

SPECIES DIVERSITY PATTERNS AT ECOTONES

Amanda Ruth Senft

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Approved by:

Robert Peet

Peter White

Dean Urban

ABSTRACT

AMANDA RUTH SENFT: Species Diversity Patterns at Ecotones

(Under the direction of Robert Peet)

This thesis aims to clarify species richness patterns at ecotones, the mechanisms underlying these patterns, and the challenges faced when trying to link diversity patterns to ecotone properties. Species present at ecotones may be characterized as coming from two sources: those that derive from additive blending of species from adjoining communities and those that are from ecotonal specialists. Diversity at ecotones is dependent on multiple factors, including environmental heterogeneity, spatial mass effect, invasive species spread, animal activities, and hybridization. To clarify the importance of these factors, I constructed vegetation transects across field/forest edges which varied in their disturbance regimes and landscape position. I found that, in general, these ecotones did not have higher species richness than the adjacent vegetation, and that the species present were mostly also present on either side of the transition, with very few species unique to the ecotone. The results of this study provide a starting point for linking patterns of diversity with ecotone properties.

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INTRODUCTION

Scientists have found little empirical evidence for universal emergent properties of ecotones (Lloyd *et al.* 2000, Walker *et al.* 2003), although many have given detailed accounts of such characteristics (e.g., Holland *et al.* 1991, Gosz 1993, Risser 1995). For example, many ecologists have made sweeping statements claiming there is higher species richness at ecotones, concluding that ecotones are areas of high conservation concern due to their diversity. Yet, as described in Chapter 1, there is little evidence supporting these claims. How then do we reconcile the difference between these asserted patterns and the lack of pattern actually documented in the literature? All ecotone characteristics, including species richness, result from the particular ecological condition and processes at the site, as well as properties of the surrounding landscape. As a case study, I focus this thesis specifically on the patterns and processes of biodiversity at ecotones. In the first chapter, I review the current literature on species diversity at ecotones, discuss the ecological mechanisms that might cause the patterns found, and suggest solutions to some of the challenges that future researchers will face. In the second chapter, I elaborate on one of the specific cases laid out in Chapter 1, ecotone diversity at a forest/field boundary. Specifically, I present a field study that looks at some of the factors contributing to species diversity at forest edges: ecotonal species and exotics.

Ecotone Concepts

It is important to touch upon what exactly is meant by the term ecotone, as this concept is often confused with related concepts, and may be used differently by other researchers. The ecotone concept is difficult to grasp because it has been and still is referred to in numerous frameworks. In this introductory section, I highlight some of the major points in the history of the application of the term ecotone and present a working definition for this paper.

The Ecotone Concept

The ecotone concept began as visually based and narrow in scope. Clements (1905) was the first to use the term, defining ecotones as stable delineations between distinct vegetation communities. This definition implies two things: firstly that ecotones refer only to vegetation and not other taxonomic groups and secondly that ecotones occur at a visually perceptible change, implying a change in physiognomy. However, it has become clear that not every taxonomic group responds similarly to ecotones. For example, Dangerfield *et al.* (2003) found that insects do not show the same community boundaries as plants. Walker *et al.* (2003) found that ecotones based on a rapid change in species composition do not always accompany changes in plant physiognomy.

Around the same time that Clements first defined ecotone, Livingston (1903), wrote about environmentally stochastic, unstable stress zones between upland plant communities in Michigan, a concept subsequently used by Dutch ecologists van Leeuwen (1966) and van der Maarel (1990) to be equivalent to ecotones. Curtis (1959) also described ecotones in this manner: tension zones between biogeographic regions, such as the intersection between northern hardwood forest types of northeastern Wisconsin and oak woodlands of

southwestern Wisconsin. Those interested in application of ecotone versus ecocline often use this definition of an ecotone. Van der Maarel (1990) discusses ecotones in terms of ecological transition zones: narrow, stochastic, unstable ecological zones possessing a mixture of two different homogenous community types. Inherent in the ecotone's sharpness is its instability; although stable ecotones are possible, they are usually man made. This tension zone concept is broader than the Clementsian definition. An ecocline, by contrast, is a stable gradient zone with relatively gradual species turnover (*sensu* Whittaker 1960).

With the advent of landscape ecology, scientists started to use 'ecotone' to refer to the boundary enclosing a relatively homogenous landscape patch. In this landscape view ecotones are still steep gradients between more homogenous patches of vegetation (Risser 1995, Fortin *et al.* 2000), but these ecotones and the patches they surround can be viewed as landscape elements. As ecologists became interested in edge effects, first for wildlife management (Leopold 1933) and then as contributors to biodiversity (reviewed in Baker and Dillon 2000), the dynamic nature of ecotones in time and space was recognized; ecotones can shift location or grow weaker or stronger. Ecotones were defined by the Scientific Committee on Problems in the Environment –Man and Biosphere Program as transitions between patches (Holland *et al.* 1991), the patch dynamics type concept resulting from disturbance theory (e.g., Pickett and White 1985). Thus, the ecotone concept went from being viewed as a small zone between communities to a dynamic, multidimensional landscape element.

Recognition of the multiscale nature of ecotones occurred when the boundary concept emerged and was coupled with the ecotone concept. Boundaries are defined as areas where the rates or magnitudes of ecological transfers like energy or nitrogen flow change abruptly in relation to those within patches (Wiens *et al.* 1985). They encompass everything

from cell membranes to lake shores to glacial margins (Strayer *et al.* 2003). Changes at the boundaries of life zones are where the ecological or environmental gradients are relatively steep. It is useful to think of ecotones as a specific type of boundary: an envelope of physical, chemical and biotic constraint around community types (Gosz 1992), or as zones between contrasting habitat patches that delimit the spatial heterogeneity of a landscape (Fagan *et al.* 2003). Boundaries are human constructs and may not have any physical properties of their own; lines on a map drawn between ecoregions may or may not correspond with any obvious physical discontinuities in nature (Strayer *et al.* 2003). In contrast, ecotones can be statistically determined based on species turnover rates.

For the purposes of this thesis, I define ecotones as zones of transition between vegetation communities or regions that can be statistically shown to represent a change in species composition. Within this zone, species turnover of vegetation is higher than at other points in the surrounding areas. Thus, along with natural ecotones between communities, anthropogenically derived edges can be classified as sharp, man-made ecotones and are discussed in this paper. Ecotones are necessarily context dependent: they don't exist without areas of relatively homogeneous composition, they don't exist without defined communities, and they are dependent on a user-defined spatial extent. This context dependence, along with the environmental factors causing the ecotone, are both influential in determining diversity patterns and are discussed later in this thesis.

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Chapter 1: FACTORS INFLUENCING SPECIES RICHNESS AT ECOTONES

Introduction

Ecotones are zones of relatively high vegetation turnover between two relatively homogenous areas. They can be conceptualized as acting at various scales such as boundaries between ecoregions, landscape patches or vegetation communities. As ecological boundaries, they have been credited with mediating flows of energy, nutrients and organisms across landscapes, and thus are important in regulating disease transmission, gene flow, and community composition (Fagan *et al.* 2003, Hansen *et al.* 1988; Wiens 1992). They are regarded as dynamic components of a landscape, supporting higher levels of productivity and providing habitat for many transient organisms. Recently, they have been shown great consideration as important for assessing climate change (Risser 1995), ecosystem health and forest patch sustainability. However, for all the grandiose characteristics attributed to ecotones, they are relatively understudied and not well understood.

One reputed characteristic of ecotones is that they have higher biological diversity than adjoining areas and thus hold high conservation value (Risser 1995, Leopold 1933, Naimen *et al.* 1988, Petts, 1990; Odum, 1983). Yet, there is a lack of strong evidence either supporting or refuting this claim. Furthermore, it is unclear as to what mechanisms would underlie such a spike in diversity and what environmental factors might influence whether this pattern is found, and if so how it might be sustained.

In this chapter, I address questions of if, why and when. Is there higher diversity at ecotones? What are the underlying processes controlling change in richness? When would we expect to find these patterns of diversity? To meet these goals, I first review the current evidence on diversity patterns to determine if higher richness is a universal, or at least frequent, property. To explain the results found in the literature, I present two patterns of ecotone richness, as well as ecological mechanisms that could cause these patterns. I then discuss the challenges to measuring diversity at ecotones in the field that may confound studies of ecotone diversity. Finally, I present recommendations for identifying diversity patterns at hypothetical ecotones.

Evidence for ecotone diversity

There are few studies that clearly show high diversity at ecotones. Shmida and Wilson (1985), Wolf (1993) and Kernaghan and Harper (2001) found higher species richness between predetermined altitudinal zones. Kirkman *et al.* (1998) and Carter *et al.* (1994) found higher species richness in wetland/upland boundaries. Brothers (1993) found higher species richness at anthropogenic forest edges. Other studies looking at grassland/forest ecotones have found species diversity at ecotones to be intermediate between the two bounded communities (Harper 1995; Turton and Duff 1992; Meszaros 1990; Meiners *et al.* 2000).

Ecotones may also have lower diversity. If an ecotone is maintained by frequent or intense disturbance, it might be less favorable for species than the communities on either side (van der Maarel 1990). Backeus (1993) and Chapman (1960) found lower species richness on sharp lake margins, which are frequently flooded. Dangerfield *et al.* (2003) studied

invertebrate composition at an ecotone between a riparian community and a semi-arid saltbush habitat in Australia and found that most taxa were either in both habitats or were faithful to one but leaked across into the other. Very few species were unique to either habitat and there was not higher richness at the ecotone.

Many studies have found that species diversity is higher than in adjacent vegetation at some ecotones but lower in others. Burk (1977) looked at a zonation from water, through wetland, to upland, with ecotones at the upland/wetland boundary, and at the wetland/water boundary. He found the highest richness within the upland/wetland ecotone and the lowest in the wet/water ecotone. Lloyd *et al.* (2000) found that species composition and richness at three different types of ecotones was intermediate between that of the adjacent communities of interest and suggested that these ecotones are more of a transition zone between a low and high richness community than a blending zone mixing species from both.

Thus, the literature suggests that enhanced diversity at ecotones is not a universal property, but depends on the properties of the ecotone in question. The remainder of this chapter is dedicated to exploring why we might find these conflicting patterns in the literature so as to provide a foundation for future studies of ecotones.

Two types of enhanced ecotone diversity

Two basic types of enhanced species richness are suggested to occur at ecotones (Figure 1.1). The first richness type is what I will call additive blending: in the region where two communities, landscape patches or biomes meet, representatives from two species pools

occur, and consequently, the ecotone has more species by virtue of being a blending or mixing zone. Secondly, ecotones could possess unique environmental conditions that are favorable to a certain group of species generally not found in the adjacent communities. Such species, here called ecotonal species, will either only be present at the ecotone, or will reach peak abundance there, increasing diversity within the ecotone.

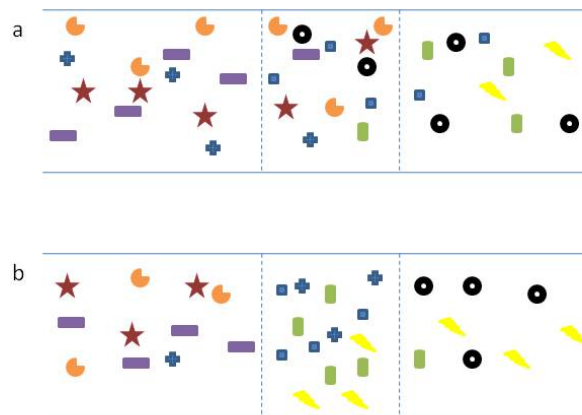


Figure 1.1: *Two hypothetical transects across a boundary showing higher diversity within the ecotone zone (within dashed lines). a) illustrates additive blending, in which the species within 2 communities coexist within the ecotone. b) illustrates ecotonal species, in which species achieve higher abundance within the ecotone.*

Additive blending

Additive blending potentially applies at all spatial scales. At the biome scale, richness increases at ecotones because the limits of the ranges of two region's species reach into the transition. Thus, species from two or more biomes occur here, making species richness

higher than in the centers of the biomes (Risser 1995). In this sense, ecotones can be thought of as “biodiversity crossroads”: places where multiple species ranges overlap. At these crossroads, species habitats can be patchier and have higher heterogeneity, thus leading to more species per unit area (Nekola and White 1999, Risser 1995). At the landscape scale, ecotones may have representatives from both communities as well as from other patch types. For example, a forest edge might have interior forest species, field species, as well as shade intolerant species from nearby edges.

Not all studies support the occurrence of higher richness through additive blending. Firstly, the zone of blending could also be a death trap for some species that are not able to withstand marginal conditions. Here, ecotones serve as population sinks (Woodroffe and Ginsberg 1998). At large biogeographical scales, some species in the ecotone are near the edges of their ranges, and it is likely that their fitness is lower than it is nearer to the range center with the consequence that survival is lower relative to establishment (Temple 1998). At a smaller scale, edge effects can reduce fitness of species adapted to the primary patch conditions. Populations of species near the edges of their ranges are often sink populations that require subsidies of dispersing immigrants. This reasoning follows the previously mentioned ecotone concept of van der Maarel (1990), who suggested lower richness at ecotones because of environmental fluctuations making the region unfavorable for plant growth; thus leading to lower species richness. Although the additive blending type of diversity enhancement makes intuitive sense, there is not a lot of observational evidence supporting its occurrence.

Ecotonal species

Richness could be higher at ecotones if there are many species particularly or uniquely suited to the conditions there. Numerous species have been reported as being ecotone specialists. For example, Weakley (2006) lists 60 species native to the Southeastern United States as occurring predominately in ecotones.

Ecotonal species would be expected to occur if environmental conditions in ecotones were intermediate between those of the adjacent communities and there were species adapted to these conditions (Jose *et al.* 1996). They may also occur if there are unique environmental conditions at the ecotone or if species need resources from both sides of the ecotone. Ecotonal species can be detected by finding those species reaching peak abundance or frequency in the ecotone (Walker *et al.* 2003).

Ecotonal species are commonly reported in sharp, anthropogenically defined ecotones between forests and fields; edges where the composition of the edge zone differs from the core areas. Baker and Dillon (2000) were the first to characterize species along patch interior to field gradient as being edge-restricted, edge-oriented, interior-restricted, or ubiquitous. Edge-restricted and edge-oriented species are typically easily dispersed, or else they would not successfully disperse to these small areas of habitat. Consistent with this prediction, Boutin *et al.* (2002) found higher numbers of more transient species in hedgerows. Some life forms may dominate at edges because they need resources from both sides, such as vines that take advantage of direct vertical sunlight from the exterior and structural support from the interior (Laurance *et al.* 2002). Many others have reported ecotonal species at forest edges, such as Burke and Nol (1998) who found species restricted to within 20 meters of the edge that didn't occur in the field or forest. Several studies have found more species that prefer the edge zone as compared to the forest interior (e.g., Gysel

1951, Watkins *et al.* 2003, Burke and Nol 1998, Fraver 1994, but see Williams- Linera 1990). Note, however, that Walker *et al.* (2003) found that even though they identified ecotonal species, there was no ecotone in their study in which the number of species reaching their maximum in the ecotone was greater than expected at random.

Mechanism/Pattern	Additive Blending	Ecotonal Species
Environmental Heterogeneity	Higher species packing at the ecotone	Unique environmental conditions present is conducive to a set of uniquely adapted species
Spatial Mass Effect	Seedlings from neighboring communities establish at the ecotone	Seedlings from neighboring ecotones establish at the ecotone of interest
Animal Densities	Animals increase pollination success and dispersal of species from adjoining communities	Animals bring in propagules from nearby ecotones
Exotics	Exotics from neighboring communities establish at the ecotone	Exotics specifically predicted to be more successfully at ecotones
Hybridization	Genes from adjacent communities forming hybrids at the ecotone	New species evolve at ecotone

Table 1.1: *Ecological mechanisms that might influence diversity patterns at ecotones.*

Mechanisms causing enhanced diversity

As described above, enhanced richness in ecotones can take the form of taxa from both core areas overlapping, leading to additive blending, or can derive from ecotonal species relatively unique to the boundary zone. Below, I describe some of the ecological mechanisms that could lead to these two types of enhanced diversity at ecotones (also, see Table 1.1).

Environmental heterogeneity

Ecotones have unique environmental and structural characteristics that may contribute to higher species richness (Risser 1995, Gosz 1992). For example, riparian zones, the transition between aquatic and terrestrial communities, are characterized by a diversity of soil types, physiognomic classes and moisture conditions. Reservoir and lake shores also have high topographic diversity, leading to higher recruitment and diversity than either the benthic or upland communities (Harper and Macdonald 2001). This high microenvironmental diversity provides more niches, leading to higher species numbers.

If single species' distributions are constrained to fewer microhabitats of smaller size, more species will be able to pack into the ecotones. The response of one species to environmental factors is amplified or attenuated across the transition zone. Conditions will be marginal for some species and species occurrences will be more sensitive to environmental heterogeneity, resulting in small-scale mosaicity (Gosz 1992; Anand and Li 2001). This is termed the mosaic effect: habitats divided into smaller patches near ecotones. However, these microsites are highly sensitive to change and disturbance, which could lead to higher mortality and thus lower richness (Gosz 1992, Hansen *et al.* 1998; Neilson *et al.* 1992).

Environmental heterogeneity could lead to diversity through additive blending if species are more tightly packed in the ecotone, but still occur on either adjacent community. If the environment at the ecotone is unique, new species might occur there, causing higher diversity via ecotonal species.

Spatial mass effect

Spatial mass effect is another mechanism that could cause increased diversity via additive blending. One measure of spatial mass effect is the disproportionate occurrence of seedlings, eggs or juveniles beyond the range of adults, resulting from continued migration of

propagules into an area where the species is not able to form a self-sustaining population (Shmida and Ellner 1984). Clearly the degree of dispersal and resultant propagule pressure is key to the importance of mass effect. Seeds may gather at forest edges, for example, because the wind speed may change at a transition, depositing airborne propagules. Seeds in transition zones and edges may have higher chance of germination than seeds in the forest due to lower predation pressure (Sork 1983). Some studies have found more species represented in ecotone seed banks, although they did not examine seed germination (Landenberger and McGraw 2004; Devlaeminck *et al.* 2005).

Although spatial mass effect can be important, the variation in its importance with ecotone type and setting is little known. At least one study of natural ecotones, found little evidence for spatial mass effect at edges (Walker *et al.* 2003). More studies are needed to document the importance of spatial mass effects in driving ecotone diversity.

Animal densities

Animal-abundance has the potential to influence additive blending at ecotones in numerous ways. For example, anthropogenic edges often have higher numbers of animal pollinators and seed dispersers (Burgess *et al.* 2005), which increase dispersal rates and viability at edges. An example is higher diversity of fleshy-fruited, bird-dispersed species at edges (Kollmann and Schneider 1999). Mammals, another dispersal agent, also show higher richness in edges (Pasitschniak-Arts and Messier 1998, Gates 1991).

In natural ecotones, there is some evidence of higher animal richness. Terrell-Nield (1986) found greater species richness of some groups of invertebrates in one scrub (ecotone) sample than in the adjacent field or woodland, but not in another scrub sample. Prous *et al.* (2004) found that invertebrate species richness was higher at cave ecotones at some sites but

not others. Pfeiffer *et al.* (2003) found particularly high ant species richness in the ecotone between steppe and desert in Mongolia. Animal species richness, like plant species richness, appears to be dependent on the ecotone's ecological properties.

Higher animal densities could also lead to more herbivory and actually lower plant species richness. For example, the rings around sagebrush stands in chaparral are caused by an interaction of herbivory and allelopathy (Swank and Oechel. 1991).

Exotic species

Exotic plant species have been purported to occur disproportionately in ecotones and thus fit the pattern of ecotone specialists, (Fox *et al.* 1997, Lloyd *et al.* 2000, Watkins 2003). Ecotones can be marginal environments for the species in adjacent communities. As many exotic species tend to be generalists, they would be expected to be at a higher abundance within the boundary zone (Allen and Knight 1984), at least in the absence of a seed source for ecotone specialists. In addition, ecotones, being of smaller spatial extent than their adjacent communities, would favor well dispersed species such as exotics. However, this higher exotic species richness may be due to the exclusion of native species richness, leading to the same or lower richness. Matlack (1994) found an opposite effect at anthropogenic edges: they were not consistently more species rich nor did they serve as entry points for ruderals or invasives. Walker *et al.* (2003) also found that exotics were not significantly higher at ecotones than in two adjoining communities. Thus, there is not yet strong evidence that the prevalence of exotics at ecotones makes a significant contribution to species richness, and it is clear that there are many circumstances where exotics do not contribute to the ecotonal diversity pattern.

Hybridization

The juxtaposition of species from different habitats at an ecotone has the potential to lead to hybridization. These hybrids may be better adapted to the intermediate conditions present at an ecotone, and may persist, increasing species richness by creating new ecotonal species. This has been shown to occur in a few isolated cases such as hybrids between *Iris fulva* and *hexagona* (Arnold 1994), between two subspecies of *Artemisia tridentata* (Wang *et al.* 1997) and between *Eucalyptus melanophloia* and *E. creba* (Drake 1980). However, these are isolated cases only involving 1-2 species. Hybridization's influence on diversity at any single ecotone appears to be insignificant.

Ecotone properties that confound diversity

Although many authors have asserted that there is often higher species richness at ecotones, the literature I have reviewed above leads to the conclusion that enhanced species richness at ecotones is not a universal property, but rather results from the particular ecological condition at the site, as well as properties of the surrounding landscape. In addition there are other factors related to measurement methods that can also bias such research results. Below, I present four major factors that directly influence the outcome of any experiment, observational study or model investigating patterns of richness at ecotones.

Type of ecotone

Causal factors provide the most conventional method for categorizing ecotones. Wilson *et al.* (unpublished), list 6 types of ecotone: environmental, switch, threshold, anthropogenic, community-coadaptation, and invasion. Environmental ecotones can occur by means of a sharp environmental gradient such as slope, soil type or soil drainage

(Dangerfield *et al.* 2003). At a biome scale, sharp changes in climate are a major factor while at the patch level, it could be soil moisture or geologic discontinuity. The switch ecotone is caused or maintained by a positive feedback loop that sharpens a gradual environmental change (Wilson and Agnew 1992). At the community scale these can include plant root growth inhibiting grasses from invading a floodplain forest or sphagnum moss lowering the pH of soil and thereby excluding competitors (Odum 1990), whereas at the biome scale the change in albedo between tundra and boreal forest leads to a switch ecotone. Threshold ecotones represent a sharp biotic response to a gradual environmental gradient (Lloyd *et al.* 2000, Risser 1995) such as the point along an elevation gradient where trees can no longer compete with shrubs and grasses. Anthropogenic ecotones are caused and maintained by human disturbance. Human disturbance often causes sharp, easily observable ecotones: forest-field edges, road cuts, and powerline right of ways. Community coadaptation ecotones assume stable, climax communities with coevolved species on either side. Lastly, invasion ecotones occur at the front of a dominant invading species.

It should be noted that the forces forming an ecotone may not necessarily be the ones maintaining it; the ecotone may be relict or contemporary (Strayer *et al.* 2003). For example, an anthropogenic ecotone may be caused by plowing but maintained by a switch based on certain animals avoiding the field. To further complicate matters, it is often the case that multiple causes contribute to the formation of an ecotone. For example, edaphic patterns may cause the formation of boundaries, but physical disturbance can alter boundary location (Wiens *et al.* 1985).

To date there has been no published research that explicitly indicates that certain types of ecotones have higher diversity while others do not. Major factors preventing this are

lack of a strong taxonomy of ecotones, general difficulties determining ecotone causation in the field, and shifting causation patterns, as discussed above. Still, some studies do suggest that the type of ecotone is an important factor in generation of diversity patterns (Walker *et al.* 2003, Lloyd *et al.* 2000). More studies are needed that explicitly link causation with ecotone richness.

Age

Another factor influencing richness at boundaries is age and stability. Boundaries that fluctuate in space and time are predicted to have lower richness than stable, long-term boundaries (Delcourt and Delcourt 1992). Ecotones that are stable over long periods of time have had more opportunities for dispersal and colonization of ecotone specialists (Gosz 1992). Boundaries can also become sharper or more diffuse over time. For example, forest edges may become less permeable over time and reinforce their own boundaries while others may disappear if they are dependent on constant disturbance. Studying ecotones of different ages without consideration of the effect of age will preclude separation of ecotone and age effects.

Sharpness

The sharpness or width of an ecotone will also affect its diversity. To illustrate I use Strayer *et al.*'s (2003) geometry of adjacency diagram (Figure 1.2). When there is a wider, more gradual transition, there is more opportunity for additive blending to contribute to richness (Figure 1.2c). When a gradient is sharp or maintained by a barrier or very frequent disturbance, it is unlikely that there will be much blending or a large enough habitat for ecotonal species with the consequence that richness will not be high (Figure 1.2b,a). If there is a unique environment between the two communities, then there is the opportunity for

ecotonal species to colonize this zone and richness will increase (Figure 1.2d). An example of this is shown in human-created edges where north- and south-facing edges have different widths and therefore may harbor different numbers of species, (Fraver 1994).

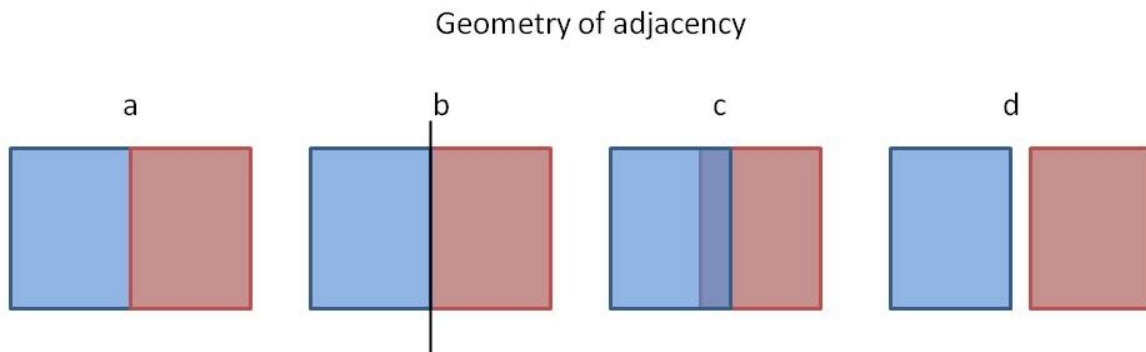


Figure 1.2: *Four types of geometry of adjacency adapted from Strayer et al. 2003: a) A boundary between two adjoining patches; b) A boundary formed by a distinct structure; c) a boundary between two overlapping patches; d) a boundary between two disjunct patches.*

User-defined factors

When designing an ecological study, there are a number of decisions that need to be made regarding the study area and sampling methods. Below, I give examples of how these sampling decisions might affect results of studies at ecotones.

1. Spatial scale

Ecotones can be defined at many spatial scales, with the decision dependent on the system and question of interest. Gosz (1993) described five levels of spatial extent and the environmental gradients most influential at each: 1. biome level: climate and topography; 2. landscape level: local weather, topography and soil; 3. patch level: the movement of vectors, species interactions, microclimate and microtopography; 4. population level: interspecies interactions, physiological controls, population genetics and microtopography; and 5. individual level: influenced by soil and physiology. The first three of these are appropriate for study of ecotones, whereas the last two are not particularly relevant. Each of the three scales of ecotones will have different causation, and thus different properties, making it difficult to draw parallels between ecotones measured at different spatial extents.

Along with spatial extent, the spatial grain size used during sampling will influence perception of ecotone richness. Although ecotone detection itself may not depend on spatial grain size (Walker *et al.* 2003), patterns of richness are scale dependent. Strayer *et al.* (2003) argue that as different grain sizes are used in observation, the perception of the same physical structure will change. As an extreme example, the grain size has to be smaller than the width of the ecotone itself, or the patterns may be meaningless. When the sample area includes not only the ecotone but the two adjacent communities, species richness will be higher as it will combine taxa from both core community types. At each grain size smaller than this, the ecotone may or may not have higher diversity per unit area, depending upon size of individuals, territory size of species, and species range size. For example, imagine an ecotone consisting mostly of grasses and sedges adjoining a savannah and a forest. At a 0.5 meter scale of observation, the ecotone might have higher richness than the forest simply due to the number of grass and sedge individuals able to fit into that area, whereas in the forest only one

individual might fit into that area. Transect designs need to take individual size into consideration to capture an accurate picture of diversity.

Patterns of species richness at ecotones might be relatively scale-independent. Stowe *et al.* (2003) did find that species richness at a *Nothofagus* treeline is scale independent. Still, there has not been much focus on studying the pattern of richness of ecotones at multiple scales of grain or extent, and species richness cannot simply be assumed to be scale independent (Lloyd *et al.* 2000).

2. Taxonomic group

Although some suspect that animal species respond to vegetation patterns in the same manner that vegetation responds to environmental gradients (Risser 1995), there is evidence showing marked incongruity in the richness patterns between different taxonomic groups (Dangerfield *et al.* 2003). The taxonomic range investigated (sea birds vs. all birds vs. all vertebrates) will also affect the results. Sisk and Battin (2002) found that bird responses to anthropogenic edges tended to vary noticeably among families and among edge types so that no simple pattern emerged regarding diversity for birds as a whole. Likewise, Rusek (1992) found that microfaunal soil organisms show an increase in diversity at the ecotone, but the same is not true for soil mesofauna. Life history traits, range size and demographic characteristics of the species group of interest will influence the patterns of diversity exhibited at ecotones. For example, if an ecotone is characterized by small-scale heterogeneity, it may be more likely to affect richness for invertebrates, which are more sensitive to microtopography, and less likely to affect the diversity of vertebrates.

Recommendations for future studies of ecotone diversity

There are many factors that influence diversity patterns at ecotones, making it difficult to tease out diversity patterns and possible underlying mechanisms. In this section, I describe three types of study ecotones, as well as research questions that should to be answered in order to better understand the patterns and processes occurring at each.

Ecoregional ecotones

An ecotone separating two ecoregions is influenced mostly by climatic and topographic change and its boundary often follows gradients on soil, topographic, and climatic maps. The ecoregion itself is defined by an observable change in vegetation associations. Richness patterns will be influenced by two competing mechanisms: increasing environmental heterogeneity at the ecotone, which will increase diversity, and lower fitness of species at the limits of their ranges, which will lower diversity. Thus, to study diversity at ecotonal boundaries, one needs to integrate range maps, data on species occurrences, and environmental data in order to answer several critical questions. 1) Is there higher environmental heterogeneity near the ecotone? 2) If so, does vegetation respond directly to this heterogeneity? 3) Do species range limits coincide with the ecoregion boundary? 4) Is there a higher number of species per unit area at the ecotone than in either ecoregion. Richness patterns for other taxa may or may not follow the same pattern; larger predators, for example, may respond to an ecoregion boundary very much influenced by a sharp elevation gradient but may not respond to an ecoregion boundary influenced by an edaphic gradient.

Forest/field boundaries

An anthropogenic ecotone separating a forest and a field is caused primarily by human disturbance. Secondly, the change in species composition is caused by soil moisture differences, light gradients, microtopography, microclimate, and the movement of dispersal vectors. There may be ecotonal species enjoying the unique edge environment. There may be additive blending of forest and field species (i.e., field species occurring in the forest and forest species occurring in the field, as a result of spatial mass effect). An opposing force is the possibility of high mortality if the ecotone represents a marginal environment for many species. To study diversity at forest/field boundaries, one should investigate species turnover at the edge, measure dispersal and establishment at the ecotone, and collect information on multiple environmental gradients. Pertinent diversity related research questions include the following. Are there specific ecotonal species at this edge, or an additive blending of field and forest individuals? Do invasive species significantly contribute to edge diversity? Does the species turnover occur at the same location as environmental turnover? How does width of edge influence diversity?

Upland-wetland boundaries

An upland-wetland boundary is primarily caused by a gradual environmental gradient, soil moisture, and will change depending on flooding frequency and intensity. Soil, micro and macrotopography and microclimate are the primary causes underlying species turnover. Here, the scale and definition of the ecotone is of utmost importance because one wetland area can contain multiple ecotones: between the upland and the wetland, between riparian and floodplain forests, between upland and open water, and between various vegetation zones connecting the wetland and upland. The pattern of richness at these ecotones will be a function of additive blending of wetland and upland species, ecotonal

species supplied by high propagule pressure from water transport, and ecotonal species adapted to a specific elevation zone, such as ecotonal species adapted to strong fluctuations in moisture at a water boundary. Important questions here include the following: How does ecotone stability relate to diversity? Is ecotone diversity at wetland ecotones scale dependent? And, does vegetation change at wetland boundaries respond directly to changes in soil moisture, or is there a threshold effect causing the turnover to be higher than expected?

Discussion and Conclusions

The question of whether diversity is higher at ecotones is complicated by numerous factors. The simple answer is “sometimes”, but a more complete answer takes into account ecotone cause, sharpness, stability, landscape position, as well as user-defined factors such as taxa of interest and sampling techniques. It is not sufficient to describe the patterns of species turnover at an ecotone; one must think about the underlying causes of that turnover, how species are responding to the environment and the relative distributions of these species along the gradient.

Ecotone properties are situational, but that does not mean that they don't lend themselves to experimental study, observational inquiry or modeling. Nor does it mean that they aren't important from a conservation standpoint. Of possible conservation concern are the much overlooked ecotonal species; species that specialize in transition zones that may be lost with increased human disturbance and climate change. This underlines the need to study diversity at higher magnification, taking into account not just patterns, but environmental, biological and ecological factors as well.

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Chapter 2: SPECIES TURNOVER AT COMMUNITY LEVEL

ECOTONES: AN EXPLORATORY ANALYSIS OF DETERMINANTS OF DIVERSITY

Introduction

Disturbance events are often responsible for creating and maintaining ecotones. They may reinforce existing boundaries, as in the case of a fire strengthening a pocosin/savannah boundary. Disturbance may create a new ecotone, as in the case of a mown field/forest boundary. Regardless of whether a disturbance is natural or human-created, we can predict that the immediate effects of an intense disturbance on an ecotone and adjoining disturbed communities will be loss of species richness, lower numbers of ecotonal species and increased sharpness. As time passes, we would expect to see an increase in richness, evidence of mass effect as propagules become established and higher numbers of exotics as they establish at the boundary.

Complicating these predictions are differences in mechanisms underlying species diversity. These include variations in environmental gradients, animal densities, mass effect potential and exotic species invasion potential. In addition, each forest-field edge on the

planet has a different species pool, disturbance regime, landscape position, age, and sharpness.

In this chapter I look at species diversity patterns across a series of disturbance-maintained edges that are similar in species composition, climate and topographic position so that I may specifically focus on the mechanisms causing species richness at these edges. These edges differ only in age (0-3 years), sharpness and aspect. This design allowed me to address the following research questions:

1. Is species richness consistently higher at these edge ecotones? Ecotones are often cited as zones of high diversity, and there is no reason to believe at the onset that forest edges are an exception (Leopold 1986, Petts 1990, Risser 1995). Species richness at ecotones is thought to be directly related to their stability (Delcourt and Delcourt 1992). A stable ecotone will have allowed species to disperse to and establish at the boundary between two communities. In contrast, an ecotone that has been very recently disturbed is not predicted to have higher richness than adjacent communities as more time is needed for species to arrive. It is unknown, however, whether an ecotone may rebound from the event faster than adjoining disturbed communities.

2. What are the relative contributions of additive blending and ecotonal species to the species composition at these edges? Are the species present in the ecotone zone the same as the species in adjacent communities or are there species that are unique to the edge environment. In this paper, I define ecotonal species as those that are exclusive to the ecotone, rather than those that just reach peak abundance there.

3. Does age, sharpness or aspect influence species richness? Species turnover per unit distance that is more rapid than on either side is a defining property of ecotones. However,

the degree of this turnover may occur over hundreds of meters or just a few. I predict that the abruptness of change at an ecotone will be higher at recently disturbed ecotones, where many of the forest species that might have been established in the field will have been lost. Sharper, younger ecotones should have few species, and north-facing ecotones will have more species due to a more gradual light and temperature gradient throughout the day.

4. Are there more exotic species in these edge ecotones than in adjacent communities? Exotic species may be more prevalent at anthropogenic ecotones (Allen and Knight 1984). Exotics tend to be generalists, making them suited for the heterogeneous and often marginal environment that ecotones provide.

Methods

Study site

The Mason Farm Biological Preserve of the North Carolina Botanical Garden, Chapel Hill, NC, provides a patchwork of stands representing various successional stages. The preserve, located in the outer Piedmont of North Carolina, is maintained for botanical and wildlife protection and diversity, as well as to provide research and recreational opportunities. The forest patches here range in age from early successional loblolly pine forest to late successional Piedmont hardwood forest dominated by oak and hickory. There is also a significant hydrological gradient in forest patches, with those in the middle of the preserve being wetter (and even occasionally flooded) than that on the western edge of our sampling area. The fields are mostly dominated by grasses and forbs. A few patches of the preserve are in shrubland, and have not been touched for at least 5 years. There are nine actively maintained fields in the preserve and two late-successional shrublands. The

shrublands were eliminated from this study as their disturbance history was unknown. Some fields were not sampled because of an existing hedgerow or a mixed mowing pattern.

Transects were placed at each field so as to maximize the differences in aspect, for a total of 17 plots (Figure 2.1). At each plot location, a GPS was used to record position and a compass for the aspect of the transect line (Table 2.1). The transects were positioned to capture the observed ecotone, and ran longer into the forest in order to accurately capture the composition of less densely packed individuals. Historical data on disturbance and field history was provided by the North Carolina Botanical Garden.

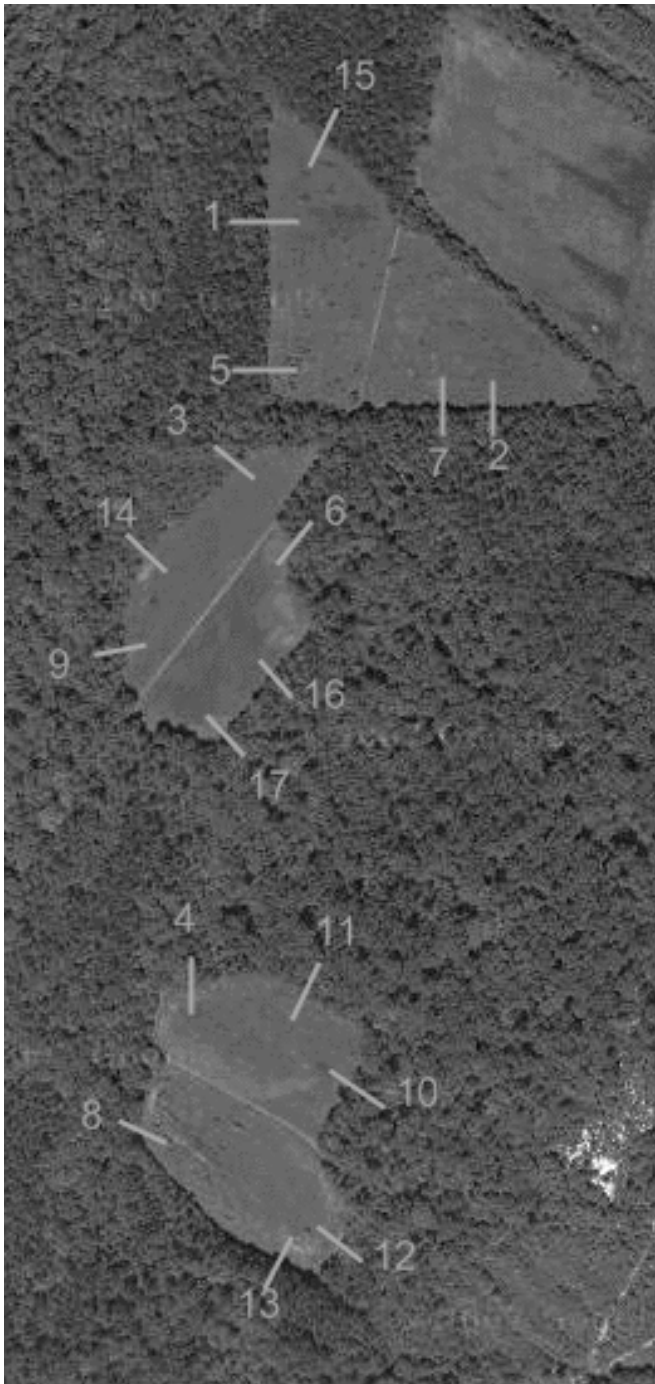


Figure 2.1: *Plot locations of the 17 transects at Mason Farm Biological Reserve. The transects indicated in the figure are approximately 45 meters long.*

Plot	Date Sampled	Plot Location	Time since last Disturbance	Type	Aspect	UTM E	UTM N
1	18-Apr-07	Mid Outer	2006	Mown	274	678993	3973426
2	08-May-07	Mid Inner	2004	Burned	190	679132	3973303
3	21-Jun-07	West Outer	2004	Burned	130	678956	3973222
4	02-Jul-07	South Inner	2005	Mown	194	678940	3972840
5	04-Jul-07	Mid Outer	2006	Mown	100	678984	3973352
6	13-Jul-07	West Inner	2006	Mown	254	678990	3973183
7	21-Jul-07	Mid Inner	2004	Mown	8	679089	3973306
8	24-Jul-07	South Outer	2006	Burned	100	678900	3972747
9	26-Jul-07	West Outer	2004	Burned	64	678880	3973092
10	23-Aug-07	South Inner	2005	Mown	289	679026	3972774
11	30-Aug-07	South Inner	2005	Mown	210	679035	3972822
12	03-Sep-07	South Outer	2006	Burned	316	679030	3972636
13	06-Sep-07	South Outer	2006	Burned	30	678987	3972651
14	12-Sep-07	West Outer	2004	Burned	108	678882	3973154
15	13-Sep-07	Mid Outer	2006	Mown	216	678997	3973495
16	18-Sep-07	West Inner	2007	Mown	315	678991	3973095
17	19-Sep-07	West Inner	2007	Mown	334	678933	3973035

Table 2.1: Characteristics of the 17 ecotone transects. Plot location indicates whether the plot was within the nature trail loop or outside of it.

Sampling

The sampling protocol is adapted from Walker *et al.* (2003) and Peet *et al.* (1998).

Prior to sampling, the protocol was tested across a diverse set of ecotones in the Francis Marion National Forest, S.C., Croatan National Forest, N.C. and Pea Island, N.C. I recorded transects across pocosin/pine savannah ecotones as well as across two salt marsh types.

These sample data were then used to test the rigorousness of the approach used.

At Mason Farm, I recorded 17 transects (sometimes referred to as plots). Each transition was measured using a 10 meter wide single belt transect. The typical transect was

approximately 45 meters in length and was subdivided into 45 contiguous, 1x10 meter belts arrayed perpendicular to the transect. Each belt was further subdivided into a 1x1 m block (Level 1), an overlapping 1x4 m block (Level 4) and the overall 1x10 m block (Level 10) (Figure 2.2). Subblocks of 0.5 meters have given similar results to 1 meter subblocks in previous studies (Walker *et al.* 2003). The subblock size also makes it easy to lump into larger blocks for determining scale dependent properties. For the purposes of this study, only the 1x10 belt size was used, as this provided the least amount of noise and resulted in the most robust ecotone boundary positions, as described below.

At each subblock, I recorded absolute abundance of herbs and trees in order to quantify changes in general compositional turnover and species richness. I recorded each species' physiognomic type (seedling, herb, shrub, grass, fern or tree) in each 1x10 rectangle. This designation was based on the largest size that the species reached in that rectangle. A single species could be assigned a different physiognomic type in different rectangles. For example, red maple could be recorded as a seedling in one rectangle, and as a tree in a different rectangle.

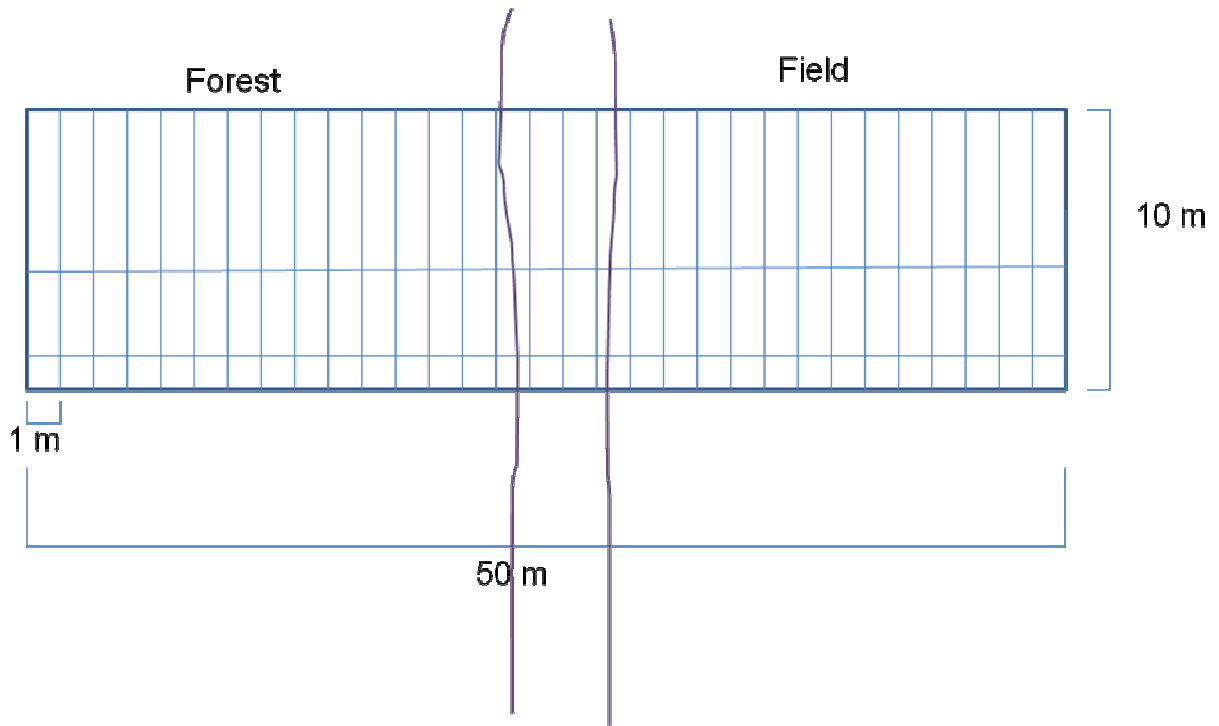


Figure 2.2: *Transect layout. The area between the purple lines corresponds to a hypothetical ecotone zone.*

Ecotone Detection

A good understanding of ecotone characteristics should lead to a statistically robust method of detecting them in the field. It is tempting to simply look for visual discontinuities in species composition, or to look at an ecoregion map and claim that the boundaries are equal to ecotones. However, upon closer inspection, a change in physiognomy (e.g., a tree line) is only a change in the composition of one group of species. In other words, an ecotone for one group of species (e.g., trees) may not be an ecotone for other groups (e.g., herbs). Detection techniques need to provide an unbiased, physiognomy-independent way of finding ecotone location.

One approach to ecotone detection is to find the location of the highest rate of change in species spatial co-occurrence (Fortin *et al.* 2000). The first detection method employed was the traditional moving split-window technique: blocking sampling points along a gradient into windows, splitting the window into two groups, finding the difference between groups, while moving the window along the gradient and finally finding the location(s) of the largest differences within a window (Whittaker 1960).

The moving split-window technique in some cases has been superseded by computationally intensive lattice and triangulation wobbling methods that are especially appropriate for two dimensional sampling (not just a linear gradient) (Fortin *et al.* 2000). Some suggest a multivariate split moving window is superior to newer techniques (Ludwig and Cornelius 1987). One can also define the midpoint of the boundary as the position of maximum rate of change in ordination scores along a length of a transect (Walker *et al.* 2003). This rate of change technique is argued to be more appropriate because ecotones are zones of rapid change rather than points of instantaneous change. Using the Walker *et al.* 2003 technique, sharpness in composition can be determined by ordination scores of individual subblocks, averaged along each meter of the transect.

I used a moving window approach to delineate the position of the maximum rate of change in ordination score along a length of a transect (Delcourt and Delcourt 1992; see Figure 2.3 for an example of this method). For this study, a 6-meter window size was used. Although previous studies have used Detrended Coorespondance Analysis to order rows, I used Nonmetric Multidimensional Scaling (NMS, Mather 1976, Kruskal, 1964), a more statistically robust method. However, in comparisons I performed, DCA and NMS gave similar location results. Using NMS in the moving window method, I determined the width

of the ecotone, as well as the locations of the upper and lower boundaries. To do this, the Axis 1 scores from the NMS ordination were plotted against position along the transect. The first derivative of this plot determined the point of maximum change in vegetation composition. The second derivative of this plot determined the points of inflection of this change, allowing me to determine the minimum and maximum points along the transect at which rapid change occurred. The belts within these points were categorized as ecotone belts. I then separated each transect into three zones: forest, ecotone and field.

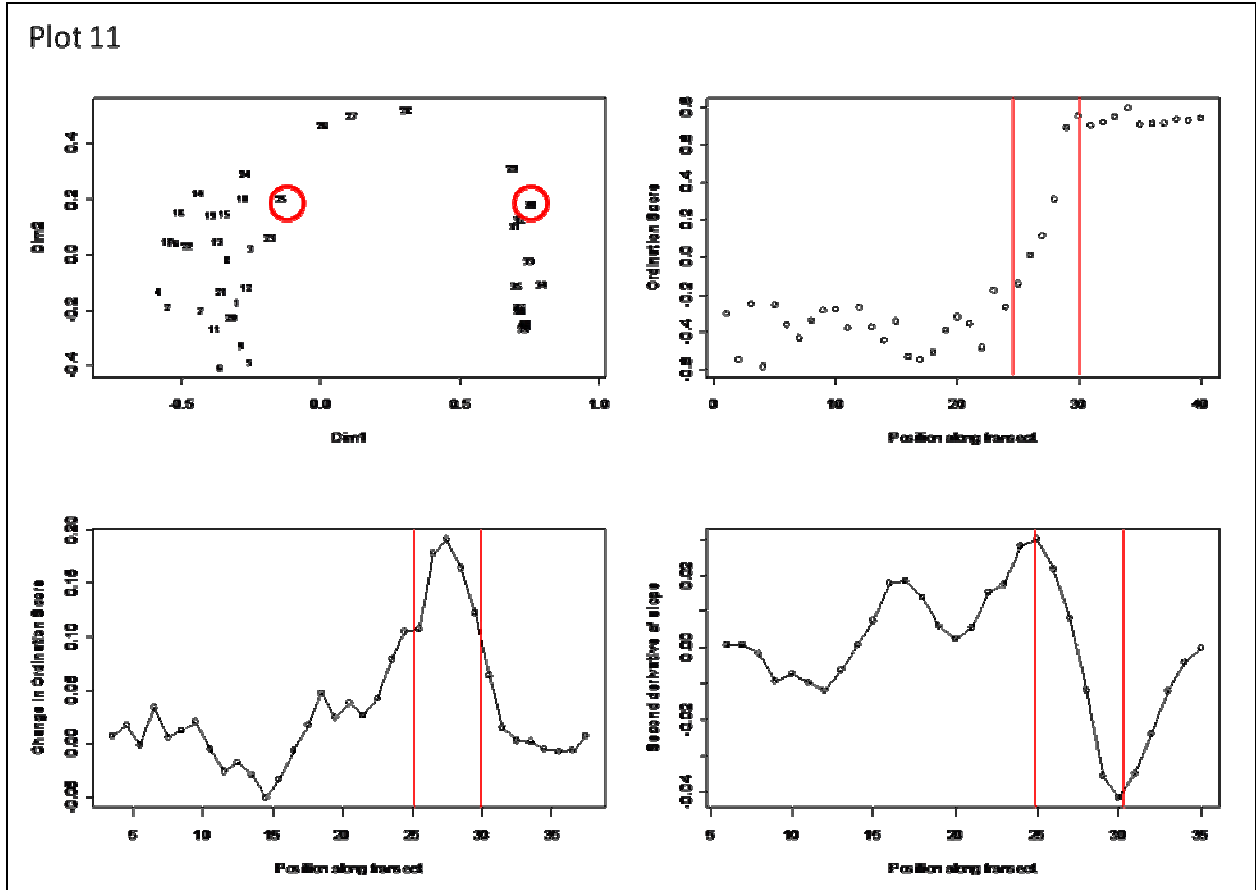


Figure 2.3: *The moving window approach to ecotone delineation illustrated using transect 11. The top left graph shows the NMS ordination, treating every belt of the transect as an ordination “plot”. The red circles and lines indicate the boundaries of the ecotone. This transect started in the forest and ended in the field. The top right graph is the plot of the belt location along the transect against the Axis 1 ordination score. The bottom left graph is the first derivative of the top right graph, the peak indicating a high rate of change in the ordination score. The bottom right graph is the second derivative of the top right graph. The maximum and minimum points on this graph determine the ecotone boundaries.*

The difference between using a visual technique to delineate ecotones and the moving window method is illustrated in Figure 2.4. A visual interpretation of physiognomic change would put the ecotone at position 28 along the transect where the herbs increase in relative abundance and trees drop out. However, there is no way to determine ecotone width using

this approach. The moving window approach tells us that the ecotone boundaries in that plot were between positions 25 and 32.

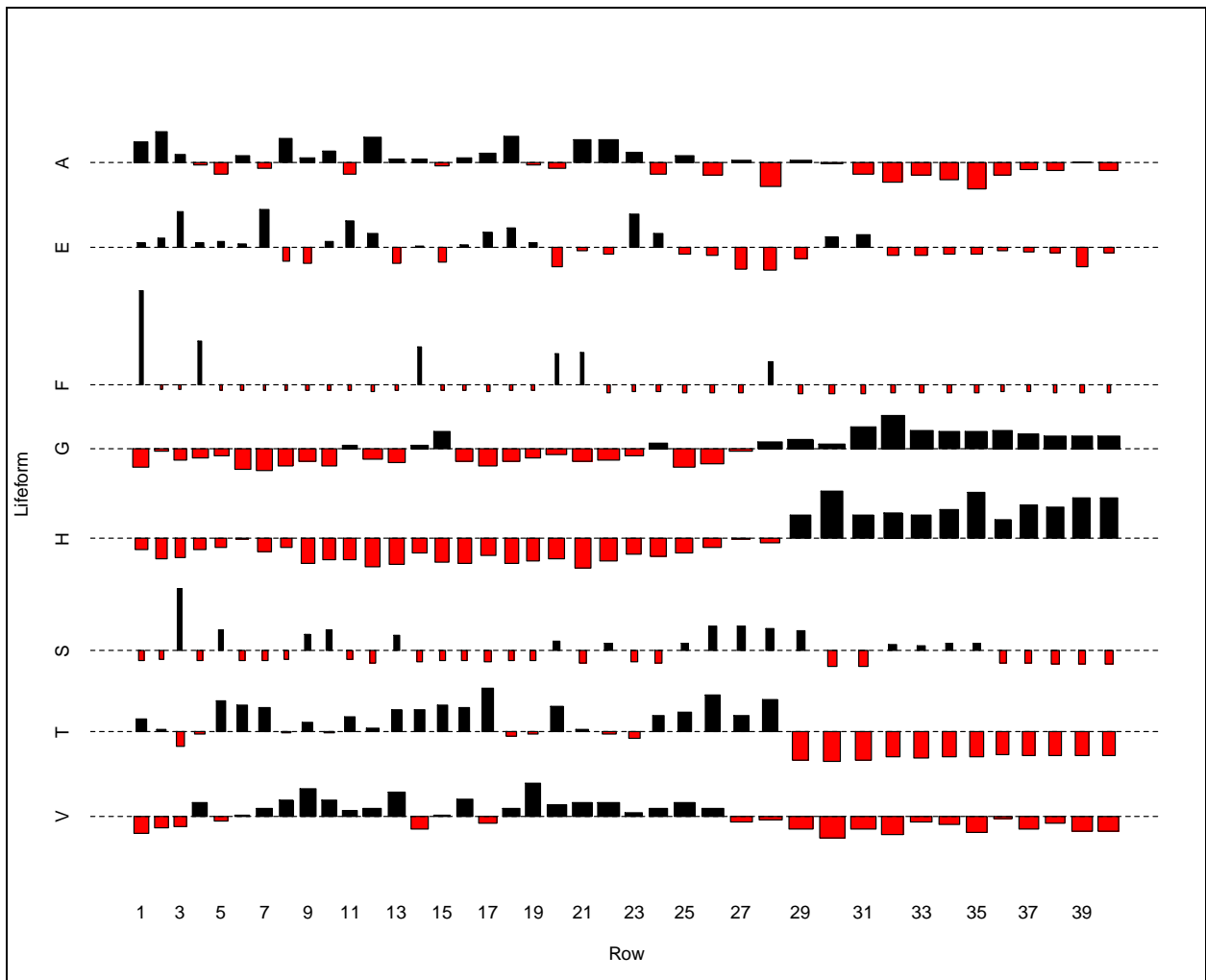


Figure 2.4: Lifeform change along transect 17. Lifeform codes are A=Sapling, E=Seedling, F=Fern, G=Graminoid, H=Herb, S=Shrub, T=Tree, V=Vine. In this association plot, the area of each box is proportional to its deviation from the expected values when the lifeform variables are assumed to be independent from each other. Red boxes indicate that the lifeform is less frequent than expected, while black indicates that it is more.

Statistical Analysis

Nonmetric multidimensional scaling (NMS) ordinations were performed at two levels. These ordinations were run in R for Windows XP (R Development Core Team 2007)

using Kruskal's Non-metric Multidimensional Scaling. The matrix used in the ordination was formed using the *vegdist* function in the VEGAN package (Oksanen *et al.* 2007), which uses the Jaccard similarity index. The first ordination was performed using only the forest data for all 17 transects. The purpose of this ordination was to explore the ecological differences between sites as a possible factor in our results. This ordination was performed using presence/absence data, using the Biodiversity R *NMSTrandom* function (Kindt and Coe 2005), which displays the ordination with the lowest stress value, given an inputted number of permutations. The second round of ordinations was performed on belts within each transect, as part of the ecotone detection method, using species abundance data (Figure 2.3). These ordinations were performed using the *isoMDS* function (MASS package, Venables and Ripley 2002), also using distance values from the *vegdist* function included in the VEGAN package.

Relationships between species richness and sharpness, age, and aspect were determined using both standard least-square regression as well as stepwise least-squares regression. Significant levels of differences between average number of total and exotic species between the ecotone and forest and field regions were determined using Student's t-tests, with a significance value set at 0.05. Exotic species designation follows Weakley 2006. Correlations between variables in the richness and ecotonal species analysis were ascertained using Pearson's product moment correlation, also with a significance value of 0.05. Aspect was transformed to "Northiness" values, or how far the value was from 180 degrees.

Results

Species Richness

Species richness per meter (i.e., 1x10m band) was not significantly higher in the ecotone for every transect (Table 2.2). Four of the plots had significantly higher richness at the ecotone, four of the plots richness values in the field which were significantly than those in the ecotone. There was no correlation between which zone had the highest species richness and age (t-value= -1.86, p= 0.0826) or aspect of the ecotone (t-value=0.868 p=0.399116). The stepwise regression showed that age, aspect, and sharpness were not masking the effects of each other, as every combination of these factors showed non-significant relationships to richness when the others were accounted for. The rest of the plots did not have richness values in the forest or field that significantly differed from that of the ecotone. Ten of the plots had an equal or higher total species count in the ecotone than either the forest or the field.

Plot	Ecotone Start Point	Ecotone End point	Length of Ecotone	Total Species in the Forest	Total Species in the Ecotone	Total Species in the Field	Average Forest	Average Ecotone	Average Field	Average Highest
1	25	35	10	47	43	40	11.68	16.45	20.31	Field *
2	15	24	9	50	57	51	16.00	24.90	22.93	Ecotone
3	21	25	4	59	47	43	19.14	28.00	23.62	Ecotone *
4	16	27	11	37	58	51	16.63	22.83	23.93	Field
5	23	28	5	32	39	52	11.43	14.66	25.08	Field *
6	24	30	6	44	54	43	13.67	24.86	23.73	Ecotone
7	21	30	9	50	57	45	17.14	24.20	24.82	Field
8	24	29	5	49	29	42	11.79	12.00	21.55	Field *
9	23	34	11	34	50	25	9.73	14.00	13.71	Ecotone
10	30	35	5	61	26	14	17.33	9.66	5.33	Forest
11	25	30	5	38	38	36	12.16	17.50	20.09	Field
12	23	34	11	43	66	36	16.65	27.00	23.00	Ecotone *
13	20	31	11	37	50	39	10.40	17.50	26.25	Field *
14	26	34	8	37	38	32	7.69	14.44	14.57	Field
15	26	32	6	37	35	28	9.77	16.29	15.44	Ecotone
16	27	32	5	42	41	26	9.11	17.50	12.44	Ecotone *
17	25	32	7	45	51	40	14.52	28.13	22.56	Ecotone *

Table 2.2: *Species richness relative to transect position. For each transect, the ecotone zone length, the total number of unique species found in each zone, and the average number of species per meter in each zone is reported.*

Visual interpretation of species richness across an ecotone often indicates a peak near the ecotone, with richness staying high into the field (Figure 2.5). In some cases, the richness values decrease with distance into the field, suggesting that longer transects could strengthen the richness-ecotone correlation.

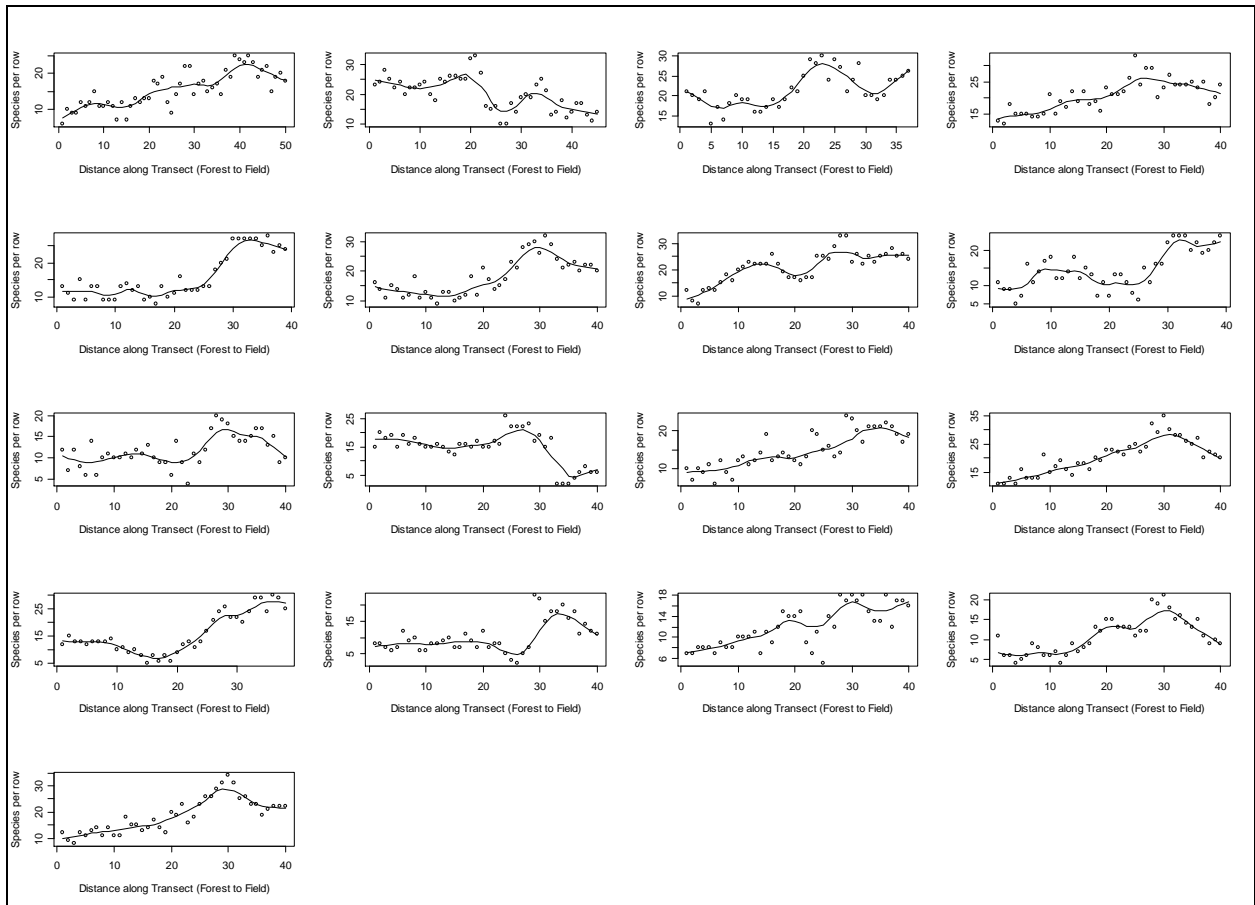


Figure 2.5: Number of species per meter along each transect (1-17 in order). Lines show a lowess smoothing function, $f=0.25$.

Ecotonal Species

All transects had at least 1 and up to 16 ecotonal species (Table 2.3). Species considered ecotonal in more than one transect include: *Quercus phellos*, *Ligustrum sinense*, *Cornus florida*, *Sisyrinchium albidum*, *Rhus copallinum*, *Festuca obtusa*, *Potentilla canadense*, *Quercus falcata*, and *Oxalis dillenii*. Ecotonal species number was not correlated with age ($cor=0.4626827$, $t = 2.0213$, $df = 15$, $p\text{-value} = 0.06146$), average richness ($cor=-0.08710251$, $t = -0.3386$, $df = 15$, $p\text{-value} = 0.7396$) or total richness ($cor=0.3700385$, $t = 1.5427$, $df = 15$, $p\text{-value} = 0.1437$) at the ecotone. Even though there was no significant

correlation with age, it is interesting to note that Plot 9, which had not been disturbed for 3 years, had the highest number of ecotonal species.

Transect	Number of Ecotonal Species	Species					
1	2	MIMUALA	QUERPHE				
2	1	LIGUSIN					
3	2	AMBRART	CARYGLA				
4	4	CERCCAN	CORNFLO	LACT1S1	SISYALB		
5	4	ASPLPLA	ELYMVIR	HYPEPRO	QUERPHE		
6	5	ALLIVIN	OENOFSS	PENSLAE	PHYSVRG	PTILCAP	
7	5	HYPEHYP	LIGUSIN	POLYACS	RHUSCOP	TRACDIF	
8	2	FESTOBT	GNAPOBT				
9	16	POTECND	ROSAMUL	QUERFLC	ROSAMUL	SCUTINT	SISYALB
		SMILBON	TRIPDAC	VITICINB	LESPBCL	OXALDIL	PINUTAE
		CAREDIG	CORNFLO	DIOSVIR	EUPAHYS	FESTOBT	
10	1	SOLACAR					
11	3	CYPE1S1	PINUECH	RUMECRI			
12	8	ASTEPIIL	EUPASER	HYPEHYP	HYPEPUN	HYPEVRG	
		JUNCEFF	QUERMCH	SYMPPAT			
13	6	ERIGANN	JUNIVIR	OXALDIL	PIPTAVE	PYRRCAR	QUERSTE
14	4	ANDRVIR	JUNCBIF	OENOFSS	POTECND		
15	2	CHAMNIC	MELALIN				
16	4	ALBIJUL	QUERFLC	RHUSCOP	RUMEACE		
17	1	OXALDIL					

Table 2.3: *Ecotonal Species found on each transect within the ecotone zone. Highlighted species were found on more than one transect.*

Ecotone Sharpness

Ecotone sharpness does not appear to have an effect on other ecotone properties except for number of ecotonal species. Ecotones ranged from 5-11 meters (Table 2.2), and was not correlated with time since last disturbance (cor= 0.1007320, t = 0.3921, df = 15, p-

value = 0.7005) or aspect ($\text{cor}=0.3230495$, $t = 1.3221$, $df = 15$, $p\text{-value} = 0.2060$). There was no correlation between length of the ecotone and species richness at the ecotone ($\text{cor}=0.182722$, $t = 0.7198$, $df = 15$, $p\text{-value} = 0.4827$) nor whether highest species richness was found in the field or ecotone. However, the number of ecotonal species was significantly correlated with length of ecotone ($\text{cor}=0.5305421$, $t = 2.4241$, $df = 15$, $p\text{-value} = 0.02845$), which one might expect from normal species-area relationships.

Exotic Species

For most of the transects there were not more exotics species at the ecotone (Table 2.4). In 16 of 17 transects, the average number of exotics was either highest in the field, or not significantly different from the number in the ecotone. Similarly, the percentage of all species that was exotic was generally highest in the field, and only significantly higher in the ecotone for 1 of the 17 transects. There were no correlations between the percentage of exotics species in an ecotone and ecotone length ($\text{cor}=0.4450479$, $p>0.05$), or age ($\text{cor}=0.1450394$, $p<0.05$).

Transect	% Forest Species that are Exotic	% Ecotone Species which are Exotic	% Field Species that are Exotic	Mean Number of Exotics in Forest	Mean Number of Exotics in Ecotone	Mean Number of Exotics in Field
1	10.88%	15.76%	28.99%	1.28*	2.64	6.13*
2	9.04%	17.60%	23.63%	1.45*	4.4	5.47
3	10.64%	13.51%	11.40%	2.05*	4	2.69*
4	16.48%	17.15%	27.46%	2.75	3.92	6.57*
5	2.28%	9.09%	12.29%	0.26*	1.33	3.08*
6	9.45%	13.71%	21.46%	1.29*	3.43	5.09*
7	14.40%	17.77%	17.22%	2.48*	4.3	4.27
8	1.41%	11.11%	23.21%	0.17*	1.33	5.00*
9	1.33%	19.64%	32.29%	0.13*	2.75	4.43*
10	15.13%	20.69%	28.13%	2.63	2	1.5
11	8.22%	9.43%	21.62%	1	1.67	4.36*
12	21.15%	21.91%	31.06%	3.52*	5.92	7.14*
13	11.54%	20.37%	26.42%	1.2*	3.67	7*
14	3.50%	19.23%	35.29%	0.27*	2.78	5.14*
15	18.75%	28.95%	33.81%	1.85*	4.71	5.2
16	4.86%	13.33%	16.96%	0.44*	2.33	2.1
17	6.34%	14.22%	18.23%	0.92*	4	4.11

Table 2.4: Percentages and average numbers of exotic species in the forest, ecotone and field sections of each transect. Asterisks indicate that the average number of exotics in the forest or field was significantly different from that in the ecotone.

Transect Position

An ordering of the 17 transects in NMS ordination space is shown in Figure 2.6. This ordination shows the differences in species composition between sites. In general, sites on the top half of the ordination space were in bottomland sites and wetter soils, as indicated by mesic species such as *Juncus effusus* and American sycamore (*Platanus occidentalis*). The bottom half of the space is occupied by upland sites that contained drier species, such as shortleaf pine (*Pinus echinata*), hickory (*Carya spp.*) and upland oak (*Quercus spp.*). For the

previous analyses, site hydrology was taken into consideration, labeling transects 3, 10, 12, 13 and 15 as mesic sites and the remainder as upland sites. However, mesic sites did not show evidence of a wider ecotone ($r=-0.03$, $p=0.9$), did not have significantly more total species at the ecotone ($r=-0.08$, $p=0.75$), nor did they have more ecotone-specific species ($r=-0.08$, $p=0.76$).

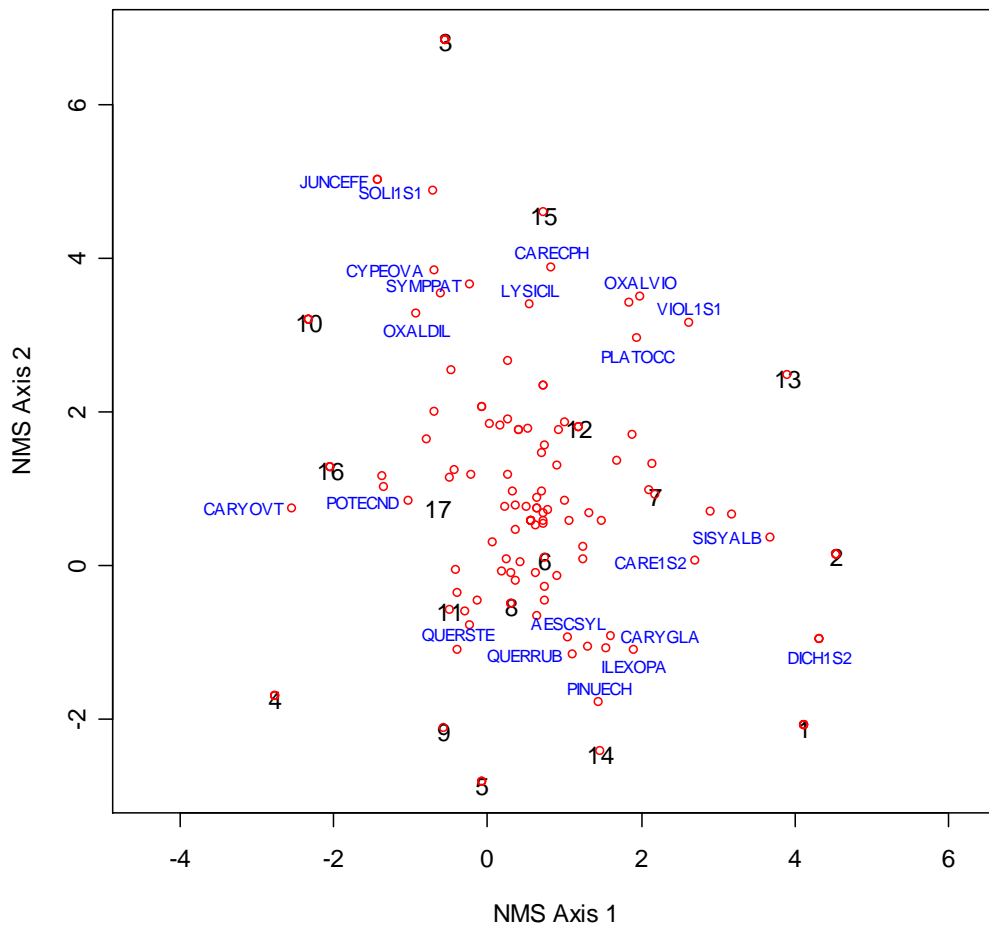


Figure 2.6: Nonmetric multidimensional scaling ordination of the 17 transects- Indicator species are labeled with acronyms consisting of the first four letters of the genus and the first three letters of the specific epithet

Discussion and Conclusions

Species richness was not consistently higher at these edges, although species per meter did appear to peak at the ecotone in most plots (Figure 2.5). This contradicts the results of studies that have specifically focused on the abundance of ecotonal species (Gysel 1951, Watkins *et al.* 2003, Burke and Nol 1998), though many studies have found a result similar to mine of overall intermediate species richness ((Harper 1995; Turton and Duff 1992). There are a few potential biotic explanations for my result. The first is that the field zone had species with small individual size with the consequence that more individuals, and therefore species, were able to pack into a single belt of a transect than in the forest or ecotone. The fields had high numbers of small ruderal species, which were adapted to the drier, sunnier conditions there. Species could also be poorly adapted to the edge conditions, as they are not stable nor do they represent optimal conditions for species adapted either to cooler forest condition or the sunnier field condition.

A visual interpretation of the species per 1x10 meter plots reveals that species richness does eventually decrease as one travels further into the field. Some of the fields had a surprisingly homogenous mixture of species once one was far enough from the edge.

Most of the species at the ecotone were not ecotone specialists, but, were also present on at least one side of the edge (Table 2.5). This suggests that additive blending is a stronger force contributing to species richness at these ecotones than ecotonal species. This does not, however, undermine the importance of ecotones as habitat for uncommon or rare species, as many botanically interesting species are present at these edges. In this study, I found that *Hypericum* species were particularly fond of these edge environments, and could be consistently found there in all of my transects.

Transect	Total # Species in the Ecotone	Species Unique to the Ecotone	Species found on at least one side of the ecotone	% Species that can be attributed to additive blending
1	43	3	40	93
2	57	1	56	98
3	47	2	45	96
4	58	4	54	93
5	39	4	35	90
6	54	5	49	91
7	57	5	52	91
8	29	2	27	93
9	50	16	34	68
10	26	1	25	96
11	38	3	35	92
12	66	8	58	88
13	50	6	44	88
14	38	4	34	89
15	35	2	33	94
16	41	5	36	88
17	51	1	50	98

Table 2.5: *Percentage of species in the ecotone that can be attributed to additive blending*

Ecotone properties such as age, sharpness nor aspect were not reliable predictors of whether species richness was higher at the ecotone. It was surprising that sharpness was not related to richness, as more edge habitat would suggest higher species numbers. It is possible that some of these relationships would prove significant with a larger sample size.

Exotic species did not significantly contribute to species richness at these edges. As the fields in the preserve are disturbed often, there is a large ruderal species pool, as well as a large number of field-adapted exotics. The forests were generally free of exotics except for *Microstegium viminium* and *Lonicera japonica*. *Celastrus orbiculata* often occurred at edges at higher abundance, but were not exclusive to them.

In this study of forest/field boundaries, I examined factors potentially influencing diversity, including ecotonal species and exotics, as well as age, sharpness and aspect of the edge. Further studies might look at other factors potentially contributing to diversity such as spatial mass effect, environmental heterogeneity and animal densities. The role of disturbance on ecotone properties is also poorly understood, and more empirical data will be necessary to tease out the relationship between types of disturbance, frequency of disturbance and species richness.

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