Plant species traits across a riparian-zone/forest ecotone

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Abstract. We examined the changes in prevalence of nine plant traits – including the presence of woody stem tissue, leaf longevity, nitrogen fixation, seed longevity, dispersal vector, pollination vector, and clonal growth form – across a riparian/forest-understory ecotone. This ecotone, found along headwater streams in boreal mixed-wood forests, supports four distinct vegetation zones: streambank, riparian, transition, and upland forest understory. The objective of this study was to identify specific trait patterns that may indicate functional responses to the changes in environmental factors such as nutrient availability and wind exposure that occur across the ecotone. The suites of plant species traits found in each zone were distinct, with a strong change in the prevalence of several traits. Wind and insect pollination, wind and vertebrate diaspore dispersal, and deciduous and evergreen leaves showed the greatest change in prevalence between the vegetation types. Some traits, including insect pollination and vertebrate diaspore dispersal, were strongly correlated within species. The consistent co-occurrence of pairs of traits in the same species suggests common responses by very different traits to the same environmental factor. This study demonstrates that an ecotone can be characterized not only as a discontinuity in species distributions or environmental factors, but also as a discontinuity in the trait spectrum. Examining ecotones from a trait perspective has strong potential for identifying the environmental factors and associated species functional responses that encourage the development of distinct vegetation boundaries.

Keywords: Clonal growth form; Dispersal vector; Leaf longevity; Nitrogen fixation; Ontario; Pollination vector; Seed bank; Trait matrix.

Nomenclature: Newmaster et al. (1998).

Introduction

Ecotones are complex and dynamic landscape features characterized by spatially rapid changes in ecological structure and function relative to the landscape as a whole (Gosz & Sharpe 1989; Delcourt & Delcourt 1992; Carter et al. 1994; Risser 1995; Stohlgren & Bachand 1997; Lloyd et al. 2000). These boundaries between adjacent communities are typically associated with either a spatial discontinuity in one or more environmental factors or a change in the disturbance regime (Wiens et al. 1985; Gosz & Sharpe 1989; Hansen et al. 1992); abrupt ecotones may be produced by positive feedback switches between the environment and vegetation even when the environmental changes are gradual (Wilson & Agnew 1992). The distribution patterns of individual species and functional groups across an ecotone can be divided into three general categories (Odum 1983; Gosz & Sharpe 1989): (1) species characteristic of each adjacent community that are typically found together in relatively low abundances at the ecotone; (2) generalist species present in both communities that do not change significantly in abundance across the ecotone; (3) specialist species of ecotones, rare in the adjacent communities, that may occur at relatively high abundance in the ecotone. Species from each of these three groups are frequently observed at both anthropogenic ecotones such as clearcut edges (e.g. Wales 1972; Williams-Linera et al. 1998), and natural ecotones (e.g. Carter et al. 1994; Stohlgren & Bachand 1997; Lloyd et al. 2000).

Most ecotone studies focus on shifts in species composition and environmental factors across the ecotone, but an alternative approach is the examination of shifts in plant trait prevalence. Trait-based analyses comparing plant communities are becoming increasingly common (e.g. Leishman et al. 1995; Mabry et al. 2000; Lavorel & Garnier 2002). A previous trait-based study of an aquatic-terrestrial ecotone (Mallik et al. 2001) found strong differences in the prevalence of a limited number of below-ground traits between floristically distinct microhabitats, suggesting that further examination

of traits at ecotones is warranted. The process of constructing a trait matrix, exploring the relationships between traits, and making functional linkages between traits and the environment provides an attractive route to a general understanding of plant community structure and function (Keddy 1992). There is a very large literature examining the functional links between plant traits and patterns of community structure (e.g. Hughes et al. 1994; Leishman et al. 1995; Landhäusser et al. 1997) that can assist in the development and evaluation of hypotheses based on the patterns found in such a study.

In this study we examine the changes in the prevalence of nine reproductive, morphologic, and physiologic plant trait classes across the ecotone between the riparian zone and plant communities in the forest understory found along small coldwater streams in northwestern Ontario, Canada. The objectives of this study are (1) to identify the traits with strong patterns of change across the ecotone, (2) to examine the interrelations between traits in this community, and (3) to use these patterns to develop testable hypotheses regarding the processes structuring the ecotone.

Methods

Study area

We selected 17 sites, that had not been recently disturbed by either clear-cutting or forest fire, along headwater streams (100 ha to 6000 ha watersheds) northeast of Thunder Bay, Ontario, Canada (49° N; 89° W). The major riparian vegetation types in the study area are swamp thickets, or dense stands of tall shrubs dominated by *Alnus incana*, and meadow marshes, or grass and sedge-dominated wet meadows. Most sites support a mixture of both vegetation types. The forests are boreal mixed woods dominated by *Picea mariana*, *Pinus banksiana* and *Populus tremuloides*. A complete description of the study area can be found in Lamb (2002) and Lamb et al. (2003).

Four major vegetation zones are found along a lateral gradient from the stream's edge to the upland forest: streambank, riparian zone, riparian-zone/forest transition, and forest. The streambank zone is a narrow strip at the bank of the active channel where large herb species are more abundant. The riparian zone is regularly flooded and highly variable in width (from 1 m to 80 m). The riparian-zone/forest transition is a zone of strong floristic change 1-2 m wide found at the limit of annual flooding. In the upland forest zone only the understory shrub and herb layers were sampled for this study.

Field sampling

At each site, four transects were established within the stream reach to collect species cover data. The first two transects were established on opposite sides of the stream at the head of the reach and the second two approximately 40 m downstream. On each transect one 1-m^2 quadrat was placed at the stream edge, one was placed directly on the riparian-zone/forest transition, and up to three quadrats, depending on riparian zone width, were spaced between the two. The position of the riparian-zone/forest transition was identified by observation of the changes in abundance of several riparian and upland forest indicator species (Lamb 2002). Three quadrats were sampled at 10-m intervals in the forest vegetation. Where the riparian zone was less than 1 m wide, the streambank, riparian, and transition zones all occurred within a single quadrat so only the three upland quadrats from that transect were retained for analysis. Since riparian widths were variable within each site, a maximum of two transects from any site crossed a narrow riparian zone. Data from each zone were thus available when the four transects were pooled for analysis. In each quadrat, the percent canopy cover of all vascular plants including shrubs and trees < 5 cm DBH was visually estimated. More rigorous methods of measuring cover such as point quadrats were impractical in the dense multi-layered vegetation of the study area.

Trait matrix

Nine morphologic, reproductive, and physiologic plant trait classes were included in the trait matrix (Table 1), with each of the nine classes subdivided into one to three presence-absence trait variables. Literature sources and field observations were the basis of the trait

Table 1. Trait classes and trait states included in the trait matrix. The stem tissue, leaf type, N-fixation, and seed bank traits were all analysed as a single presence-absence variable. The remaining traits were all scored as two or three variables, with species potentially positive for more than one variable within the trait class. See App. 1 for the criteria used to score each trait.

Trait class	Trait states
Stem tissue	Woody; herbaceous
Leaf type	Deciduous; evergreen
N-fixation	Present/absent
Seed bank	Persistent; transient
Potential mycorrhizae	Vesicular-arbuscular mycorrhizae
Infection	Ectomycorrhizae; ericoid mycorrhizae
Diaspore dispersal vector	Vertebrate; wind; water
Pollination vector	Insect; wind; self
Clonal growth method	Rhizome; resprouting; layering
Clonal growth form	Phalanx; guerrilla

matrix. Efforts were made to find local sources, and information was compared between multiple sources whenever possible. The published information was supplemented with field observations, especially excavations of root and rhizome systems. The criteria used to score each trait are listed in App. 1, and the complete trait matrix and source references are presented in App. 2.

Of the 154 vascular plant species found in the study area (Lamb 2002) 51 were included in the trait matrix. The criterion for including a species in the trait matrix was that it had been found in at least 10% of the quadrats in either the riparian zone or the forest understory. The rarer species were eliminated for three reasons: (1.) Many of them were found fewer than $5 \times$, and thus are a very minor component of the community. (2.) Many are poorly studied making it impractical to collect trait data. (3.) Vegetative individuals of many rare species could not be reliably separated from a closely related species, so all cover observations were ascribed to the more common species.

Data analysis

For each site mean cover values for each species in each zone were calculated from every quadrat that fell into that zone at that site. Mean cover values for each species were divided by total plant cover within that zone at that site to avoid bias caused by variation in total vegetation cover between zones. A summary of the prevalence of each trait in each zone was calculated by multiplying the zone $\times$ species matrix of vegetation data by the species $\times$ trait matrix to obtain a zone $\times$ trait matrix. The value in each cell of this new dataset is the sum of the relative cover of each species observed in that zone that was positive for that particular trait.

The change in the arcsine-transformed prevalence of each trait between the four zones was examined using a one-way ANOVA (Zar 1996) blocked by site. An $\alpha = 0.003$ was considered significant (experiment-wise $\alpha = 0.05/18$ traits). Relations among traits were examined using pairwise Pearson correlations (Zar 1996). Due to the high probability of significant relationships occurring when so many pairwise combinations are examined only strong correlations ($r \geq |0.63|$ ($r^2 > 0.4$); $p < 0.001$) were examined further. A binomial test (Zar 1996) was used to determine whether the number of strong correlations found was greater than would be expected by chance ($p = 0.05$).

Results

Nine of the 18 traits examined showed a significant change in prevalence across the ecotone, with others displaying non-significant trends (Fig. 1). Several traits, including deciduous leaves, wind and water-borne diaspore dispersal, wind pollination, rhizomatous clonal growth, nitrogen fixation, and the phalanx clonal growth form, all declined in prevalence from the streambank to the forest. Another group of traits, including vertebrate diaspore dispersal and ericoid mycorrhizae, displayed the opposite pattern, increasing in prevalence from the streambank to the forest. Traits that did not change significantly in prevalence over the ecotone included woody stem tissue, ectomycorrhizae, V-A mycorrhizae, methods of clonal propagation, and the formation of a long-term seedbank. Two traits, insect pollination and ectomycorrhizae, displayed more complex patterns. The overall trend displayed by insect pollination was for a significant increase in prevalence from the streambank to the forest, but the non-significant trend toward a lower prevalence within the riparian zone indicates that insect pollination may be less important in that zone.

Table 2. Pairs of traits exhibiting pairwise Pearson correlations with $r \geq |0.63|$ and $p < 0.001$. Group 1 comparisons are between traits that are rarely or almost always found together in the same species. Group 2 comparisons are significant because the first trait (nitrogen fixation) co-occurs with the second trait in the dominant species *Alnus incana*. Group 3 comparisons highlight pairs of traits that may be associated for physiological or morphological reasons or that may represent functional trade-offs between traits.

| Group	Comparison	R
Group 1	Insect pollination vs. wind pollination	-0.935
	N-fixation vs. ectomycorrhizae	0.664
	Vertebrate dispersal vs. hydric dispersal	-0.717
	Deciduous vs. ericoid mycorrhizae	-0.782
	Woody tissue vs. ectomycorrhizae	0.704
Group 2	N-fixation vs. guerrilla	-0.767
	N-fixation vs. resprouting	0.686
	N-fixation vs. wind dispersal	0.722
Group 3	Ectomycorrhizae vs. guerrilla	-0.742
	Ectomycorrhizae vs. layering	0.797
	Ectomycorrhizae vs. resprouting	0.728
	Guerrilla vs. layering	-0.780
	Guerrilla vs. resprouting	-0.684
	Insect pollination vs. phalanx	-0.861
	Vertebrate dispersal vs. insect pollination	0.828
	Vertebrate dispersal vs. phalanx	-0.881
	Vertebrate dispersal vs. wind pollination	-0.811
	Wind pollination vs. phalanx	0.836
	Woody tissue vs. layering	0.736
	Woody tissue vs. resprouting	0.815
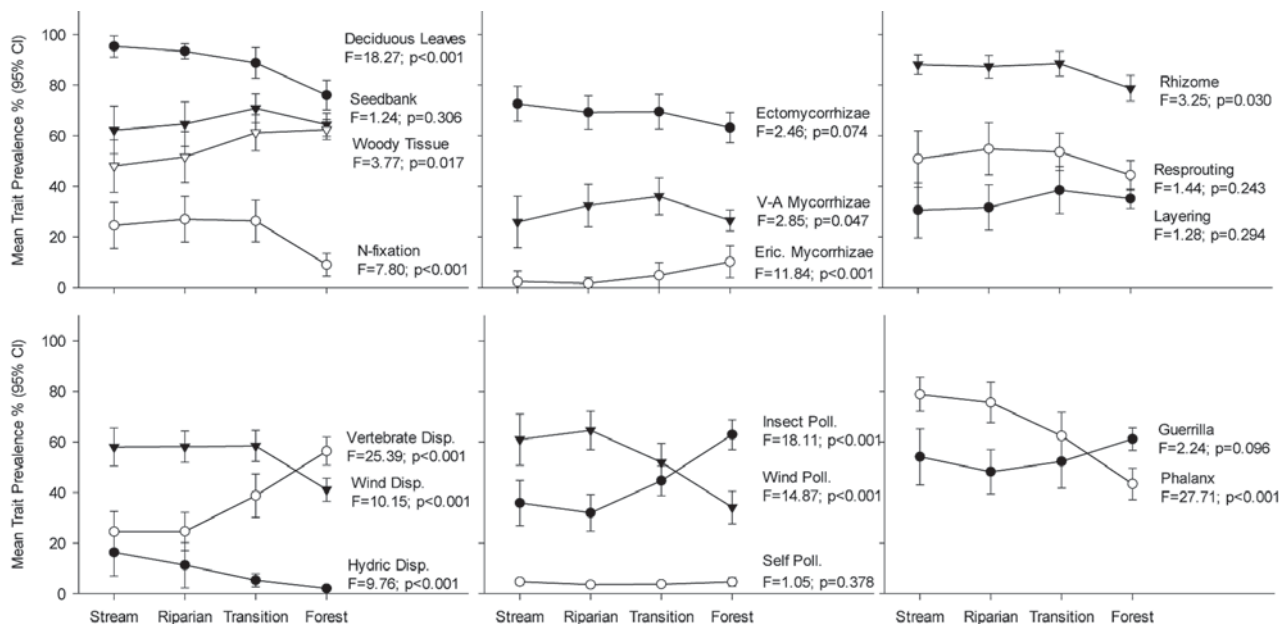
Fig. 1. Changes in mean trait prevalence across the riparian-forest ecotone. Error bars are 95% confidence intervals. *F*-ratios and *p*-values from one-way ANOVA, comparing zones are presented; those with $p \leq 0.003$ should be considered significant (experiment-wise $\alpha = 0.05$).

Similarly, there was a non-significant peak for ecto-mycorrhizae in the riparian-zone/forest transition.

There were 20 strong correlations ($r \geq |0.63|$; $p < 0.001$) between traits among the 153 possible correlations (Table 2). The proportion of strong correlations found (0.13) is significantly higher ($p < 0.001$) than that expected by chance (0.05×153 or 7.65 correlations). These strong correlations fall into three general categories. The first group includes negative and positive correlations between traits that either consistently or only rarely co-occur in the same species, for example wind and insect pollination. The second group includes strong positive correlations between a rare trait, nitrogen fixation, and other traits with which it co-occurs in the highly abundant species *Alnus incana*. The third group of correlations do not have clearly trivial interpretations, for example the negative correlation between the guerrilla growth form and layering and the strong positive correlation between insect pollination and vertebrate dispersal.

Discussion

The results of this study demonstrate that an ecotone can be characterized not only as a discontinuity in species abundance and distribution but also as a discontinuity in traits. These shifts in the prevalence of traits may represent functional responses to the shifts in environmental conditions found at the ecotone. For example, the shift from the high prevalence of wind dispersal in the riparian zone to the high prevalence of vertebrate dispersal in the forest is in accord with the typically low abundance of wind-dispersed species observed in the understory vegetation of forests (Howe & Smallwood 1982; Willson et al. 1990; Hughes et al. 1994). This pattern favouring vertebrate dispersed species may be due to limited wind penetration into the understory of the closed canopy forests (Hughes et al. 1994), while wind dispersal may be more effective in the more open riparian vegetation. A second pattern with a potential functional explanation is the decline of species with deciduous leaves from the riparian zone to the forest. Deciduous species tend to have higher rates of photosynthesis than evergreen species, but at a cost of lower nutrient-use efficiency, shorter growing season, and higher herbivory risk (Chabot & Hicks 1982; Aerts 1995; Landhäusser et al. 1997). The higher photosynthetic potential of deciduous leaves may be an advantage in a richer and wetter riparian zone, while ever-

green leaves may be at an advantage in a drier forest environment. Studies examining the differences in wind patterns and the soil nutrient regime between zones to test these hypotheses further could easily be implemented. Similar functional explanations could be likely found in the literature for many of the other trait patterns identified in this study. For example, the need for forest understory species to identify and exploit small patches of sunlight may favour the guerrilla growth form in the forest understory (Lovett Doust 1981). This may explain the switch from phalanx to guerrilla clonal growth forms observed between the streambank and riparian zones and the forest understory. The process of identifying a range of potential hypotheses and then selecting the most promising for further study is one of the most useful aspects of this type of trait analysis.

The V-A mycorrhizae and guerrilla clonal growth form traits displayed non-significant peaks and depressions within this ecotone. These trends within the ecotone deserve further attention. Ecotonal species have been observed (e.g. Lloyd et al. 2000), so why not ecotonal traits? Are there traits that confer specific advantages to species in an ecotonal habitat, and equally, do ecotone-specialist species have unique complements of traits? Exploring these questions would provide much insight into the forces influencing the evolution of ecotone-specialist species.

Many of the correlations observed among traits are simply obvious negative associations between traits that rarely co-occur in the same species or positive associations between pairs of traits that co-occur in a dominant species. These relationships are clearly trivial and should be ignored, but other associations are more interesting. For example, the positive correlation between vertebrate diaspore dispersal and insect pollination suggests two potential explanations. If limited wind penetration into the forest understory (Hughes et al. 1994) is a major factor structuring this community, then it should not be surprising that the two traits should be often found in the same species. This explanation is supported by a similar, though much weaker, correlation between wind dispersal and wind pollination ($r = 0.476$; $p < 0.001$). Alternatively there could be a deep-seated phylogenetic or physiological association between the two traits leading to the association. These associations and potential explanations can serve as starting points for further investigation into the evolutionary forces that shape suites of plant traits.

The traits used in this study reflect aspects of the reproductive and resource use strategies of many plant species, but other traits may also be important. For example, flooding and high soil moisture are factors critical in structuring riparian vegetation (Naiman & Décamps 1997). A series of traits that accounted for the

strategies commonly used by riparian species to withstand or avoid the effects of flooding (e.g. Blom & Voesenek 1996) would likely display very strong shifts in prevalence across the ecotone, and would allow a much more complete set of potential hypotheses to be developed.

This study has examined the changes in the trait structure of the plant community across the riparian-zone/upland ecotone found along small streams in northwestern Ontario. We have demonstrated that there are shifts in the prevalence of traits across this ecotone similar in form to the shifts in species abundance and distribution found at many other ecotones. Potential functional explanations can be found for many of these trait patterns that would be easily testable in future studies.

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