographic mosaic of coevolutionary interactions, such as between plants and terrestrial herbivores, that can have cascading effects on other organisms that must also adapt toward an optimal diet (Thompson 2005).

The effects of interspecific interactions can be transmitted across ecosystem boundaries thereby affecting organisms spatially disjunct from where the interactions occurred (Murakami and Nakano 2002, Knight et al., 2005, Spiller et al., 2010, Wesner 2010). Organism fluxes across ecosystem boundaries are known to be a major factor in determining ecosystem function in recipient systems (Polis and Hurd 1996, Huxel and McCann 1998, Nakano and Murakami 2001). These fluxes from donor habitats may vary across space due to a geographic mosaic of interspecific interactions occurring in the donor habitat. As local consumers should be adapted to the traits of prey transported across boundaries, the coevolutionary processes occurring in the donor ecosystem may dictate ecosystem function in the recipient system. Local adaptation in the recipient system can arise from mechanisms acting through at least two levels of the ecological hierarchy: through phenotypic shifts in the traits of individuals (which may be genetic or plastic), and through altered species composition of communities that are recipients of cross-system fluxes. Indeed, there is evidence in stream–riparian–forest environments that community-

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level variation in riparian tree species composition generates local aquatic community adaptation through leaf fluxes into adjacent rivers (Kominoski et al., 2011). For this paper, we use the term adaptation in its broadest generic sense as any change in the community that results in members that are more suited for their environment. Our definition makes no presumption about the contribution of genetic shifts within a species to that change. Adaptive change could arise from physiological shifts within individuals, microevolutionary shifts within populations, or species sorting within communities.

Stream habitats are tightly interconnected with the terrestrial surroundings (Nakano et al., 1999, Sabo and Power 2002, Fukui et al., 2006). For example, aquatic macroinvertebrate communities of forested streams depend on terrestrial leaf litter, though the relative importance of leaf litter varies depending on stream width. Streams with a narrow channel width receive less sunlight and more leaves per unit of water. As a consequence, leaf-shredding species dominate smaller streams while collector/filtering species extract fine particulate organic matter from the turbid waters of larger streams (Vannote et al., 1980). Local macroinvertebrate community composition also depends on the successional stage of the riparian forest. For example, aquatic leaf litter breakdown rates of certain tree species are higher in stream reaches surrounded by those same riparian tree species (Kominoski et al., 2011). These differences in macroinvertebrate composition in association with differences in stream size and differences in riparian vegetation may reflect an adaptive shift in the community that should increase the efficiency of energy utilization (Vannote et al., 1980).

While previous research has shown ecological shifts favoring increased ecosystem efficiency in response to differences in species composition and rates of subsidy inputs, the consequences of individual variation in food resources has not been investigated. Abundant evidence of macroinvertebrate community adaptation to other forms of variation in riparian ecosystems (tree species composition and quantity of leaf input relative to stream width) makes this forest-stream consumer community an ideal system to test for adaptation to intraspecific differences in cross-ecosystem subsidies. Here we use leaf inputs into streams as a model to show that individual variation within riparian tree species generates adaptation of consumer communities across ecosystems. Adaptation of macroinvertebrates to the leaves supplied by trees should be evident because the generation time of trees is multiple orders of magnitude longer than that of decomposers, allowing natural selection to shape decomposer communities to most efficiently decompose leaves growing in the immediate area. Additionally, feedback interactions of aquatic decomposers on their resource providers should be minimal (trees receive no direct fitness impact if their leaves are readily eaten after

being shed into the river), and therefore should allow for an assessment of the unidirectional impact of intraspecific trait variation on decomposer communities. Using a reciprocal transplant experiment across four rivers in the Olympic Peninsula of Washington, we show that aquatic decomposer communities have locally adapted to more efficiently feed on the leaves dropping from specific individual trees growing along the banks of their river.

MATERIALS AND METHODS

Study sites

We studied aquatic decomposition at eight stream reaches in the Olympic Peninsula of Washington State, USA. Two deployment sites were on each of four rivers: the South Fork Pysht, Hoko, Little Hoko, and Sekiu (see Appendix A for river descriptions). The riparian zones of all eight sites consisted of early successional forest dominated by red alder with small numbers of bigleaf maple (*Acer macrophyllum*), western hemlock (*Tsuga heterophylla*), and other conifers. Common understory vegetation included salmonberry (*Rubus spectabilis*), vine maple (*Acer cinereus*), thimbleberry (*Rubus parviflorus*), salal (*Gautheria shallon*), and sword fern (*Polystichum munitum*).

Methods background

Compared to dried senescent leaves, fresh green leaves decompose more quickly, support higher macroinvertebrate diversity, and fall into streams in large quantities during the summer growing season (Stout et al., 1985). To measure leaf fall during summer months in rivers of the Olympic Peninsula, we deployed 0.6 m wide pieces of 6.4-mm wire mesh nets in the Hoko and Little Hoko Rivers to catch floating leaf litter over 24-h periods in July and August. Trapped leaves were enumerated and categorized by tree species and dominant leaf color (estimated by eye). Mass of leaf litter was calculated using the mean fresh mass of red alder leaf data sets from the Hoko River ($n = 540$ samples, mean = 0.658 g/leaf) and the Little Hoko River ($n = 492$ samples, mean = 0.507 g/leaf).

Field experiment

To test for the direct and indirect effects of individual variation within red alder on decomposition rates, we carried out a reciprocal transplant design in which leaves from individual trees growing along rivers were enclosed in mesh leaf packs and were either placed in the river they grew adjacent to, or in a different river (4.5–26 km away). The experiment was replicated in two different pairs of similar sized rivers (between two third-order streams, South Fork Pysht River and Little Hoko River, and between two fourth-order streams, Sekiu River and Hoko River). We asked whether individual trees exhibited variation in decomposition rates across all rivers to establish whether there was detectable variation in traits among individuals. We also tested whether rates

of decomposition of leaves from the same individuals were higher in their “home” river than in the “away” river; such a pattern would indicate adaptation of the decomposer community to the specific genotypes/phenotypes of individual trees living locally along the river banks.

We conducted two rounds of reciprocal transplant experiments: between the South Fork of the Pysht (see Plate 1) and Little Hoko rivers from 9 July to 26 July 2012 and between the Hoko and Sekiu Rivers from 1 August to 17 August 2012. Five red alder trees growing in the riparian zone immediately upstream of each of the eight aquatic deployment sites were used. For each experimental run, we used 20 trees (or 40 trees in total). From each of these 40 trees, we hand-picked 52 fresh, green leaves and sealed them in plastic bags. Leaves with little or no visible damage from herbivores and/or pathogens were used. For each individual tree, we constructed four leaf packs with 12 leaves each using 19×15.25 cm bags made of 4.75 mm mesh nylon seine netting. Using 4.75-mm mesh netting allowed colonization by most stream macroinvertebrates. Crayfish and larger caddisflies (*Dicosmectus* and *Psycoglypha*) were observed feeding through the mesh openings but were usually too large to enter the bags. We deployed 20 leaf packs at each site (one pack per site for each of 20 trees; Appendix B illustrates the experimental design).

Initial masses of leaf packs were recorded and packs were strung with cable ties onto a steel reinforcing bar, which laid on the stream bottom perpendicular to the flow and was pinned at either end by two other bars pounded into the stream bottom at a 45° angle (see Plate 1). Leaf packs were deployed for 17 or 18 days at each site. During removal, cable ties were snipped, and leaf packs were placed inside sealed plastic bags. Leaves were removed from mesh bags and gently washed with water to dislodge macroinvertebrates and silt. Leaves were blotted dry with paper towels and weighed to the nearest centigram. Several bags were lost from the upper Sekiu River site, which created a slightly unbalanced design.

Statistical analyses

Regression analyses were conducted using SYSTAT (Systat Software, Chicago, Illinois, USA) and R (R Development Core Team 2013). Percentage of leaf mass remaining per leaf pack was calculated and all statistical analyses were completed using the general linear model module of SYSTAT. Breakdown rates were arcsine-square-root transformed to meet assumptions of normality for statistical analyses and results are reported on the untransformed scale. We used an analysis of variance, controlling for variation arising from individual tree effects (a random effect), to compare mean decomposition rates among experimental treatments (the fixed effect) using planned orthogonal contrasts: (1) home river vs. away river reciprocal

transplant treatments, (2) home site vs. away site packs within the home river, and (3) upstream vs. downstream location within the away river. We also partitioned the variance explained by individual tree into components arising from the early vs. late season experimental runs, the source population within experimental run, and individuals within source populations to further probe the scale of individual variation. Note that variation between the two experimental runs could be attributed to individual tree differences, environmental differences among experimental rivers, experiment duration, and temporal differences in environmental conditions. Percentage of leaf mass lost is reported in terms of fresh leaf mass, where the final leaf masses were weighed as blotted dry masses and then converted to fresh mass using the regression equation (fresh mass = $0.941[\text{blotted mass}] - 0.00337$) generated from the lab experiment (Appendix C). Because we suspected there might be asymmetry in adaptation to leaves based on location of a leaf source, we also compared whether upstream and downstream decomposition within the home river varied between individuals depending on whether leaves were derived from an upstream or downstream source, by testing whether the difference in decomposition rate of individual trees differed from zero for trees from upstream and from downstream sources, using paired *t* tests.

RESULTS

Measurements of summer leaf litter fall into streams during four 24-h leaf collection periods indicated red alder (*Alnus rubra*) comprised 95–98% of all leaf litter entering reaches of the Hoko and Little Hoko Rivers. Of this litter, 23–34% of leaves were entirely green, while 37–53% of leaves were mostly green (Appendix D). Entirely green leaves were trapped on average at a rate of $59 \text{ g}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$ at the Little Hoko River and $38 \text{ g}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$ at the Hoko River. Mostly green leaves were trapped on average at a rate of $108 \text{ g}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$ at the Little Hoko and $58 \text{ g}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$ at the Hoko River. Because fresh, green leaves from red alder trees enter streams in large quantities during the summer growing season for aquatic decomposers, we used red alder in the reciprocal transplant experiment.

In our reciprocal transplant experiment, we found significant direct and indirect effects of intraspecific trait variation on decomposition rates. Aquatic decomposition rates were highly variable among individual red alder trees within a river (Table 1, $F_{32, 105} = 5.34$, $P < 0.001$; Appendix E). Beyond this individual variability, there was significant across-river local adaptation: leaves decomposed more in their home river location than their away river (home sites vs. sites on away river, Table 1, $F_{1, 105} = 9.36$, $P = 0.003$). Seventy-eight percent of trees' leaves decomposed more quickly at their home river than the away river, which differed significantly from the 50% expected by chance (Appendix F). Even within the same river, decomposition rates

TABLE 1. Analysis of variance comparing aquatic decomposition rates of replicate red alder leaf packs from individual riparian trees that were deployed in the immediately adjacent river (home sites), the same river at a different site (away site, home river), and a different river (away river).

Source	df	SS	MS	F	P (F = 1)
Leaf source	3	0.169	0.056	4.41	0.006
River: home vs. away	1	0.119	0.119	9.36	0.003
Home vs. away sites within home river	1	0.046	0.046	3.58	0.061
Upstream vs. downstream within away river	1	0.006	0.006	0.43	0.51
Individual tree	39	4.780	0.123	9.62	<0.001
Experimental run effects	1	1.856	1.856	15.34	0.008
Source location within experimental run	6	0.728	0.121	1.78	0.13
Individual tree within source location	32	2.176	0.068	5.34	<0.001
Error	105	1.338	0.013		

Notes: Indented lines are planned orthogonal contrasts decomposing the main effects. Upstream and downstream are the relative position of incubation sites within the home or away river. Variance arising from mean decomposition rates of individual trees across all treatments is partitioned into effects of experimental run (variation in individuals used, river sites used, and time of year) and residual effects are due purely to individual differences.

at away sites tended to be lower than at home sites, although the magnitude of difference was not as large as the among river comparison, but approached statistical significance (Table 1, $F_{1,105} = 3.58$, $P = 0.061$; Fig. 1). Of 37 trees, 22 (59%) had their leaf packs decompose most rapidly in the home river at the site immediately adjacent to where the tree was growing compared to 25% expected by chance (Appendix F). In light of the near significance of within-river adaptation and the unidirectional flow of rivers, we more fully investigated the pattern by categorizing each tree by its location relative to the deployment sites: the home site where the tree was located was either upstream or downstream of the away site within the home river. Leaves incubated downstream of their source tree tended to break down at similar rates (difference in decomposition $0.088\% \pm 3.68\%$ [mean \pm SD], $n = 17$ replicates; paired t test, $P = 0.54$) as leaves incubated at the home site of their source tree. In contrast, leaves incubated upstream of their source tree broke down more slowly than leaves at the home site of their tree (difference in decomposition $1.1\% \pm 0.77\%$, $n = 18$ replicates; paired t test, $P < 0.001$). This result was not caused by simple differences in decomposition rate in upstream vs. downstream locations: the rates of decomposition of leaves placed at their home sites did not differ between upstream ($23.5\% \pm 2.18\%$) and downstream ($20.0\% \pm 2.73\%$) locations (t test, $P = 0.45$), and no systematic differences existed in decomposition rates for leaves of individual trees placed in upstream compared to downstream sites in away rivers (Table 1, $P = 0.51$)

DISCUSSION

Biodiversity ranges from phenotypic diversity within species to diversity among species, but most ecological studies have been restricted to studying only effects of among-species biodiversity on ecosystem processes. This study shows that differences among individuals

in one ecosystem can shape the structure of another ecosystem through fluxes across boundaries. We found significant variation in aquatic leaf decomposition among individual red alders, a pattern also observed in other tree studies (LeRoy et al., 2006, Marks et al., 2009). Here, we extend these findings to show that stream consumer communities are locally adapted to intraspecific variation in subsidies from riparian to riverine ecosystems. Green leaves were a substantial and consistent food resource available in these streams for aquatic decomposers during their growing season, a time when high quality resources are vital. Natural

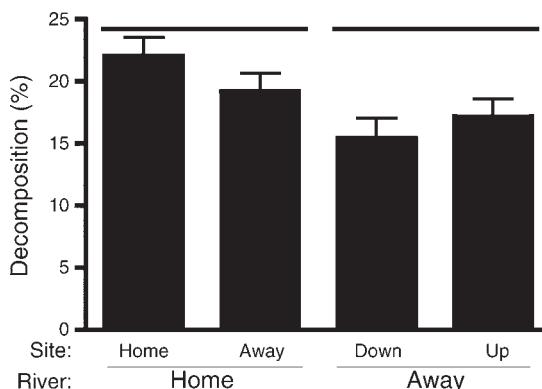


FIG. 1. Leaf decomposition by river deployment location. Four leaf packs from each of 10 trees at each of four rivers were deployed at two sites at the home river and two sites at the away river ($n = 160$ leaf packs). The x -axis describes home vs. away location at two scales: by river and by sites within river. There is one upstream and one downstream site per river (e.g., river away, site down is a leaf pack incubated at the farthest downstream site on the away river where "away" is relative to the source tree that those leaves came from). The y -axis is decomposition (mean \pm SE) measured as percentage of leaf mass lost from ANOVA after factoring out effects of individual tree identity. Mass lost was calculated using final mass that was adjusted to a fresh leaf mass scale using a regression equation (Appendix C). Bars sharing an overhead line are not significantly different from each other ($P > 0.05$).



PLATE 1. (Top) Typical river reach and (bottom) example of leaf pack deployment system for experimental study of stream community adaptation to leaves of individual red alder (*Alnus rubra*) trees. Note the branches of red alder hanging over the river (foreground of top photo) and the fallen green leaf of a red alder lying on the stream bed (bottom photo). Photo credit: J. T. Wootton.

selection should drive community composition to consist of organisms that can efficiently feed on the most commonly available resources. We found that aquatic decomposers do indeed process locally derived leaf litter significantly faster than leaf litter originating from other riparian zones, a pattern consistent in two independent reciprocal transplant experiments using a pair of two small rivers and a pair of two medium-sized rivers.

We also found evidence that aquatic communities more rapidly decomposed leaves of individual trees to which they were regularly exposed within rivers. This was strongly evident at the across-river scale. At the within-river scale, even though the overall analysis was not quite significant ($P = 0.061$), we found a clear and highly significant pattern at the within-river scale once we accounted for each tree's upstream vs. downstream location. In the within-river treatments, leaves from trees growing at away sites that were upstream of the deployment site decomposed as quickly as leaves from trees growing at that deployment site. The leaves from

upstream trees could realistically be washed downstream and used by the local community. Downstream leaves never float against the current to fuel upstream communities, hence these communities were less adapted to downstream trees. Thus, the aquatic decomposer community rapidly processed leaves only from trees the community could have realistically adapted to over time both at large (across-river) and smaller (within-river) scales.

A corollary is that upstream decomposer communities might be more strongly adapted to their home leaves. Upstream communities might receive leaves from a smaller number of trees, and might benefit from even stronger adaptation to the less diverse resource pool, if a specialist–generalist tradeoff exists. We found no evidence, however, of more rapid decomposition in upstream compared to downstream home sites. This result could indicate that there is no cost of decomposers adapting to upstream leaves, so decomposers adapt to any resources regularly available. Or, any effects of stronger adaptation in upstream locations could be

masked if these stretches of river experience more stressful biotic and abiotic conditions. Alternatively, leaves were floating into upstream sites from even further upstream or other locations outside the riparian zone so that there was no substantial asymmetry in the variety of food resources to which local decomposers would adapt.

We attribute the differences observed in leaf loss to biotic processes (evident by the large number of macroinvertebrates collected from each leaf pack and visible chewing patterns from larger caddisflies). Abiotic conditions such as sunlight, water turbulence and leaching could all cause leaf mass loss. Our laboratory experiment (Appendix C) shows that leaching in tap water caused negligible leaf mass loss. Additionally, at each deployment site, home and away leaf packs were intermixed so that there would be no systematic differences in the abiotic conditions affecting each group.

We do not know the basis of the individual leaf variability. There are a number of potential sources of within-species variation including genetic variation in trees, induced plant defenses, and ontogenetic changes in the phenotype of different aged red alder stands. Each of these sources of variation could feasibly create spatial clustering of leaf traits that would explain why we found individuals within populations to decompose at more similar rates than between populations. Limited gene flow could cause nearby trees to be close relatives whereas natural selection could create phenotypic differences between locations where spatial variation exists in terrestrial insect loads or microclimatological conditions. Although we have no information on the red alder genetic structure, plants show substantial phenotypic plasticity, and may express different levels or types of plant defenses when terrestrial herbivore loads and composition vary spatially (Mooney et al., 2009, Ali and Agrawal 2012). Additionally, natural disturbance or logging often creates local gaps that are colonized by a cohort of trees of relatively uniform age. These cohorts could exhibit spatial variation in traits if the genotype of the recruitment pool varies through time because of biased pollen flow or seed dispersal, large-scale temporal variation in environmental conditions, or genetic drift, or if phenotypic effects such as age-related changes in leaf traits vary through time (Donaldson et al., 2006). All of these mechanisms can create spatial variation that can indirectly exert an influence on the function of other ecosystems through cross-system flow.

The result of this variation is direct effects on the quality of leaves available for consumers: certain trees decomposed readily at all locations while others hardly broke down even at their home location. Many environmental variables such as soil nutrients, hydrology, and sunlight intensity affect leaf traits in ways that can directly affect both herbivory and decomposition rates. For example, leaves with high nitrogen concentrations are particularly valuable food sources for

terrestrial insects (Mattson 1980). Leaf palatability is also influenced by leaf thickness and toughness, which can depend on sunlight intensity, water availability, and leaf age (Coley 1980, Sariyildiz and Anderson 2003). Beyond the direct effects of leaf quality and regardless of the specific drivers of this intraspecific variation, this trait variability provided a medium on which the decomposer community could adapt to individual trees over time. This local adaptation to leaf traits was strong enough to be detectable despite high intraspecific variation in inherent decomposition rates.

The local adaptation pattern observed from our experiment could be caused by a number of factors. First, decomposers may be physiologically or morphologically acclimating to the leaf traits of resources abundant in their lifetimes. Second, species of decomposers might evolve over time to be composed of individuals with traits that maximize efficient resource use. Third, the community could be adapting via taxon sorting among macroinvertebrate and/or microbial decomposers, as species that more efficiently dealt with local resource traits outcompete less efficient species. The latter two hypotheses predict that varying successional age of the riparian zone will generate differences in decomposition efficiency as the community adapts over time to the growing riparian trees, whereas the first hypothesis predicts a more rapid physiological response. More detailed information on both the macro- and micro- decomposer communities is necessary before these mechanisms can be fully sorted out. Regardless of the mechanism, it is clear that ecosystem decomposition rates adapt to individual variability of resources entering through leaf flux.

Although the exact mechanism of the adaptation process is not known, the key properties of these results correspond to those of geographic mosaics of coevolution. Genetics and/or environmental variation in biotic and abiotic conditions across the geographic range of a tree species appears to have caused local clustering or a mosaic of leaf traits. It follows from our results that effects of coevolutionary dynamics, especially where geographic mosaics exist, are likely to indirectly dictate the functioning of neighboring ecosystems through cross-boundary fluxes.

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SUPPLEMENTAL MATERIAL

Appendix A

Location, morphology, and environmental characteristics for four rivers used in the local adaptation experiments ([Ecological Archives E095-005-A1](#)).

Appendix B

Illustration of experimental design for reciprocal transplant experiments ([Ecological Archives E095-005-A2](#)).

Appendix C

Background experiments for determining the methods used for evaluating leaf decomposition measurements ([Ecological Archives E095-005-A3](#)).

Appendix D

Leaf litter fall into rivers during summer months ([Ecological Archives E095-005-A4](#)).

Appendix E

Individual tree variation in leaf decomposition rates across four rivers ([Ecological Archives E095-005-A5](#)).

Appendix F

Nonparametric comparisons of decomposition rates in reciprocal transplant experiments ([Ecological Archives E095-005-A6](#)).