Plant community composition, species coexistence, and community assembly in the riparian zones of small streams in New York State

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Abstract of the Dissertation

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Many mechanisms may contribute to the diversity and composition of an ecological community. In riparian habitats, which are often described as both very diverse and very susceptible to biological invasions, flood disturbances may be a predominant structuring mechanism. In this dissertation I use several approaches to describe the mechanisms governing the diversity and composition of riparian plant communities along small streams. I performed a systematic literature review of the role of disturbances in facilitating plant invasions in general and in riparian plant communities in particular. General trends in the effects of disturbance on plant communities may be difficult to detect in part because of the breadth of events described by the term “disturbance”. In field studies, I found that riparian plant communities and nearby upland areas did not differ in diversity or species composition at a local scale, but riparian communities harbored more species regionally, suggesting that the riparian zones of small streams may serve as a reservoir of regional species richness. Variation in the composition of riparian plant communities of small streams throughout the Upper Hudson watershed (NY) was correlated with annual mean temperature, soil texture, and the abundance of wetlands in the surrounding landscape, and community composition was spatially autocorrelated. In greenhouse experiments, plant growth and survival under flooding conditions were found to vary among species and among and various types of flood effects, suggesting that while floods may exclude some regional species from the riparian zone, it is likely not the only mechanism controlling riparian community composition. Finally, I used information on plant traits to investigate how introduced species might establish and succeed in riparian communities. I found that introduced and native species differ substantially in many plant traits, suggesting that introduced species might be able to succeed in these communities and coexist with native species by virtue of their dissimilarity and the associated potential for reduced competition with natives. The research presented in this dissertation taken together provides a deeper understanding of the factors controlling the diversity and composition of riparian plant communities along small streams.

Dedication Page

To my parents, Richard and Susan, who first inspired my love of nature and botany.

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Chapter 1: Introduction

A major goal in the field of ecology is the characterization of mechanisms that govern the diversity and composition of communities. One such mechanism is disturbance, which has been hypothesized to affect not only diversity (Connell 1978) and species composition (Rao et al. 1990), but also biomass accumulation (Mou et al. 1993), primary production (Houser et al. 2005), nutrient dynamics (Vitousek 1985, Evans et al. 2008), and ecosystem energetics (Sprugel 1985). Additionally, disturbed habitats are also thought to be especially vulnerable to species invasion (Hobbs and Huenneke 1992, Burke and Grime 1996, Alpert et al. 2000, Lake and Leishman 2004).

Riparian plant communities provide an example of a system that experiences a range of disturbances through flooding, which may have strong effects on plant community composition and diversity. Riparian plant communities are often highly species-rich compared to surrounding upland areas (Gregory et al. 1991, Naiman et al. 1993, Naiman and Décamps 1997, Goebel et al. 2003). Riparian habitats are also widely considered to be more prone to invasion by introduced plants than upland areas (DeFerrari and Naiman 1994, Planty-Tabacchi et al. 1996, Stohlgren et al. 1998, Alpert et al. 2000, Tickner et al. 2001). The riparian zone is characterized by strong hydrologic processes caused by proximity to flowing water and consequent flood events (Junk et al. 1989, Naiman et al. 2005), which are likely to have a strong influence on the composition of plant communities in this habitat (Pollock et al. 1998, Bendix and Hupp 2000). Riparian plants are influenced by flowing water and floods in several ways. Roots are deprived of oxygen when floodwaters saturate the soil. Fast-flowing water may cause physical damage to plants, and may remove existing vegetation, providing an opportunity for new vegetation to establish. Floods may also deposit sediment in the riparian zone as the floodwaters recede. Sediment deposition may crush small seedlings. If larger plants are bent over by floodwaters, they can be buried under sediment, hindering their ability to photosynthesize. However, sediment deposition may also benefit riparian plants via the addition of nutrients to the soil. These consequences of flood disturbances, taken together, are likely to have a strong effect in structuring the diversity and composition of riparian plant communities. If so, riparian plant communities may differ in diversity and composition from nearby upland areas due to the influence of flooding.

However, the general relationship between disturbance and diversity is far from clear. While theory predicts that diversity peaks at intermediate levels of disturbance (Connell 1978), observed relationships between disturbance and diversity in ecological communities are variable (Mackey and Currie 2000, 2001, Kimbro and Grosholz 2006, Haddad et al. 2008, Miller et al. 2011, Fox 2013). General trends in nature may be elusive because ‘disturbance’ is an umbrella term encompassing a wide range of ecological and environmental phenomena, any of which may differ in consequences for different members of a community.

Consequently, the diversity of riparian plant communities may be best understood not by a broad attribution to flood disturbances, but by an integration of specific consequences of flood events on vegetation, and the consideration of additional factors that might contribute to diversity and species composition. Flood events have many simultaneous consequences, as described above, but also differ in characteristics (e.g., frequency, severity) among rivers. In particular, the riparian zones of small streams experience a very different hydrological environment than those of larger rivers. Plant communities along small streams may therefore differ from communities along large rivers, and patterns observed in the plant communities of large river floodplains may not hold for riparian plant communities along streams. Small streams may also be considered of particular ecological importance as they comprise the majority of any given river network (i.e., there are many more small streams than large rivers). Therefore, they may play a disproportionate role in the structuring of the regional composition of plant communities, through both the connectivity they provide across the landscape (Décamps 2011) and the sum total of land area that they comprise.

The diversity and composition of communities can be described not only in terms of species richness and species identity, but by the types and range breadth of the traits of species within communities. Trait-based approaches are increasingly useful in many subdisciplines of ecology, and the particular plant characteristics of interest are likely to differ among these subdisciplines. One valuable classification is the concept of “response” and “effect” traits by Lavorel and Garnier (2002). Effect traits are of primary interest in ecosystem ecology, referring to characteristics of organisms thought to affect ecosystem processes. Response traits are those that are likely to affect an organism’s response to environmental conditions, including abiotic conditions or disturbances. Identification of trait syndromes and characterization of the trait composition of plant communities can be used to help understand how communities respond to their environment (McGill et al. 2006, Haddad et al. 2008). Differences in relative trait abundance between habitat types, such as between riparian and upland plant communities, may suggest how (or if) the mechanisms that govern species co-existence in those habitats differ.

The goal of this dissertation is to identify the factors that influence the diversity and composition of riparian plant communities of small streams. In this work, I focused on the riparian zones of small streams in the Upper Hudson Watershed (New York). I addressed the composition of riparian zones across multiple spatial scales by using multiple lines of evidence (greenhouse experiments comparing responses of upslope and riparian species, surveys of local community composition, and surveys of regional species turnover). Working across scales provides a broader perspective of the factors that may influence community composition. For instance, hydrology might drive differences between riparian and upland plant communities at a local scale, while riparian plant communities may differ regionally due to broader environmental characteristics. Greenhouse experiments were used to test for differences in responses of confamilial pairs of upslope and riparian plant species to riparian conditions (i.e., specific consequences of flooding), to identify conditions that might benefit some species or act as mechanisms to exclude other species. Local-scale field surveys were used to compare the composition of riparian and upslope plant communities, to understand the characteristics that distinguish riparian plant communities when compared to nearby upslope plant communities, which share similar overall climatic environments except for the influence of the stream itself (i.e., flooding). I used information about species richness, abundance of introduced species, and trait diversity to make inferences about the mechanisms governing assembly of riparian communities of small streams. I also carried out a systematic literature review of studies of disturbance in riparian plant communities to identify which specific types of disturbances are most and least often studied. The goal of this systematic review was to identify potential gaps in the literature on disturbances in riparian communities.

I asked the following specific questions:

1) What types of disturbances are studied most often in relation to biological invasions and riparian plant communities? How can specific types of disturbances be usefully categorized to better understand where there might be gaps in our knowledge of disturbance in these systems? (Chapter 2)
2) Is species richness higher in riparian plant communities of small streams than in nearby upland communities? Do riparian and upland communities differ in

species composition? Do riparian plant communities contain more introduced species than upland areas? Do riparian and upland plant communities differ in their trait diversity or trait composition, when considering traits likely to affect plant responses to resource availability, responses to environmental conditions, and ability to persist through or re-establish after disturbances? (Chapter 3)

3) What variation exists at regional scales in the riparian plant communities of small streams, and what environmental factors contribute to the diversity and composition of these communities? (Chapter 4)
4) Do different species of plants respond differently to different aspects of a flood event (i.e., submergence, burial under sediment, and nutrient addition)? Do plant species characteristic of riparian and upland areas differ in their responses to these events? (Chapter 5)
5) Can information about the plant traits considered in Chapter 3 inform our understanding of how introduced species succeed in riparian zones? (Chapter 6)

These questions examine riparian plant communities at several scales, from individual species to local and regional spatial scales. Because communities are likely to be influenced by different factors at different spatial scales, integrating information about plant communities across these scales may contribute to a more general understanding of the mechanisms that contribute to plant community diversity, composition, and biological invasions in riparian zones. In particular, this dissertation examines these factors in the riparian zones of small streams, which have to date been understudied in comparison to the floodplains of large rivers. Taken together, the chapters in this dissertation provide a better understanding of the composition of riparian plant communities along small streams, the factors that might govern their diversity and composition at both local and regional scales, and a potential mechanism for the success of introduced species establishing in these communities. More broadly, this dissertation offers insight into the ecology of plant communities and potential mechanisms governing their assembly and diversity.

Chapter 2: A review of disturbance concepts and their applications in species introductions and riparian plant communities

Introduction

Disturbances have long been considered important in determining patterns in vegetation distribution (White and Jentsch 2001). The disturbance regime is thought to be one important contributor to the determination of community composition (White 1979). Several classic hypotheses regarding the diversity of biological communities incorporate disturbance (e.g., the intermediate disturbance hypothesis (IDH), Connell 1978; the dynamic equilibrium concept, Huston 1979). The relationship between disturbance and diversity in particular has produced a great deal of theory and empirical research. For instance, while IDH predicts that diversity will be maximized at intermediate disturbance levels, varying relationships between disturbance and diversity have been observed empirically (Mackey and Currie 2000, 2001, Shea et al. 2004, Miller et al. 2011). One review of empirical studies of the diversity-disturbance relationship found that 46% of terrestrial studies conformed to IDH, while 23% were inconclusive and 17% showed relationships other than that predicted by IDH (Kershaw and Mallik 2013). A number of mediating factors may contribute to variation in the diversity-disturbance relationship. Disturbance regimes can be characterized by their magnitude, frequency, intensity, and duration (Shea et al. 2004). These characteristics of a disturbance can interact to produce different diversity-disturbance relationships (Miller et al. 2011, Hall et al. 2012). Diversity-disturbance relationships may also vary with resource availability (Laliberté et al. 2013). Tradeoffs between r- and K- selection are another influential factor. A mechanistic model by Bohn et al. (2014) showed that under intense selection for r-strategists (colonizer species with a high seed production and fast growth rate), diversity declined with increasing disturbance, while in scenarios selecting for K-strategists (strong competitors with large biomass), diversity increases as disturbance increases. Different species or functional groups may also differ in their response to disturbance (Seifan et al. 2013). Across an experimental fire frequency gradient, tree species richness was shown to be highest in unburned locations, while forb richness was maximized under biennial fire regimes, and richness of annual plants was highest in areas experiencing near-annual fires (Peterson and Reich 2008). Without considering these additional factors, it may be difficult to make adequate comparisons of the role of disturbance among systems or for different types of disturbance.

In addition to the many factors that mediate the diversity-disturbance relationship in communities, variation in how studies measure or define diversity may contribute to the breadth of relationships observed in empirical studies. For example, simulations of disturbance (modeled as a chance of removal at each time step of the simulation) support IDH when used to model species richness, but predict a continual increase of species evenness with increasing disturbance rather than the classic hump-shaped relationship (Svensson et al. 2012). Species richness, evenness, Shannon index, and other diversity indices may each have different relationships with disturbance. Svensson et al. (2012) argue that studies evaluating the diversity-disturbance relationship need to present *a priori* logical hypotheses (i.e., predicted mechanisms) regarding the relationship between disturbance and a specific measure of diversity.

Much as there are many possible descriptors of diversity, there are many concepts of disturbance, and no single operational definition of the term disturbance exists that is used consistently throughout the ecological literature. The term disturbance has been applied across many ecological contexts, often inconsistently or ambiguously (Rykiel 1985). For ecological theories of the impacts or importance of disturbance in natural communities, ambiguity in the operational definition of this term can result in inconsistency simply due to the same terminology being applied to different phenomena (Regan et al. 2002, Hodges 2008). More broadly, a synthesis of current understanding of disturbance may similarly benefit from increased clarification of operational definitions and the inclusion of *a priori* predicted mechanisms and responses in disturbance studies.

There have been few literature reviews categorizing how studies have approached the concept of disturbance and its effects, in part because of the breadth of use of the term (White and Jentsch 2001). Many different definitions for disturbance in ecological communities have already been put forth (e.g., Grime 1977, Paine and Levin 1981, Pickett and White 1985, Menge and Sutherland 1987, Pickett et al. 1989, Reynolds et al. 1993, Mackey and Currie 2000, Shea et al. 2004). The term disturbance is probably so broadly defined as to be effectively meaningless in the absence of more specific characterization. The best path to make progress in understanding disturbances in communities, then, is not to create a novel, singular definition, but to begin to conceptualize questions past research has addressed regarding the effects of disturbances and develop a framework into which disturbances might be categorized.

The goal of this chapter was to summarize existing definitions of disturbance, and then develop a framework to categorize the way that previous research has conceptualized disturbance. This framework includes three major dimensions differentiating disturbance studies: 1) a focus on causal agents versus on effects; 2) a focus on abiotic versus biotic factors; and 3) temporal duration of the disturbance. I then used two systematic reviews of literature on disturbance in plant communities to demonstrate the use of this framework and to examine how studies in particular subsets of plant ecology have looked at disturbance in the context of this framework. The first systematic review examined the body of literature investigating the role of disturbances in facilitating biological invasions for plants and invertebrate animals. The second review focused on the role of disturbances in structuring riparian plant communities. The goal of these systematic reviews was to identify areas of ecology that deal with the effects and importance of disturbance that have been well-studied within plant ecology, and areas that would benefit from additional focus in future.

Existing definitions of disturbance

It is not possible to construct a single definition of disturbance that is both unambiguous and that applies in every context in which ecologists use the term. Disturbance definitions vary in whether they emphasize a causal agent or an effect, and what in particular qualifies as a cause or as an effect of disturbance. For biological communities, both Grime (1974) and Paine and Levin (1981) define disturbances in terms of specific effects on a system. Grime considered disturbance as the partial or total destruction of biomass, and Paine and Levin (referring to mussels) considered it to be measurable effects on the rate and size of patches created in a patchy environment where space is a limiting resource. Other definitions emphasize nutrient availability as the limiting resource, wherein disturbances alter nutrient availability in the system of interest (Mackey and Currie 2000; Shea et al. 2004).

In contrast, other concepts of disturbance focus on various causal agents rather than the responses of organisms within communities. For example, Menge and Sutherland (1987) considered disturbance agents as being either physical, physiological, biological, or predatory/grazing. This description contains both biotic and abiotic agents as potential disturbances. According to Menge and Sutherland’s definition, physical disturbance is produced by a mechanical force, such as the movement of air, water (snow, rain), and soil or sediment. Physiological disturbances might include factors such as temperature and salinity and drought or flooding, although these could be also be considered stress, defined by Grime (1977) as conditions that restrict production. Menge and Sutherland define biological disturbances as those caused by the activity of other organisms, such as trampling, burrowing, or digging.

Definitions of disturbance may also be defined by the temporal duration with which they impact communities. Some definitions emphasize that disturbances are discrete events (Sousa 1984, Pickett and White 1985) or abrupt changes (Reynolds et al. 1993). However, not all definitions of disturbance in the literature specify a discrete event or effect. Many self-identified disturbance studies focus on permanent alterations to the environment, such as considering urban or agricultural areas to be generally ‘disturbed’ compared to rural forested areas (see the systematic reviews below).

A proposed framework for classifying disturbance studies

I identified three major dimensions that differentiate many different definitions of disturbance used by ecologists such as those described above. These dimensions can be used to categorize studies of disturbance and identify operational definitions (Table 2-1). First, a disturbance may be conceptualized either as a causal agent or as an effect. Second, a disturbance may be either biotic or abiotic. Third, disturbances can vary in temporal scale, from discrete events to permanent shifts in the environment. Below, I describe a systematic literature review in which I categorized studies within this framework.

Systematic review methods

Disturbances are thought to play an important role both in biological invasions and in riparian ecology, highlighting a need to examine the literature on disturbances in these systems and identify potential gaps in our understanding. The probability of an introduced species’ success in a novel habitat has been attributed to levels of disturbance in the recipient community (e.g., Elton 1958, Hobbs and Huenneke 1992). Introduced species are also thought to be especially common in riparian zones, with disturbance (often flooding) again being a potential driver (Hood and Naiman 2000, Richardson et al. 2007). Because disturbances are commonly studied in these contexts, these bodies of literature provide valuable examples for reviewing the breadth of operational definitions of disturbance within these contexts and for the use of the three-dimensional disturbance framework described above.

Two systematic reviews were used. The first included a subset of the literature from a previous systematic review of biological invasions (Lowry et al. 2013), and included studies that examined the effects of disturbance on the success of introduced plant species. I categorized these studies within my conceptual framework of disturbances. I then performed a second systematic review to identify published studies describing the effects of disturbance on the success of introduced species within riparian zones in particular.

The role of disturbance in plant invasions

Papers addressing the role of disturbances in the success of introduced species were drawn from a database of the literature on non-native, introduced and invasive species of plants and invertebrate animals (Lowry et al. 2013). This database was constructed based on a search of the ISI Web of Science core collection between January 1, 1900 and September 29, 2011, using the following search string:

> TOPIC = (INVASI* OR INVADER OR ALIEN OR EXOTIC OR RUDERAL OR WEED OR NON-NATIVE OR INTRODUCED OR NATURALIZ*) AND TOPIC = (PLANT OR INVERTEBRATE OR ECOLOG* OR EVOLUT* OR MARINE OR TERRESTRIAL OR FRESHWATER OR AQUATIC) NOT TOPIC = (CANCER* OR CARDIO* OR SURG* OR

CARCIN* OR ENGINEER* OR OPERATION OR MEDIC* OR CROP OR ROTATION OR OVAR* OR POLYNOM* OR PURIF* OR RESPIRAT* OR "INVASIVE TECHNIQUE").

This search was then restricted using the Web of Science "refine" function to exclude journals from non-relevant fields (e.g., medical, engineering), and further restricted by manually screening abstracts and articles for relevance. Lowry et al. (2013) classified all papers in the database according to which hypothesis for the success of introduced species the authors were testing (e.g., the enemy release hypothesis, fluctuating resources, or environmental disturbance). Here, I included the papers on plants classified as testing a disturbance hypothesis. Figure 2-1 outlines the paper selection process from the initial search to the final set of papers included.

Plant introductions in riparian zones

The hypothesis that disturbances facilitate biological invasions is a natural fit for the riparian zone. Riparian zones are often thought to be highly invaded (DeFerrari and Naiman 1994, Planty-Tabacchi et al. 1996, Stohlgren et al. 1998, Alpert et al. 2000, Tickner et al. 2001), potentially due to frequent flood disturbances. Therefore, I conducted a second literature review, not derived from the Lowry et al. (2013) review, to examine studies examining factors contributing to the success of introduced plant species in riparian zones.

I searched the ISI Web of Science core collection for papers published between January 1, 1900 and February 3, 2015, using the following search string:

TOPIC = (INVA* OR EXOTIC OR INTRODUCED OR NON-NATIVE) AND TOPIC = (RIPARIAN OR FLOODPLAIN) AND TOPIC = (PLANT) AND TOPIC = (FLUVIAL OR HYDROGEOMORPH* OR FLOOD* OR HYDROCHOR* OR DISPERSAL OR LINEAR OR DISTURBANCE) AND TOPIC = (RIVER OR STREAM).

This search returned 434 papers, the titles and abstracts of which were then screened for relevance to the current review. Papers were included in the review if they examined the role of a disturbance or disturbances (as identified by the authors) in the establishment or distribution of an introduced species in the riparian zone. Figure 2-2 outlines the process of paper selection from the initial search results to the final set of papers included in the review.

Results

The role of disturbance in plant invasions

In the database of the biological invasions literature provided by Lowry et al. (2013), I identified 303 papers that addressed some disturbance-based hypotheses for determining the success of introduced plant species. The majority of these papers (n = 231) used plants as a study system, which were then used for this review (Figure 2-1, Appendix A). Field observation studies were the most common type of research (58%), followed by field experimental studies (30%). Relatively few theoretical, modeling, or non-field experimental papers examined the hypothesis that disturbance facilitates plant invasions.

Almost half (46%) of the studies focused on a single introduced species, while some (12%) addressed from 2 to 10 species, and the remaining 42% of papers asked community-level questions regarding species introductions (Figure 2-3). The vast majority of studies examining the effects of disturbance on plant invasions were performed in terrestrial systems (93%), with few studies focusing on wetlands, estuaries, marine, lotic or lentic systems. This paucity may in part result from the search terms used in the systematic review, which may have excluded topics such as marine algal invasions, although it is likely that the majority of studies of plant invasions are performed in terrestrial systems.

Approximately 28% of the studies addressed multiple potential disturbance agents simultaneously, or quantified their results both in terms of disturbance agents and disturbance effects. Of these, over two-thirds (69%) identified an abiotic disturbance agent, evenly split between anthropogenic agents (e.g., proximity to roadsides or the construction of trails) and non-anthropogenic agents (e.g., hurricanes). The remaining studies framed their discussion of disturbance primarily in terms of biotic causal agents (15%), biotic effects (9%), or abiotic effects (6%) (Figure 2-4). The most commonly studied topics were current anthropogenic influences (35%), fire (16%), disruption of the soil or substrate (11%), and removal of vegetation (10%). Overall, the vast majority of the studies examined a causal agent of disturbance, while only 10% defined disturbance as an effect such as removal of biomass (Figure 2-4).

Studies were also classified in terms of whether the disturbances they examine represented discrete (and potentially recurring) events, historical events from which a system is now in recovery, or a permanent or semi-permanent shift in the environment. Fires and floods were considered discrete events, changes in vegetation on abandoned agricultural land was considered a historical event, and alteration to a river’s flow regime through the construction of a dam a permanent shift. An almost equal number of studies addressed either permanent shifts or discrete disturbance events (47% each), and very few papers described recovery from a historical event as a disturbance (Figure 2-5).

Plant introductions in riparian zones

Of the 434 papers identified in the initial literature search, 156 were determined to be relevant and included in this review. Criteria for inclusion and exclusion are given in Figure 2-2. These papers are listed in Appendix B. In contrast to the systematic review including all plant systems, for riparian zones there was a near-equal number of field experimental and field observational studies (both 47%), and again relatively few greenhouse, garden, laboratory or modeling studies. While hydrological factors were by far the most common disturbance agent studied in this context, other disturbances were also included. Some studies examined more general anthropogenic impacts in the riparian zone, agricultural encroachment, or the effects of fire on riparian vegetation (Figure 2-7). Discrete events and permanent shifts were similarly abundant in the literature (52% and 46%, respectively), while relatively few studies focused on reversal of a historical shift in the environment, such as abandonment of agriculture (2%; Figure 2-8).

Discussion

This chapter represents an effort to systematically describe and categorize the studies that have been published to date regarding disturbances in two areas for which disturbance is potentially of particular ecological importance: biological invasions and riparian plant communities. Disturbance and biological invasions, as well as the interplay of these two, have received a great deal of attention for many decades. Many definitions of disturbance have been proposed, as have many hypotheses of factors responsible for invasion success. The way we conceptualize disturbance affects our thinking about the role of disturbance in ecological systems, and the concept of disturbance used in a given study may have important implications for the inferences that can be made from that study.

I found that most studies examining the role of disturbance in the success of introduced species examined abiotic agents of disturbance, whether anthropogenic in nature (e.g., increased density of developed areas in the landscape) or non-anthropogenic (e.g., natural fires or floods). Many of the anthropogenic studies compared “disturbed” areas, meaning those that have experienced general human development and anthropogenic influences, to areas relatively unaffected by humans. Comparisons addressing a broad disturbed versus undisturbed dichotomy may provide different inferences regarding the effect of disturbance than studies that examine a specific or discrete disturbance event. The non-anthropogenic agents of disturbance largely fell into the category of discrete disturbance events, best fitting the definition of disturbance outlined by Pickett and White (1985), which describes a disturbance as any discrete event that causes some disruption to the community, ecosystem or population. Relatively few studies defined disturbance as an effect (e.g., the definitions of Grime (1977) or Paine and Levin (1971)). Studies that define disturbance as an effect ask fundamentally different questions of biological invasions than do studies defining a disturbance as some sort of causal agent. For example, a study defining a disturbance as a flood event (a causal agent) may seek to determine the degree to which biomass was removed by that flood, whereas under Grime's definition, the removal of biomass itself is the disturbance (an effect).

While floods or particular aspects of flooding were by far the most commonly studied disturbances regarding biological invasions in the riparian zone, some studies did look at other effects, such as fire or forest management. Most studies addressed either the effects of natural flood events or on the effects of an altered flow regime (e.g., following damming of a river) in either facilitating or hindering the success of introduced species. Natural flood events and anthropogenically altered flow regime are fundamentally different types of disturbance. A natural flood is a discrete event, while alteration of the flow regime permanently shifts the nature of the habitat. Additionally, a community may be adapted to a particular flow regime, such that its composition already reflects the natural pattern of flooding, while alteration to that flow regime might produce distinct changes in community composition or facilitate the establishment of introduced species (Aguiar et al. 2001, Stromberg et al. 2007, Beauchamp and Stromberg

2008, Catford et al. 2011). Both natural flooding and changes to the natural flow regime might be considered disturbances, but they differ in temporal scale and may have different effects. Studies examining specific aspects of a flood event were less common in this study; these largely defined disturbance in terms of a particular effect (clearing of vegetation, alteration of channel morphology, sediment deposition, or nutrient addition). In the future, additional studies focused on specific aspects of flood events may contribute to a more mechanistic understanding of the role of disturbances in riparian invasions.

Future synthesis and generalization about the role of disturbance in ecology may benefit from additional attention to mechanistic details of disturbance, such as those that have been identified in studies of the relationship between disturbance and diversity. This relationship can depend on the magnitude, frequency, and intensity of a disturbance (Shea et al. 2004, Miller et al. 2011, Hall et al. 2012), resource availability (Laliberté et al. 2013), and types of selection pressure facing plants in a community (Bohn et al. 2014). Different species or functional groups may also differ in their responses to disturbance (Peterson and Reich 2008, Seifan et al. 2013). Just as all of these factors mediate the relationship between disturbance and diversity, they may also affect observed relationships between disturbance and biological invasions and other ecological phenomena. In the systematic review of biological invasions, many studies focused on comparing broadly “disturbed” and “undisturbed” areas, without pinpointing specific agents beyond human development and other anthropogenic influences on the environment. Studies such as these can provide broad-scale inferences about where invaders might succeed, but studies of more specific disturbances may be more informative about mechanisms of invasion. Similarly, while many studies in the systematic review of invasions in riparian zone focused on floods, relatively few of those address specific aspects of flooding (e.g., submergence, burial under sediment, or increased nutrient availability). Additional studies in future that examine these more specific causal agents may contribute to a detailed mechanistic understanding of the role these disturbances play in facilitating invasions in the riparian zone.

This review points to a need for more specificity in studies that examine the effects of various types of disturbance for facilitating biological invasions in plant communities. Many disparate types of events have been classified under the umbrella term “disturbance”, and it is unlikely that a consensus on the effects of disturbance will be reached when the term is used so broadly. The framework presented in this chapter provides a set of dimensions in which to categorize disturbances that is complementary to distinguishing disturbances by their magnitude, frequency, or intensity. In the future, an extension of this framework that also incorporates those factors may be useful in synthesizing the outcomes of disturbance studies and provide a more detailed, mechanistic understanding of the role of disturbance in biological invasions.

Tables

Table 2-1 A framework for categorizing studies of disturbance in ecological systems considering three dimensions: 1) Focus on causal agents versus on effects; 2) Focus on abiotic versus biotic factors; and 3) Temporal scale of the disturbance. Specific disturbances described in the studies included in the systematic review were summarized within this framework. Anthropogenic influences are indicated by †. Empty boxes indicate that no studies were found that fell into that category.

	Causal Agent		**Effect/Response**	
Temporal scale	**Abiotic**	**Biotic**	**Abiotic**	**Biotic**
Discrete event (days)	• Flood – inundation • Flood – scouring • Flood – sediment deposition • Flood – nutrient addition • Fire • Wind • Wave	• Browsing or grazing (beaver, deer, cattle†) • Tree fall	• Flood – nutrient addition • Physical disruption of soil or substrate	• Vegetation removal (including logging† or clearcutting†)
Medium-term (months)	• Drought	• Browsing or grazing (beaver, deer, cattle†)		
Long-term (> 1 year)	• Damming of river† • Urbanization† • Agriculture† • Change in fire regime • Altered climate	• Browsing or grazing (beaver, deer, cattle†)	• Change in hydrologic regime	
Long term (consequences of removal of disturbance agent)	• Dam removal † • Abandonment of agricultural fields		• Restoration of natural hydrologic regime	• Cessation of vegetation removal (e.g. logging†, clearcutting†)

Figures

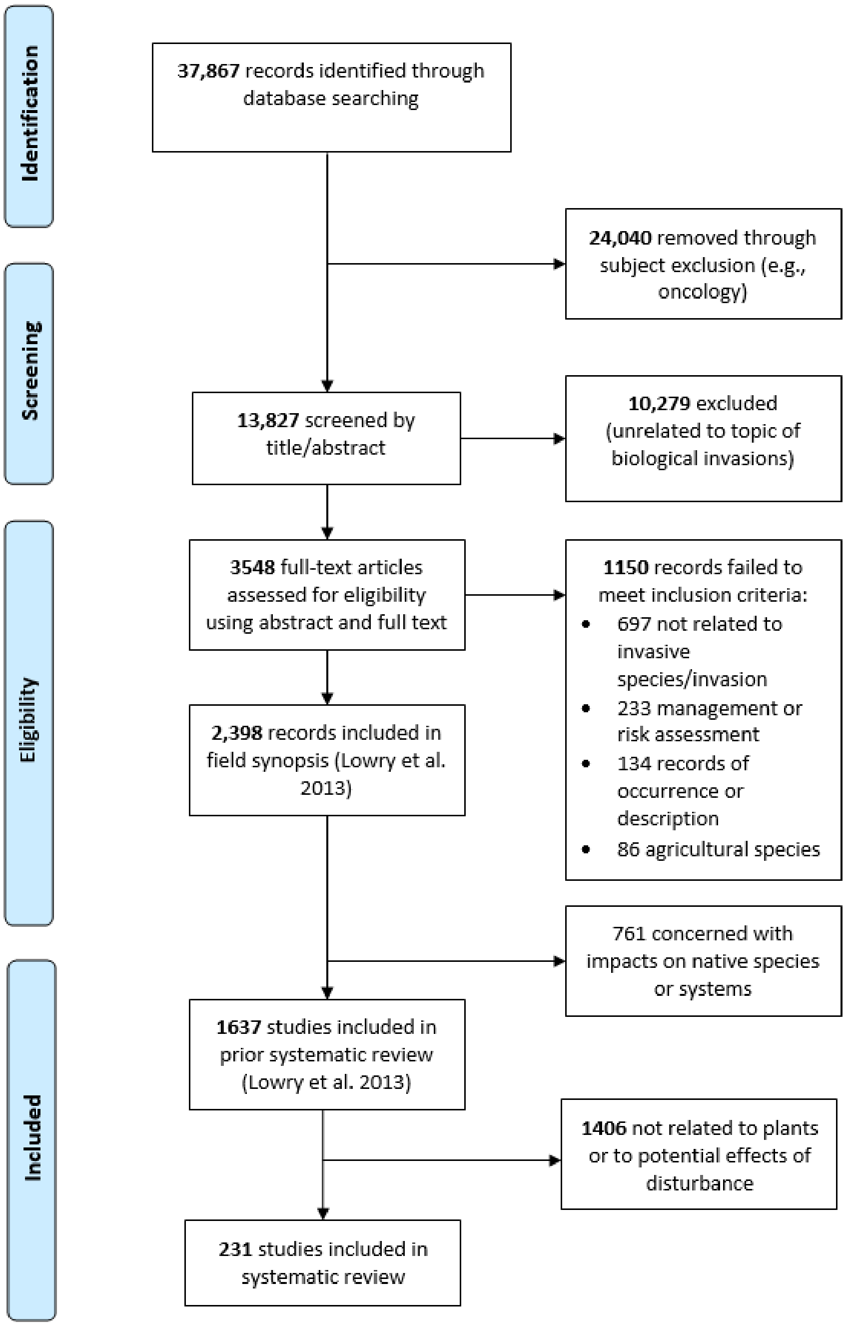


Figure 2-1 Flow chart detailing the process of literature collection, record review, and elimination for the original Lowry et al. (2013) systematic review, and additional screening of papers for the systematic review of disturbance in biological invasions presented here.

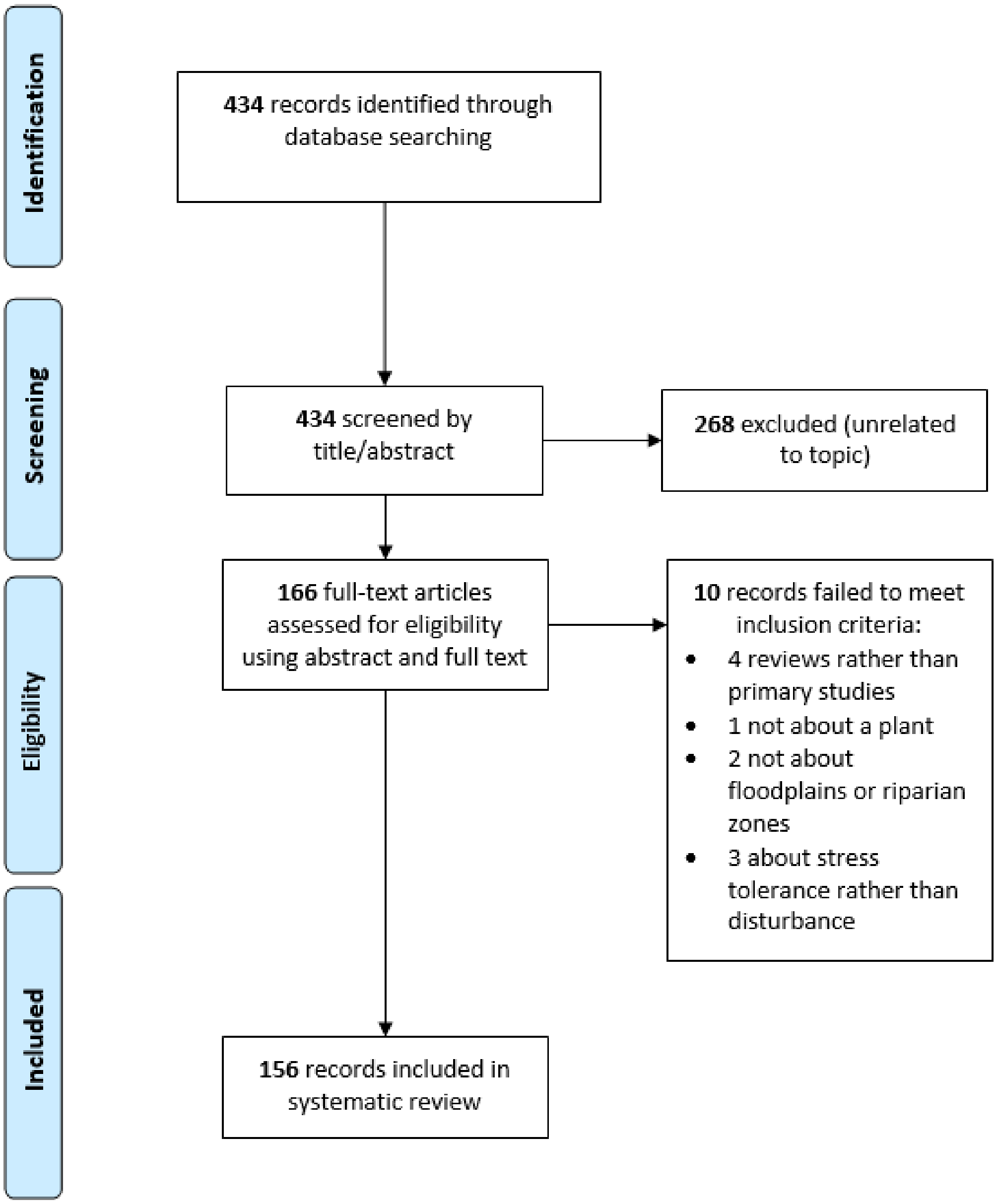


Figure 2-2 Flow chart detailing the process of literature collection, review, screening, and elimination of papers for the systematic review of introduced species in riparian zones.

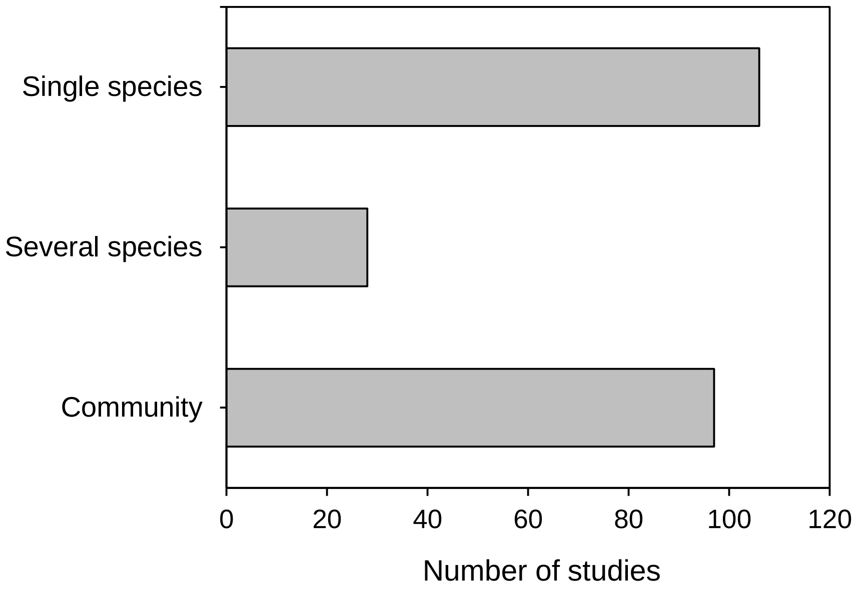


Figure 2-3 The principal level of focus of each study in the systematic review of disturbance in biological invasions.

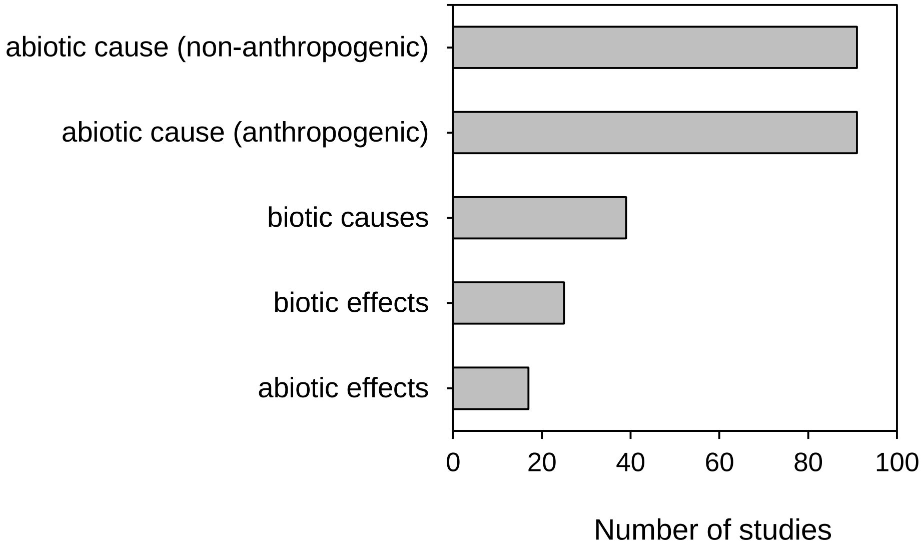


Figure 2-4 Number of studies in the systematic review of disturbance in biological invasions that address each of these broad types of disturbance.

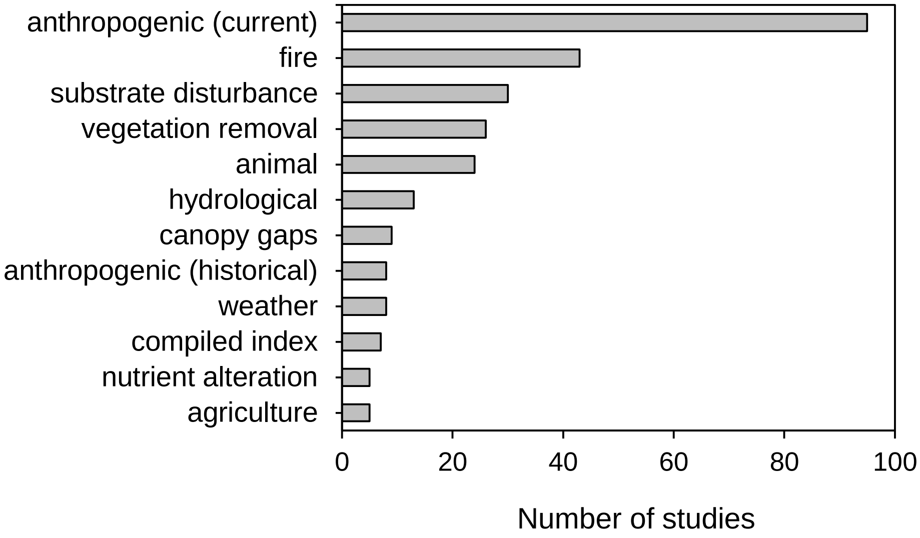


Figure 2-5 Number of studies in the systematic review of disturbance in biological invasions addressing each of these specific disturbances. “Compiled index” refers to studies that used a general index of disturbance incorporating many different factors to describe the relative disturbance of different areas, rather a single disturbance agent.

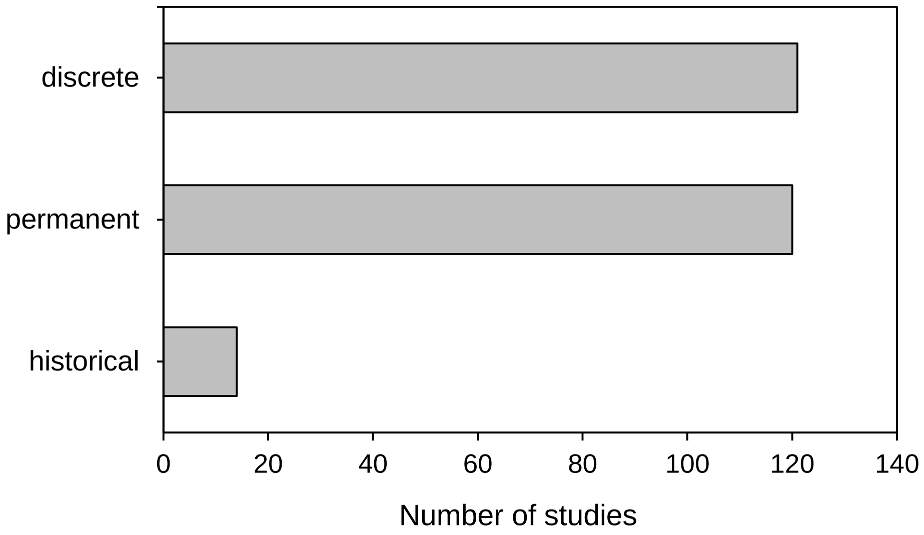


Figure 2-6 Number of studies in the systematic review of disturbance in biological invasions that focus on discrete events, permanent shifts in a system, or reversals of a historical shift.

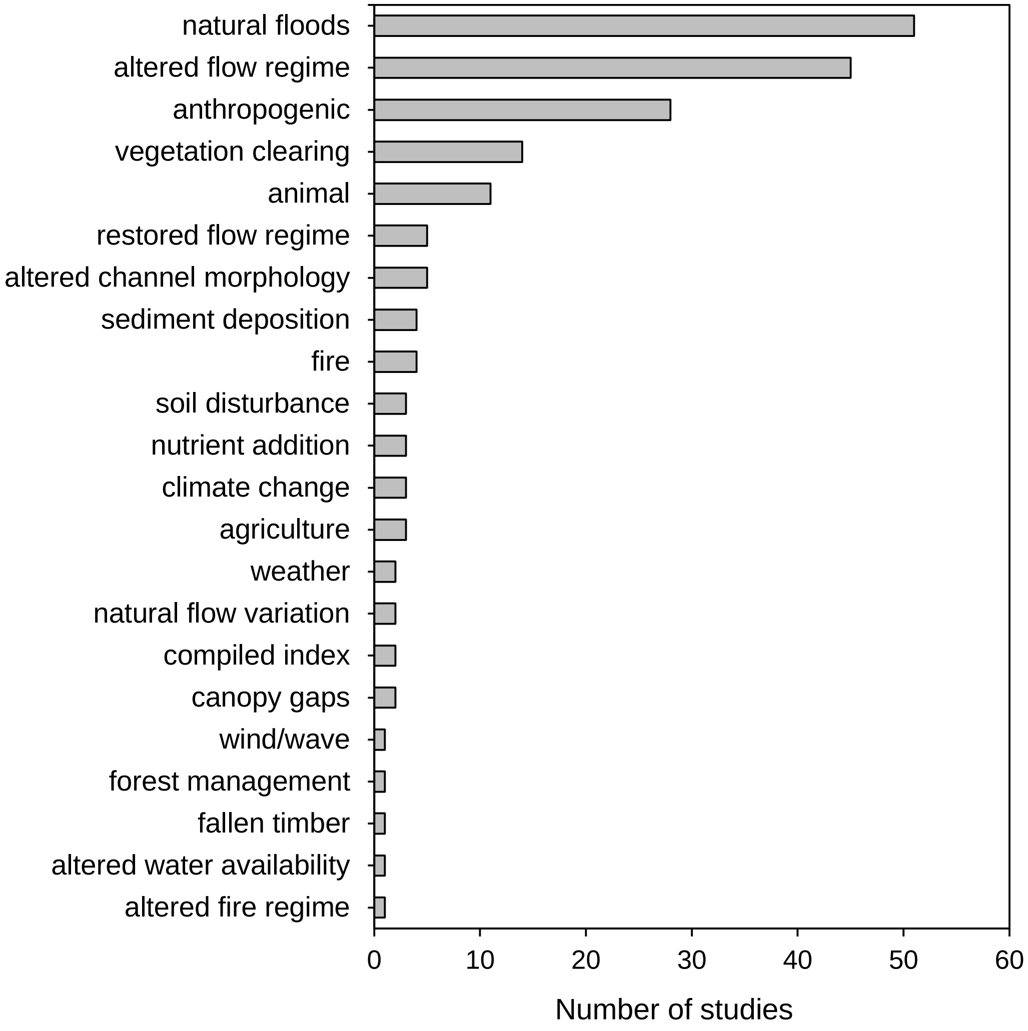


Figure 2-7 Number of studies in the systematic review of riparian zones that addressed each of the disturbance agents listed.

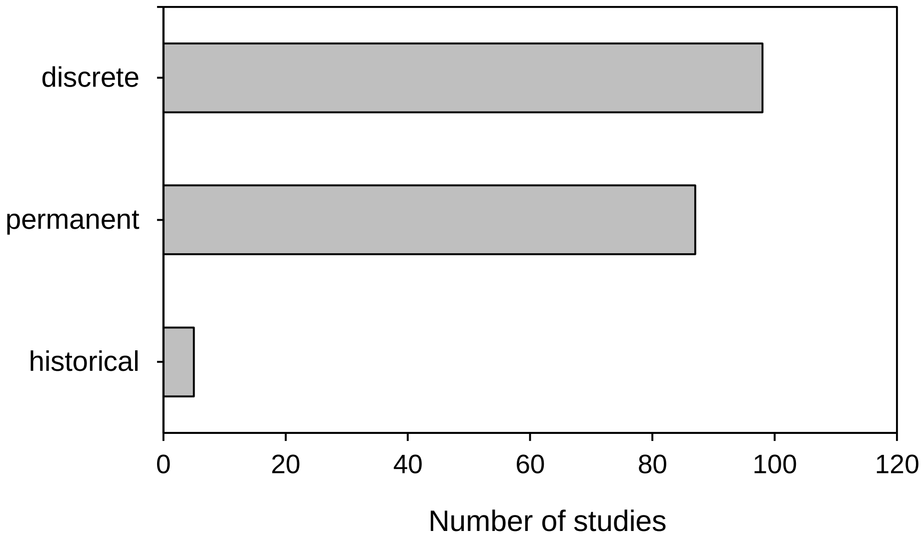


Figure 2-8 The number of studies in the systematic review of introduced species in riparian zones that could be classified as studying a discrete event, a permanent shift in the environment, or recovery from a historical effect on the environment.

Chapter 3: Small stream riparian zones as a reservoir of regional plant species richness

Introduction

Riparian zones, defined as “areas along streams and rivers that are periodically inundated by flowing water” (Naiman et al. 2005), have been shown to support plant communities that are more diverse than those found in nearby upland habitats (Salo et al. 1986, Nilsson et al. 1989, Gregory et al. 1991, Naiman et al. 1993, Naiman and Décamps 1997, Brown and Peet 2003, Goebel et al. 2003, Biswas and Mallik 2010). While riparian plant communities may share some characteristics with communities in the surrounding landscape due to regional environmental conditions and a shared regional species pool, they may also differ due to the influence of the adjacent stream or river. Factors such as soil moisture, nutrient availability, topography, and the intensity of flood disturbances vary over small spatial scales in the riparian zone (Salo et al. 1986, Naiman et al. 1993, Naiman and Décamps 1997), while the surrounding upland landscape is likely to be more environmentally consistent at similar spatial scales. Species richness has been shown to be positively correlated with the occurrence, frequency, intensity and duration of floods (Brown and Peet 2003, Jansson et al. 2005, Violle et al. 2010), and disturbance through flooding may maintain high levels of diversity in riparian zones by interrupting natural successional patterns (Connell 1978, Peet 1992).

In addition, riparian zones typically contain more introduced species than associated uplands (DeFerrari and Naiman 1994, Planty-Tabacchi et al. 1996, Stohlgren et al. 1998, Alpert et al. 2000, Tickner et al. 2001). Stream channels may facilitate rapid spread of introduced species across the landscape (Thébaud and Debussche 1991, Pyšek and Prach 1993, 1994, Edwards et al. 1994, Hood and Naiman 2000), and flood disturbances may create opportunities for novel species to establish (Kalliola and Puhakka 1988, Tickner et al. 2001). The relative strength of hydrologic processes, regional environmental characteristics, and the regional species pool in determining the composition of plant communities may determine patterns at the local and regional scale. If hydrologic processes are a stronger influence on species composition than the regional environment and species pool, there might be more differences in species composition between adjacent riparian and upland areas than among various riparian areas across a region. However, the riparian zones of small streams have a relative lack of hydrologic connectivity through regular flood pulsing as compared to the floodplains of large rivers. Consequently, the regional environment and regional species pool may have a greater influence than hydrology on the composition of riparian zones along small streams. In this case, species composition of these riparian zones may be similar to that of adjacent uplands because of shared environmental conditions.

There is some evidence that the high biodiversity of riparian zones may not be a general rule or global pattern (Sabo et al. 2005, Sabo and Soykan 2006, Stromberg 2007). To date, studies demonstrating high riparian biodiversity relative to uplands have primarily considered the riparian zones of large rivers; only limited information is available for the riparian zones of smaller streams (Richardson and Danehy 2007). Small streams differ in important ways from larger rivers, and the community structure of their riparian zones may reflect these differences. The small size of the riparian zone of a small stream leads to an overhanging tree canopy in forested areas, and the effects of this shading may have a strong influence on community composition. Small stream channels are also often less predictable in the timing of their flood events (Junk et al. 1989), which may prevent the development of a characteristic assemblage of plants suited to the riparian environment (Daleo et al. 2009). If disturbance events prevent resources from becoming limiting, species with greatly overlapping niches will be able to coexist, and a pattern of community composition reflecting competitive exclusion and limiting similarity will not establish in that community. Instead, species present in these communities at any given point in time may primarily reflect colonization processes and early environmental filters (e.g., Katabuchi et al. 2011) or tradeoffs for species that are successful colonizers versus those that are successful competitors (Bohn et al. 2014).

Recently, many ecologists have advocated the use of plant trait information to approach questions about species co-existence and community assembly to make inferences about the mechanisms governing community composition (Shipley et al. 2006, McGill et al. 2006, Ackerly and Cornwell 2007, Violle et al. 2007, Messier et al. 2010). Contrasting the trait diversity and composition of different communities may provide another dimension by which to assess biodiversity overall. Plant traits vary among the species within a community, as well as across environmental gradients (Kleyer 1999, Pausas et al. 2003, Violle et al. 2010). Plant traits are often usefully described as either response traits (those which mediate their response to environmental conditions) or effect traits (those which determine their effect on ecosystem properties) (Lavorel and Garnier 2002, Suding et al. 2008), although not all plant characteristics must fall into one of these two categories. Variation in response traits within a community is an additional way to describe the diversity of that community, just as species richness describes an aspect of diversity. Species may need a certain suite of response traits to succeed in particular environmental conditions, and species with similar traits may be in strong competition for similar niche space. A trait-based approach to describing the composition of communities may facilitate inferences about the mechanisms determining the diversity and composition of plant communities.

To test whether diversity and composition of riparian and upslope plant communities of small woodland streams differed, I surveyed plant communities along second- and third-order streams in central NY and compared these species assemblages with those found in adjacent uplands that are elevated above the regular influence of flooding. I quantified both species richness and the abundance of each species. I also examined the prevalence of native and introduced species in these communities, in terms of species richness, abundance of each species, and percent ground cover of herbaceous plants. Further, I examined the degree of plant species turnover between riparia and adjacent uplands and among the streams. Finally, I compared the trait composition and trait diversity of riparian and upland plant communities based on several plant traits, selected for possible relevance to a species' ability to establish or thrive in the riparian environment with regard to resource availability, ability to persist through or re-establish after disturbances, or other environmental conditions.

Methods

Field methods

I surveyed riparian plant communities at two sites along each of three streams in the Upper Hudson watershed (Figure 3.1) – Kayaderosseras Creek (1 = 43.01310°N, 73.84237°W; 2 = 43.01950°N, 73.83039°W), Ballston Creek (1 = 42.96628°N, 83.82181°W; 2 = 42.95915°N, 73.81998°W), and Indian Kill (1 = 42.88205°N, 73.94018°W; 2 = 42.87092°N, 73.90864°W). These streams are located in a suburban to rural landscape interspersed with deciduous forests. The streams are found in wooded areas within this suburban-rural-forest matrix. I also surveyed plant communities located upslope of each of these riparian zones. All surveys were completed between July 31 and September 3, 2012. Kayaderosseras Creek is 55 km in length, arising in the southern edge of the Adirondack Park and concluding in Saratoga Lake. Although the

Kayaderosseras changes in stream order along its length, all study sites were located along a third-order reach of the stream (Horton 1945, Strahler 1957). At the Kayaderosseras study sites, the creek is approximately 10 meters in width and 1 meter at its deepest point during average waterflow. Ballston Creek is a third-order stream that arises from the north end of Ballston Lake and runs approximately 8 km to its outlet in Round Lake. Ballston Creek is approximately 5 meters wide and 50 cm deep at its deepest point during average waterflow at the study sites. Indian Kill is a second-order stream approximately 10 km in length and concludes in Alpaus Kill, 2 km upstream of the point where Alpaus Kill meets the Mohawk River. At the Indian Kill study sites, the stream is about 5 meters wide; the deepest point during average streamflow at one site is approximately 50 cm, and at the other site is approximately 1 meter. These focal streams do not contain USGS stream gauges, as the vast majority of gauges in New York State are located in much larger rivers. Therefore, a more detailed description of streamflow information (e.g., daily variations) is not available. However, these three streams are broadly similar in flow regime, and because they are located in the same region, they should have similar flow regimes as driven by seasonality and regional rainfall patterns.

I selected two study sites along each focal stream where I documented the presence and abundance of vascular plant species along four transects parallel to the stream channel – two at the edge of the streambank and two at higher elevations upslope (Figure 3.2). Each streambank transect was located along the greenline, a standard location for sampling riparian vegetation defined as a clear linear grouping of plants near the water’s edge that has at least 25% overall vegetation cover (Winward 2000). The greenline is often not at the edge of the average stream flow, but rather some distance away. Substrate between the greenline and the edge of the water is highly disturbed, and may contain only regenerating seedlings and occasional larger plants. The selection of the greenline as a sampling location represents a regularly vegetated area that still experiences a degree of disturbance, not the most disturbed portion of the riparian zone. This greenline is equivalent to the floodplain or bank in the riparian geomorphic classifications of Hupp and Osterkamp (1985). The bottom of the greenline transect was placed along the greenline, such that the entirety of the width of the transect included vegetated areas within the greenline. These greenline transects were therefore parallel to the stream. Upslope transects were also parallel to the stream and to the greenline transects. To place upslope transects, I used a clinometer to identify points on the slope that were elevated 1 m above the greenline transect, and ran the upslope transect along these points. Vegetation at this elevation is expected to be removed from the regular influences of these small streams (e.g., flooding; scouring). For instance, although the study streams do not contain streamflow gages, the second-order Glowegee Creek (the nearest stream to Kayaderosseras Creek that contains a USGS streamflow gage), has an annual peak water height approximately 0.75 m above its average flow, below the 1m elevation defined here for upslope transects.

Transect lengths varied between 24 and 65 meters, in order to accurately encompass the assemblage of species contained within a particular topographic unit (e.g., an erosional or depositional bank) at each location. Plants were recorded in twenty 1m x 0.5 m quadrats placed randomly along each transect, such that each transect, regardless of length, sampled a total of 10 m^2 across quadrats. Quadrats were rectangular rather than square to minimize the elevational variation encompassed within the sampled area, because the topography perpendicular to the stream is often steep. This method allowed an equal area to be sampled even along transects differing in length. Quadrats were placed along the bottom edge of the greenline, with the long axis of the rectangular quadrat oriented parallel to the stream. I recorded the number of individuals of each vascular plant species observed in each quadrat. I also recorded visually estimated % ground cover for herbaceous species. This sampling regime provided data for 3 streams, 2 sites per stream, 2 elevations (greenline and upslope) per site, 2 replicate transects per elevation at each site, and 20 plots per replicate transect, for a total of 480 plots surveyed. I identified all species possible in each quadrat, visually estimated the percent cover of each, and counted the number of individuals for those species where it was possible to discriminate individuals. For visual cover estimates, I used Daubenmire's modified Braun-Blanquet cover class scale (T: < 1%; 1: 1-5%; 2: 6-15%; 3: 16-25%; 4: 26-50%; 5: 51-75%; 6: 76-95%; 7: 96-100%) (Bonham et al. 2004). Because very few large woody plants fell within the quadrats, species abundance was recorded for shrubs and trees rooted within 0.5 m of either side of the transect line to maximize inclusion of species rooted along each transect.

Species identification followed Gleason and Cronquist (1991). Of the 243 total species observed, twenty could not be identified because of a lack of reproductive material, and in most cases, very little vegetative material present. However, they were identifiable as being distinct from observed named species. These were classified as unique morphospecies for inclusion in analysis. Eight additional samples were identified only to genus. Each identifiable species was defined as native or introduced to the United States using the USDA PLANTS database (http://plants.usda.gov; data accessed 2013). All species observed are listed in Appendix C (Table C-1).

Statistical analysis

I examined four characteristics of plant communities (response variables) along each transect: 1) species richness (number of species) in the transect, 2) total number of individuals of each species in the transect, 3) percent cover of herbaceous plants, and 4) trait diversity. To determine trait diversity, I obtained information on 19 traits of interest from the TRY Plant Traits Database and contributors to the database (Niinemets 1999; Niinemets 2001; Kerkhoff et al. 2006; Kattge et al. 2011; http://www.try-db.org). Traits were chosen for possible relevance to a species' ability to establish or thrive in the riparian environment with regard to resource availability, ability to persist through or re-establish after disturbances, or other environmental conditions. I used the R package *FD* to calculate the trait diversity of each transect. The trait diversity index is based on an abundance-weighted sum of squares that takes into account both character values (traits) and the abundance of each of those values to describe the breadth of traits within that community (Mason et al. 2005).

I fit multiple candidate generalized linear models (GLMs) of increasing complexity, either containing no explanatory variables (Model 0), only stream (Model 1, S = stream, meaning the three different streams included in the study), site within stream (Model 2, I = site), and bank type (i.e., riparian or upslope) within site within stream (Model 3, B = bank type). Species richness and abundance of individual plants were each modelled using a Quasi-Poisson model, $Y_i \sim QuasiPois(\lambda_i, \phi)$, where the underlying intensity of the Poisson process is modelled as a function of Stream, Site, and Bank Type:

$$0: log(\lambda_i) = \lambda$$

$$1: log(\lambda_i) = \lambda + S_i$$

$$2: log(\lambda_i) = \lambda + S_i + I_{ij}$$

$$3: log(\lambda_i) = \lambda + S_i + I_{ij} + B_{ijk}$$

and the overdispersion parameter ϕ was not estimated from or influenced by site characteristics but was estimated separately for each of models 0 through 3.

Percent data (vegetation cover) were modeled using a Quasi-Binomial model, $Y_i \sim QuasiBinom(n, p_i, \phi)$, where the associated probability was modelled as a function of Stream, Site, and Bank Type:

$$n = 100$$

$$0\colon logit(p_i) = p$$

$$1\colon logit(p_i) = p + S_i$$

$$2\colon logit(p_i) = p + S_i + I_{ij}$$

$$3\colon logit(p_i) = p + S_i + I_{ij} + B_{ijk}$$

and the overdispersion parameter ϕ was not estimated from or influenced by site characteristics but was separately estimated for each of models 0 through 3.

Although the family of binomial distributions is not ideal for modelling percentage data, using the Quasi-Binomial distribution allowed the incorporation of the spatially nested structure of the sampling design, and is a reasonable if not ideal distribution for percentage data. The binomial family of distributions models the probability of a given number of observations in *n* total events. Using a binomial distribution to model percent data implicitly assumes that these data are a number of observations out of 100 events, and not a true proportion between 0 and 1. The beta distribution would be a better fit for cover data, as it is defined between [0, 1], and is a more natural fit for true proportion rather than count data. As cover was visually estimated in discrete categories, a multinomial model may have provided an appropriate fit, but this would have precluded the use of nested models. Given all of these compromises, I chose a Quasi-Binomial distribution for these models.

The explanatory power of each model was compared to the previous model using a chi-squared test of deviance reduction (Hastie and Pregibon 1992, Guisan et al. 2002). In this approach, a significant increase in explanatory power indicates a significant contribution of the added explanatory variable in the more complex model (e.g., a significant reduction in deviance from Model 2 to Model 3 would indicate significant explanatory power of bank type on the response variable). The hierarchical nature of this model testing parallels the structure of a nested ANOVA. I compared the results of this analysis to those using a more conventional nested ANOVA approach to note if there were any disparities due to the statistical methodology.

I also used GLM to test for differences in the abundance of native and introduced species, using three response variables: species richness, number of individual plants, and herbaceous cover. The models used were the same as described above, with the addition of a fifth model (Model 4) including species origin (native or introduced) as a final explanatory variable to be tested against the nested spatial variables. Species richness and abundance of individual plants were each modeled using a Quasi-Poisson distribution, $Y_i = QuasiPois(\lambda_{i,}\phi)$, where the underlying intensity of the Poisson process was modelled as a function of Stream, Site, and Bank Type:

$$0: log(\lambda_i) = \lambda$$

$$1: log(\lambda_i) = \lambda + S_i$$

$$2: log(\lambda_i) = \lambda + S_i + I_{ij}$$

$$3: log(\lambda_i) = \lambda + S_i + I_{ij} + B_{ijk}$$

$$4: log(\lambda_i) = \lambda + O_i + S_j + I_{jk} + B_{jkl}$$

Vegetation cover was modeled using a Quasi-Binomial model, $Y_i \sim QuasiBinom(n, p_i, \phi)$, where the the associated probability was modelled as a function of Stream, Site, and Bank Type:

$$n = 100$$

$$0: logit(p_i) = p$$

$$1: logit(p_i) = p + S_i$$

$$2: logit(p_i) = p + S_i + I_{ij}$$

$$3: logit(p_i) = p + S_i + I_{ij} + B_{ijk}$$

$$4: logit(p_i) = p + O_i + S_j + I_{jk} + B_{jkl}$$

I used the R package *vegan* to perform non-metric multidimensional scaling (NMDS) ordinations of Bray-Curtis dissimilarities among transects using a species by site abundance matrix. I also conducted an analysis of similarity (ANOSIM) to determine if there were differences among the three streams or between streambank and upslope sites in abundance-weighted community composition. I conducted a second ANOSIM to compare abundance-weighted trait composition between streambank and upslope sites using a trait matrix.

I compared the species richness of riparian and upslope transects at the regional scale using a species rarefaction curve (i.e., comparing the species present regionally in all riparian sites to those in all upslope sites). I used the function *specaccum* within the *vegan* package to find the species rarefaction curve across all quadrats sampled in the riparian zone and all quadrats sampled upslope. I used 999 permutations to find the mean species rarefaction curve and its standard deviation for riparian sites and for upslope sites, subsampling all quadrats without replacement in a random order in each permutation (Gotelli and Colwell 2001).

Results

Species richness and abundance

At the local scale, species richness did not differ significantly between greenline and upslope transects, neither overall ($\chi^2 = 12.68$, p = 0.8370) nor for introduced ($\chi^2 = 7.592$, p = 0.7357) or native ($\chi^2 = 6.284$, p = 0.9521) subsets of the community (Table 3.2). Greenline transects (n = 12) contained a mean of 2.8 (± 0.28 SE) species m^{-2}, and upslope transects (n = 12) contained a mean of 1.8 (± 0.25 SE) species m^{-2} (Figure 3.3A). Greenline and upslope transects had similar richness of introduced species (0.4 ± 0.09 SE and 0.3 ± 0.07 SE m^{-2} respectively). Natives appeared more abundant in greenline than upslope transects, although this difference was not significant, as stated above (2.0 ± 0.24 SE and 1.4 ± 0.20 SE m^{-2} respectively; Figure 3.4A). Native species were more abundant than introduced species by all three measures of abundance: species richness ($\chi^2 = 336.43$, $p < 0.0001$), abundance of individual plants ($\chi^2 = 3087.28$, $p < 0.0001$), and herbaceous cover ($\chi^2 = 4.6058$, $p < 0.0001$).

On average, greenlines contained almost twice as many individual plants (i.e., the total number of individuals, irrespective of species identity) as did their paired upslope sites (36.9 ± 4.45 SE and 20.2 ± 4.97 SE individuals m^{-2} respectively; $\chi^2 = 960.6$, $p = 0.0462$; Figure 3.3B). This difference remained significant when just considering native individuals (26.4 ± 4.12 SE and 11.8 ± 2.13 SE m^{-2} respectively; $\chi^2 = 1085$, $p = 0.0400$). The same trend was observed for introduced individuals, although it was only marginally significant (6.7 ± 1.58 SE vs. 3.5 ± 1.34 SE m^{-2}; $\chi^2 = 324.8$, $p = 0.0581$; Figure 3.4B). Mean herbaceous cover did not differ between the greenline (45% ± 8.8% SE) and upslope (27% ± 6.2% SE) transects ($\chi^2 = 1.283$, $p = 0.3339$; Figure 3.3C). This was true both native (37% ± 7.5% SE and 21% ± 4.0% SE for greenlines and upslope respectively; $\chi^2 = 1.333$, $p = 0.3588$), and introduced species (7.5% ± 2.0% SE vs 6.3% ± 2.8% SE respectively; $\chi^2 = 0.2762$, $p = 0.1136$; Figure 3.4C).

While at the local scale individual stream reaches were not more diverse at the greenline compared to upslope sites, at the regional scale, the total number of species observed across all greenline sites (n = 198 species) was greater than total number of species observed in upslope sites (n = 156 species) as indicated by non-overlap of 95% confidence intervals on species accumulation curves (Figure 3.7).

Species richness differed among streams ($\chi^2 = 40.16$, $p = 0.012$, Table 2, Figure 3.5A) and ranged from 1.9 ± 0.37 SE species m^{-2} (Ballston Creek, n = 8 sites) to 2.9 ± 0.35 SE species m^{-2} (Indian Kill, n = 8). The number of native species ($\chi^2 = 59.68$, $p = 0.0005$; Table 3.2) also differed among streams, although the number of introduced species did not ($\chi^2 = 5.483$, $p = 0.276$, Figure 3.6A). The number of native species ranged from 1.4 ± 0.21 SE species m^{-2} (Kayaderosseras Creek) to 2.3 ± 0.28 SE m^{-2} (Indian Kill); introduced species richness ranged from 0.2 ± 0.09 SE m^{-2} (Ballston Creek) to 0.5 ± 0.08 SE m^{-2} (Kayaderosseras Creek). Individual abundance (i.e., the number of individual plants within a quadrat) did not differ among streams ($\chi^2 = 228.3$, $p = 0.218$) (Table 3.2, Figure 3.5B), nor did abundance of just native individuals ($\chi^2 = 134.7$, $p = 0.441$) or introduced individuals ($\chi^2 = 123.9$, $p = 0.097$) (Table 3.2, Figure 3.6B). A significant portion of the total variance in herbaceous cover was accounted for by differences among the three streams ($\chi^2 = 1.325$, $p = 0.029$). This was also true for herbaceous cover of only introduced species ($\chi^2 = 1.348$, $p < 0.0001$), but not for native herbaceous cover ($\chi^2 = 0.5147$, $p = 0.279$) (Figures 3.5C, 3.6C). Additionally, differences between streambank and upslope sites explained a significant portion of the observed variance in the total abundance of individuals ($p = 0.040$). Coefficients and dispersion parameters for the fitted GLMs can be found in the supplementary material (Appendix C, Tables C-2 through C-5). Results for the ANOVA approach did not differ substantively from those of the GLM approach, except in two cases. With the GLM, there was a significant difference between greenline and upslope communities in overall abundance of individual plants and in abundance of native plants, which were not significant in the ANOVA approach ($p = 0.079$ and $p = 0.069$ respectively) (Appendix C, Table C-6).

Trait diversity and composition

Trait diversity was 0.74 ± 0.03 SE among streambank sites, and 0.73 ± 0.03 SE among upslope sites and did not differ significantly between streambank and upslope sites ($\chi^2 = 0.1186$, $p = 0.180$; Table 3.2). There was also no difference in trait composition between streambank and upslope plant communities (ANOSIM; $R = 0.0164$, $p = 0.268$; Figure 3.8).

Species composition

Species composition significantly differed among the three stream locations (ANOSIM; $R = 0.365$, $p = 0.001$; Figure 3.9). However, there was not a significant difference in community composition between streambank and upslope sites (ANOSIM; $R = 0.064$, $p = 0.128$).

Discussion

Unlike previous studies that have focused on larger rivers (Salo et al. 1986, Gregory et al. 1991, Naiman et al. 1993, Naiman and Décamps 1997), I found no statistically significant differences in species diversity, vegetative cover, or trait diversity overall or within native and introduced subsets of riparian and upslope plant communities along small streams in northern New York State; however, the density of individuals was greater in riparian than upland sites. At a regional scale (across all sites), riparian zones harbored significantly more species than did upslope communities, as shown in the species rarefaction curve (Figure 3-7). This suggests that for the metrics of community composition used in this study, differences in regional environmental conditions or in the regional species pool may have a greater influence on the plant community than does the influence of the abiotic environment of the stream. The similarity of trait composition between streambank and upslope plant communities suggests that the regional accumulation of species within the riparian zone reflects accumulation of species with similar traits, rather than an accumulation of trait diversity.

While I found no significant differences between greenline and upslope communities in total species richness or number of introduced species, previous studies on riparia of larger streams suggest that riparian zones are higher in diversity compared to the surrounding landscape, and are also more vulnerable to species invasion (Pyšek and Prach 1993, Planty-Tabacchi et al. 1996, Stohlgren et al. 1998, Hood and Naiman 2000, Brown and Peet 2003). One possible explanation for this difference is that relatively few streams were considered in this study. There were, on average, 50% more species in the greenline than in upland sites (1.8 vs. 2.8 species m^{-2} respectively), though this difference was not significant. If this study were treated as a pilot study to guide additional vegetation surveys in this area, sixteen additional transects (four additional streams, over twice that included in this study) would be needed to obtain sufficient power ($\beta = 0.84$; $\alpha = 0.05$) to find the difference in species richness observed in this study significant, assuming the observed variance remained the same with the increased sampling. Additionally, sampling vegetation more broadly throughout the landscape (i.e., a greater spatial extent) might represent a greater breadth of ecological and environmental conditions, in which different patterns might be observed. It is also possible that a significant difference would be found between riparian zones and the surrounding landscape by selecting upslope transects at a higher elevation (and thereby a greater horizontal distance). However, gauged streams of similar size in the region do not generally show an annual peak flow higher than 1 m above the average flow (data derived from streams with archived flow height data within the Mid-Atlantic watershed, http://waterdata.usgs.gov/usa/nwis/).

Small differences in diversity between the riparian zone and uplands might be expected here for a variety of reasons. Along smaller streams, the absolute distance between plants that experience flood disturbances and those that do not is often quite small. For example, in the second-order Glowegee Creek (the nearest stream to Kayaderosseras Creek, which contains a USGS streamflow gage), the annual peak gage height is approximately 0.75 m higher than the average height of the stream throughout the growing season. For many small streams, this degree of elevational change away from the streambed occurs over a short horizontal distance. In this study, riparian and upland transects varied between 4 and 25 m of horizontal separation with a 1 m change in elevation as a consequence. Riparian zones of small streams are likely to experience very similar environments to upslope plant assemblages due to this proximity, with the exception of the influence of the stream itself. It is also possible that plant roots extend from the upland into riparian water sources, in which case these two zones may not represent radically different environments. Flowing water and flood events will affect established riparian vegetation, and the stream may also contribute to seed dispersal and colonization. The riparian zones of small streams are often under a closed canopy, and shaded similarly to upslope communities (Vannote et al. 1980). Additionally, the underlying hydrology of riparian and upslope sites at this spatial scale is very similar, due to lateral water pathways moving downslope under the soil. In contrast, greater absolute distance is needed to escape the flooding influence of a larger river, which is likely to introduce additional environmental differences between floodplains and uplands beyond the direct influence of the stream itself. For large streams and rivers, the effects of flooding on community composition may be small compared to other factors such as light availability, unlike the case of smaller streams, where flooding is likely to be the predominant differentiating factor. Flood disturbances can directly increase light availability in large floodplains, while in the riparian zones of smaller streams in forested areas, the canopy coverage of the surrounding area provides a more constant reduction in light availability that is not as profoundly influenced by flooding (Vannote et al. 1980).

The timing, duration, frequency, and magnitude of flood events differ between small streams and large rivers. Flood events in small streams may correspond more strongly with individual rainfall events, peaking and receding rapidly, while these are dampened into attenuated, longer high-flow events in larger channels downstream (Dunne and Leopold 1978, Vannote et al. 1980, Montgomery and Bolton 2003). In large rivers, floods are largely predictable, and plant communities in the floodplains may be maintained at an early successional stage (Junk et al. 1989), such as in Odum’s (1969) pulse-stability concept. This may be the process that maintains high species richness in riparian zones in the cases where it has been observed. Different hydrologies may have different consequences for patterns in streambank vegetation. From an organismal perspective, unpredictable floods may act as catastrophic events that periodically “reset” the physical and biotic environment (Junk et al. 1989), perhaps leading to different patterns and dynamics in the riparian plant communities of small streams than those observed in communities experiencing more regular disturbance regimes. Therefore, patterns in the riparian plant communities of small streams might differ from those observed in larger floodplains due to flooding patterns alone.

I also found a significant difference in species identity among streams, although not between riparian zones and uplands within a site. A meta-analysis by Sabo et al. (2005) similarly found no overall differences in diversity in studies comparing riparian and upland habitats, but did find that spatial variation in species composition was much higher in riparia than uplands. The size of the rivers used in this meta-analysis is not given, and may have been weighted toward larger rivers. In a study of the riparian zones of small streams, Goebel et al. (2003) found that while individual stream reaches were not more diverse than a given upland site, riparian areas when pooled together were more diverse than the uplands as a whole, again consistent with the results of the present study.

Understanding the composition of the riparian plant communities of small streams in particular is critical to developing a broader understanding of the general contribution of riparian zones to biodiversity. Small streams differ both hydrologically and ecologically from larger rivers, and comprise the vast majority of the total linear length of river systems in most watersheds (Richardson and Danehy 2007). While the riparian zone of one particular reach of a small stream may not make a substantial or disproportionate contribution to regional plant diversity, it appears likely that the riparian zones of small streams may be quite important when considered collectively because of the variation they contain at the regional scale. Under the model of the intermediate disturbance hypothesis (Connell 1978), the banks of small streams may be too frequently disturbed to develop higher diversity than nearby upslope areas in a single location. However, not all streambanks are alike – regional patchiness, turnover, and chance colonization by different species may be maintaining higher diversity collectively along the banks of small streams in a region.

Tables

Table 3-1 Traits selected from the TRY-DB Plant Traits Database for use in trait diversity and composition analysis.

	Trait
Leaf traits	C (mg/g dry leaf)
	N (mg/g dry leaf)
	P (mg/g dry leaf)
	K (mg/g dry leaf)
	C:N
	N:P
	Specific leaf area (cm^2/g dry leaf)
	Leaf weight ratio (% of plant)
	Stomatal conductance per leaf area
Stem traits	Stem specific density (g/cm^3)
	Wood dry mass (% of plant)
Root traits	N (mg/g dry root mass)
	Rooting depth (cm)
Seed traits	Number of seeds per reproductive unit (tussock or individual plant)
	Seed protein content per mass (%)
	Seed mass (mg)
Other	Relative growth rate (g/g/day)
	Photosynthesis (nmol CO_2/g dry leaf/s)
	Leaf respiration (nmol CO_2/g dry leaf/s)

Table 3-2 Model comparisons (chi-squared test) of GLMs for each response variable. Models increase in complexity from 0 to 3, representing the nested structure of the sampling. Model 0 contains only an intercept and no predictors. Model 1 includes the three streams as a predictor Model 2 includes the streams as well as sites within streams. Model 3 contains all predictor variables (bank type, site, and stream). The explanatory power of each model was tested against the previous model. Significant p-values at α = 0.05 are marked with asterisks (*).

Model	**Residual df**	**Residual Dev.**	**df**	**Deviance (χ^2)**	**p**
Number of species					
Model 0	23	116.18			
Model 1	21	76.014	2	40.16	0.0124*
Model 2	18	68.463	3	7.551	0.6481
Model 3	12	55.785	6	12.68	0.8370
Number of native species					
Model 0	23	120.06			
Model 1	21	60.385	2	59.68	0.0005*
Model 2	18	53.663	3	6.722	0.6328
Model 3	12	47.379	6	6.284	0.9521
Number of introduced species					
Model 0	23	52.151			
Model 1	21	46.668	2	5.483	0.2758
Model 2	18	40.775	3	5.893	0.4288
Model 3	12	33.193	6	7.582	0.7357
Total abundance of individuals					
Model 0	23	22086			
Model 1	21	2295.8	2	228.3	0.2183
Model 2	18	1905.3	3	1090	0.0023*
Model 3	12	944.80	6	960.6	0.0462*
Total abundance of native individuals					
Model 0	23	3019.6			
Model 1	21	2884.9	2	134.7	0.4408
Model 2	18	2160.0	3	724.9	0.0318*
Model 3	12	1074.8	6	1085	0.0400*
Total abundance of introduced individuals					
Model 0	23	1271.8			
Model 1	21	1147.9	2	123.9	0.0971
Model 2	18	696.42	3	451.5	0.0007*
Model 3	12	371.61	6	324.8	0.0571
Herbaceous cover					
Model 0	23	6.5543			
Model 1	21	5.2298	2	1.325	0.0290*
Model 2	18	3.8972	3	1.333	0.0681
Model 3	12	2.6138	6	1.283	0.3339

Model	**Residual df**	**Residual Dev.**	**df**	**Deviance (χ^2)**	**p**
Native herb cover					
Model 0	23	5.8203			
Model 1	21	5.3056	2	0.515	0.2793
Model 2	18	4.1720	3	1.134	0.1317
Model 3	12	2.8390	6	1.333	0.3588
Introduced herb cover					
Model 0	23	2.3483			
Model 1	21	0.9998	2	1.349	< 0.0001*
Model 2	18	0.6540	3	0.346	0.0049*
Model 3	12	0.3777	6	0.276	0.1136
Trait diversity					
Model 0	23	0.2935			
Model 1	21	0.2911	2	0.002	0.9144
Model 2	18	0.2787	3	0.012	0.8184
Model 3	12	0.1601	6	0.119	0.1802

Table 3-3 GLM model comparisons (chi-squared test of reduction of deviance) comparing the diversity of native and introduced species (richness, number of individuals, and vegetative cover). Models increase in complexity from 0 to 4. Model 0 contains only an intercept. Model 1 includes the three streams as a predictor. Model 2 includes the streams as well as sites within streams. Model 3 contains bank type (greenline or upslope), site, and stream. Model 4 contains species origin in addition to the nested spatial factors. The explanatory power of each model is tested against the previous model. Significant p-values at $\alpha = 0.05$ are marked with asterisks (*).

Model	Residual df	Residual Dev.	df	Deviance (χ^2)	p
Number of species					
Model 0	47	508.64			
Model 1	45	467.70	2	40.95	0.0006*
Model 2	42	457.24	3	10.45	0.2913
Model 3	36	447.66	6	9.590	0.7536
Model 4	35	111.23	1	336.43	< 0.0001*
Total abundance of individuals					
Model 0	47	7378.6			
Model 1	45	7224.1	2	154.58	0.2435
Model 2	42	6359.3	3	864.73	0.0012*
Model 3	36	5081.9	6	1277.4	0.0007*
Model 4	35	1994.6	1	3087.3	< 0.0001*
Herbaceous cover					
Model 0	47	11.990			
Model 1	45	11.515	2	0.4751	0.1032
Model 2	42	9.8738	3	1.6416	0.0013*
Model 3	36	8.8121	6	1.0618	0.1184
Model 4	35	4.2062	1	4.6058	< 0.0001*

Figures

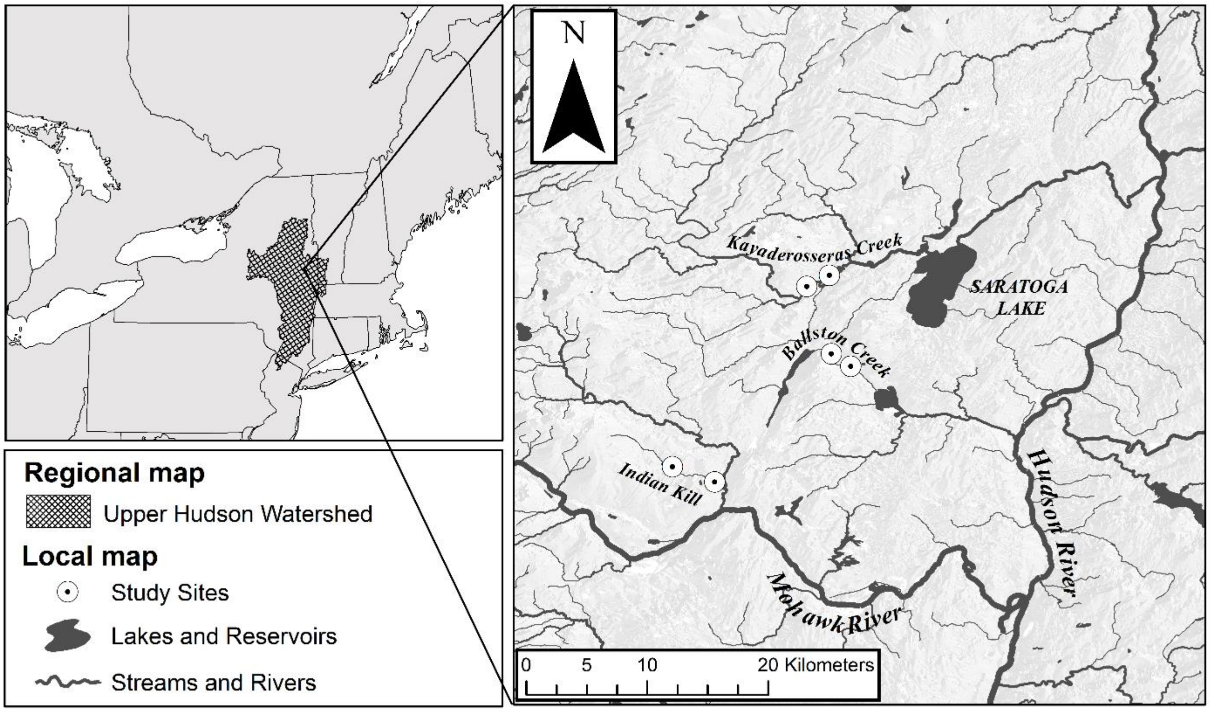


Figure 3-1 Map of the study area in the Upper Hudson watershed (central NY, USA), showing focal streams and locations of the six study sites.

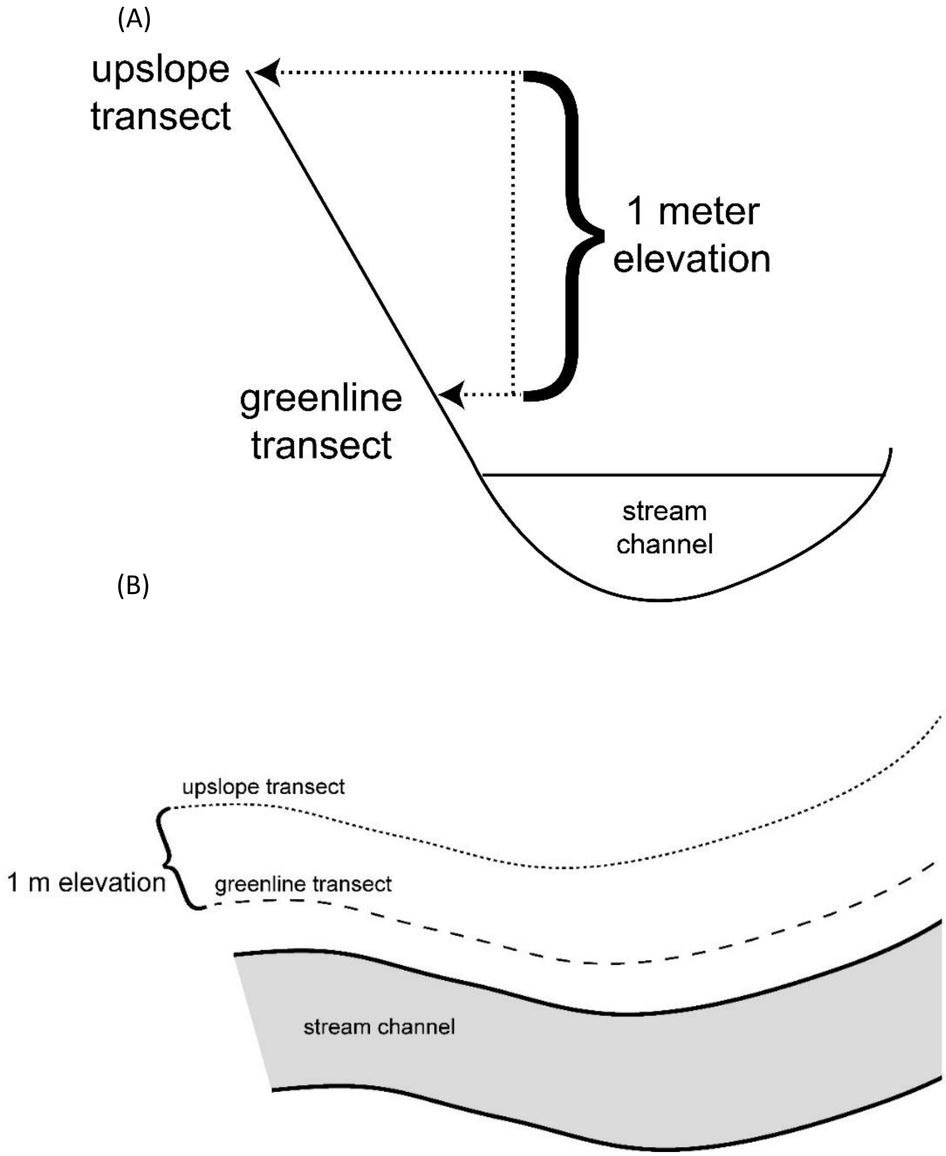


Figure 3-2 (A) Longitudinal diagram of placement of greenline and upslope transects. Both transects were parallel to the stream channel. Upslope transects were placed 1 m in elevation (vertical) above the greenline transects. The horizontal distance between transects therefore depended on the slope of the land away from the stream channel. (B) Overhead view of the placement of transects. Both greenline and upslope transects were placed parallel to the stream channel. Greenline transects were placed at the greenline, defined as the closest clear linear grouping of plants to the water's edge with at least 25% vegetation cover (Winward 2000). Upslope transects were parallel to greenline transects and to the stream, located 1 m in elevation above the greenline transect.

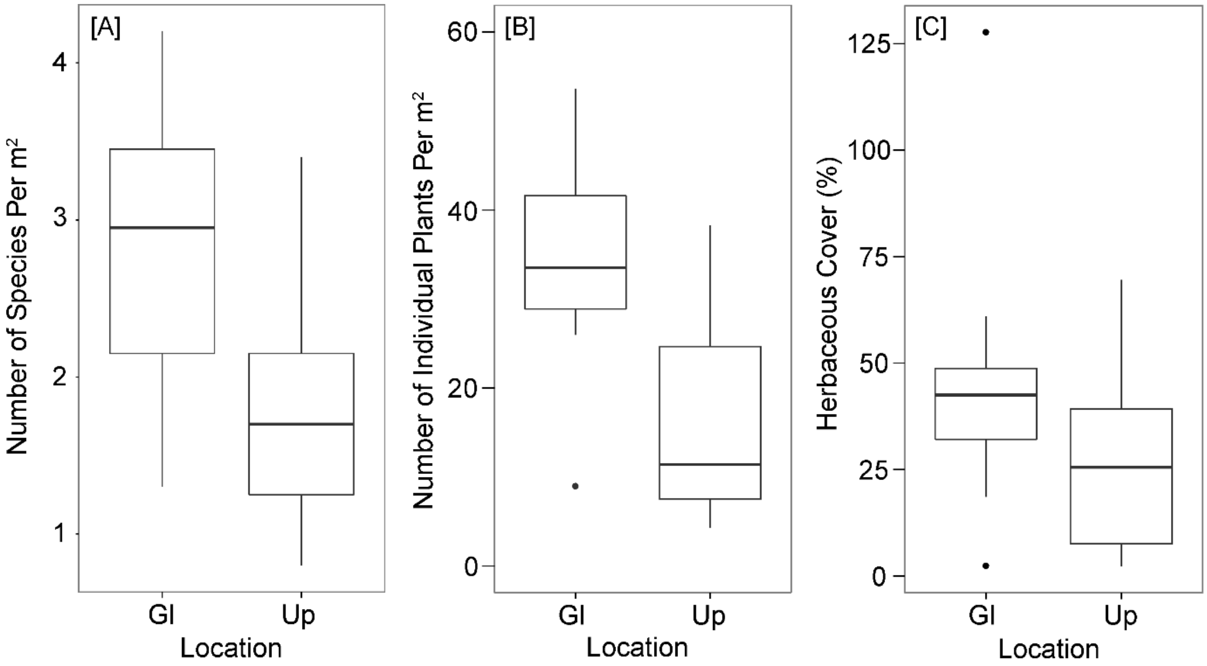


Figure 3-3 Greenline (Gl) and upslope (Up) diversity. Tukey boxplots comparing community composition variables between greenline and upslope transects. The top and the bottom of the box indicate the first and third quartiles, respectively; the line inside the box indicates the median. Whiskers extend to the highest and lowest values within 1.5 times the interquartile range; data that extend beyond the end of the whiskers are plotted as individual points. No factors significantly differed between greenline and upslope transects. (A) Number of species m^{-2} in greenline and upslope transects; (B) Total abundance of individuals m^{-2} in greenline and upslope transects; (C) Herbaceous cover in greenline and upslope transects.

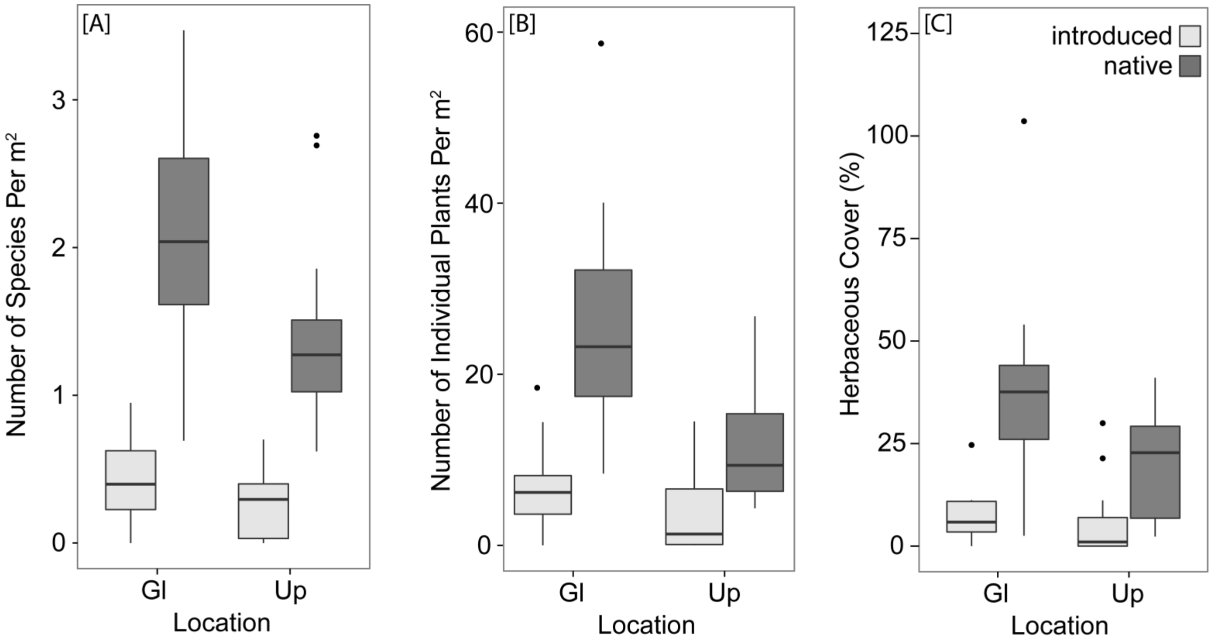


Figure 3-4 Tukey boxplots comparing community composition variables between greenline (Gl) and upslope (Up) transects, showing native and introduced species separately. The top and the bottom of the box indicate the first and third quartiles, respectively; the line inside the box indicates the median. Whiskers extend to the highest and lowest values within 1.5 times the interquartile range; data that extend beyond the end of the whiskers are plotted as individual points. No factors significantly differed between greenline and upslope transects. (A) Number of native and introduced species m^{-2} in greenline and upslope transects; (B) Total abundance of native and introduced individuals m^{-2} in greenline and upslope transects; (C) Herbaceous cover of native and introduced species in greenline and upslope transects.

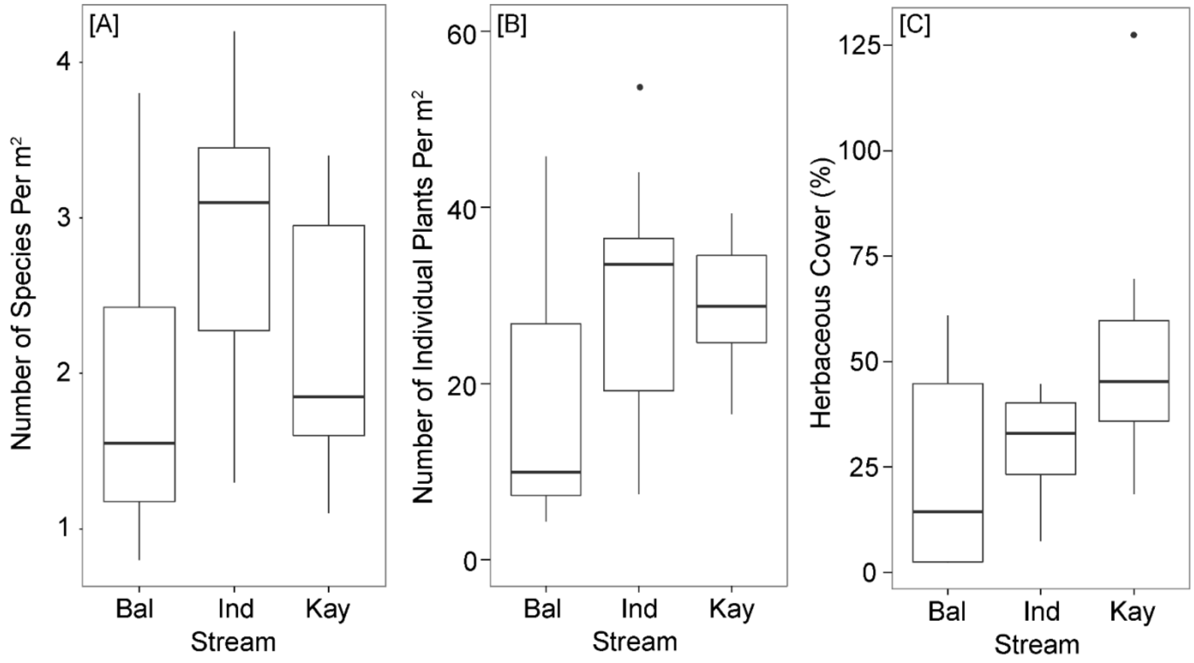


Figure 3-5 Tukey boxplots comparing community composition variables among streams. The top and the bottom of the box indicate the first and third quartiles, respectively; the line inside the box indicates the median. Whiskers extend to the highest and lowest values within 1.5 times the interquartile range; data that extend beyond the end of the whiskers are plotted as individual points. The number of species per m^2 (A) differed significantly among the three streams (Table 3-1). “Bal” = Ballston Creek; “Ind” = Indian Creek; “Kay” = Kayaderosseras Creek. (A) Number of species m^{-2} at each stream; (B) Total abundance of individuals m^{-2} at each stream; (C) Herbaceous cover at each stream.

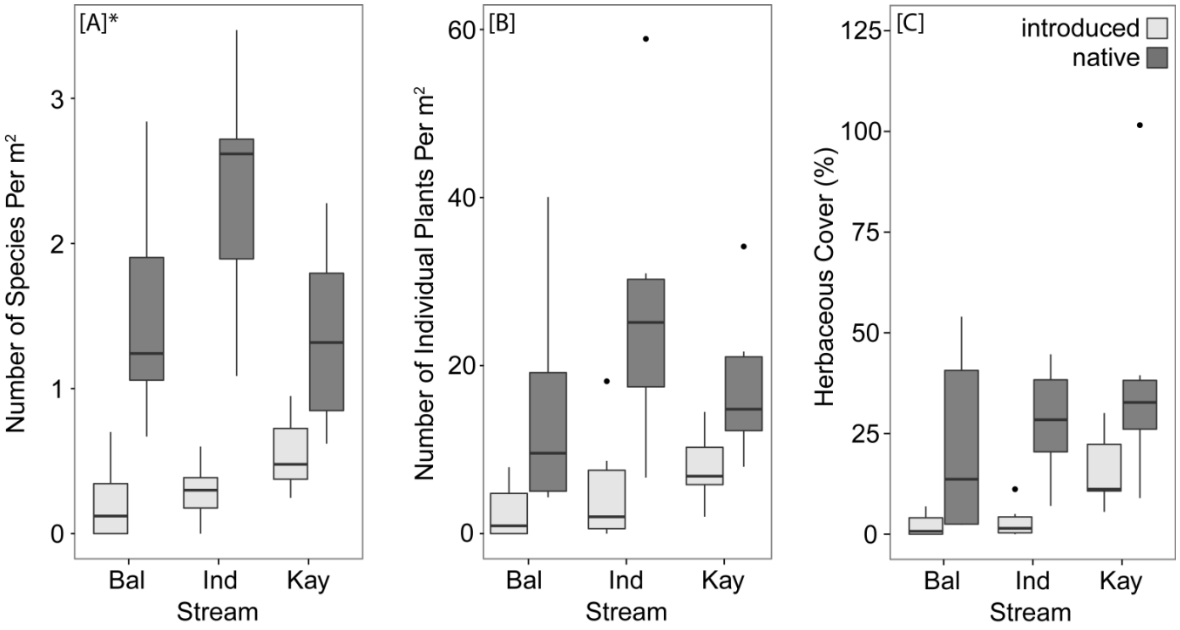


Figure 3-6 Tukey boxplots comparing community composition variables among streams, showing native and introduced species separately. The top and the bottom of the box indicate the first and third quartiles, respectively; the line inside the box indicates the median. Whiskers extend to the highest and lowest values within 1.5 times the interquartile range; data that extend beyond the end of the whiskers are plotted as individual points. Only A, average species richness, was significantly different among streams (*) (Table 3-1). “Bal” = Ballston Creek; “Ind” = Indian Creek; “Kay” = Kayaderosseras Creek.

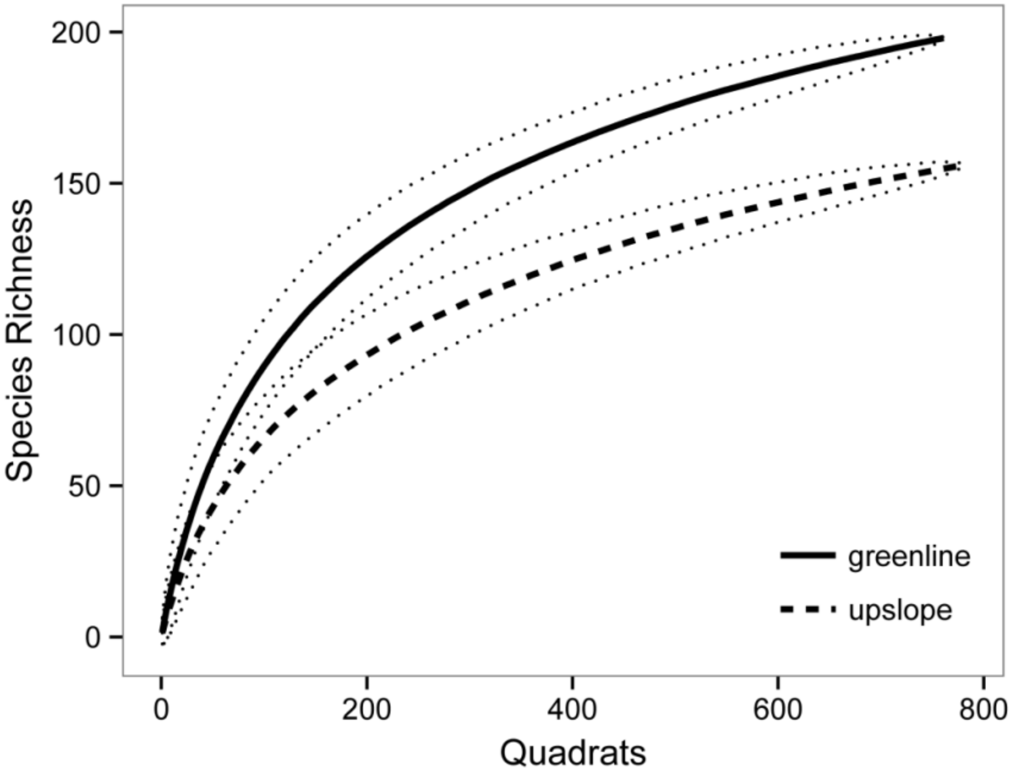


Figure 3-7 Mean species rarefaction curves (cumulative number of species observed) for greenline transects (solid line) and upslope transects (dashed line), generated by 999 permutations of sampling all quadrats in the dataset in random order. Confidence intervals (95%) on each SAC are shown with dotted lines. A total of 198 species were found across all greenline transects; 156 species were found across all upslope transects.

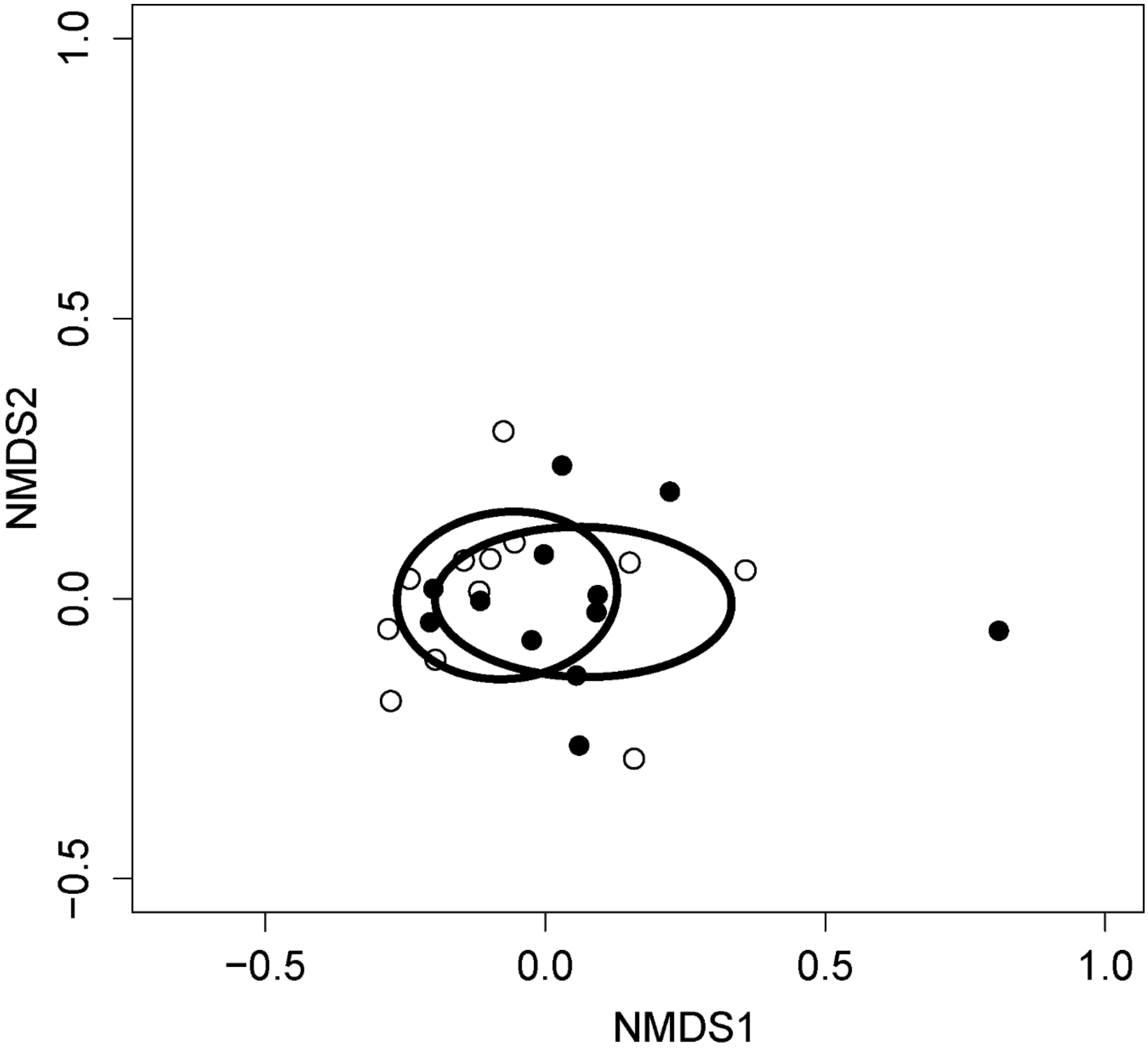


Figure 3-8 NMDS ordination of trait dissimilarity measures among transects (2D stress = 0.11). Greenline and upslope transects are distinguished by closed and open points, respectively. Ellipses represent 1 SD around the centroid of each group.

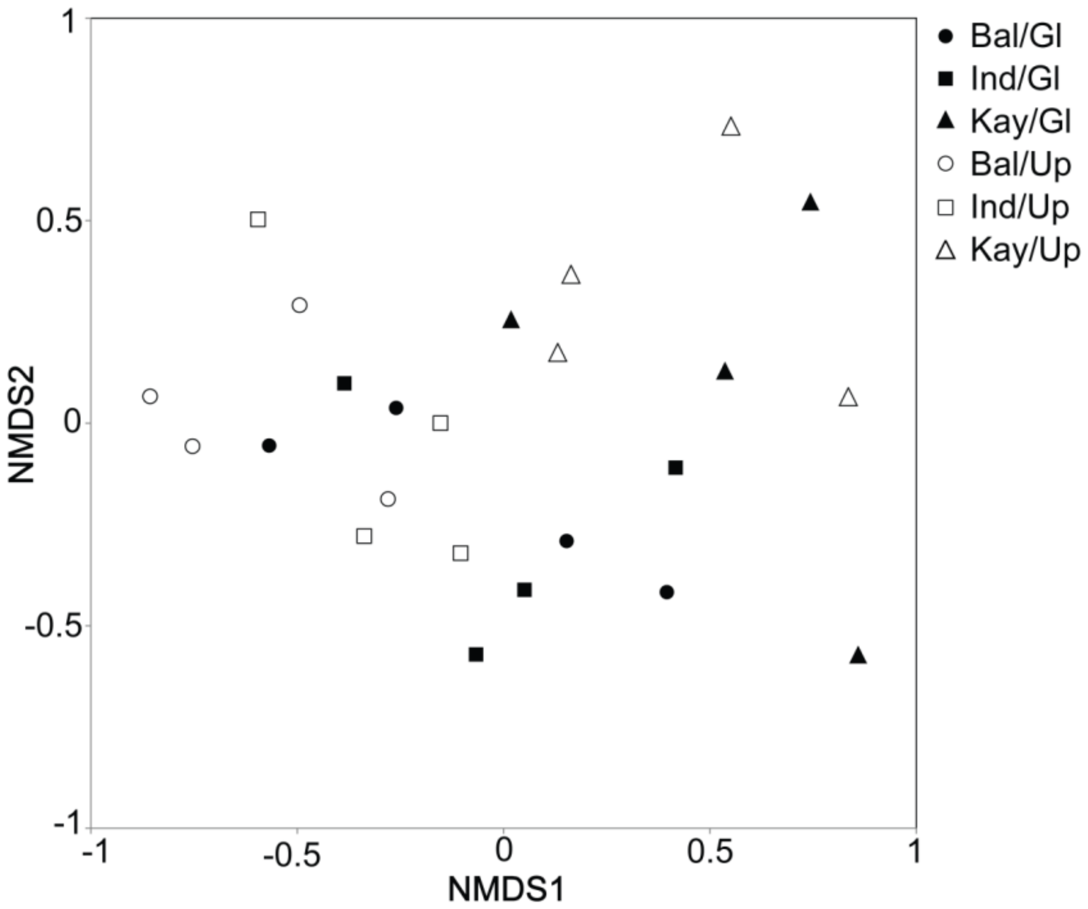


Figure 3-9 NMDS ordination of Bray-Curtis dissimilarity measures (i.e., dissimilarity in species composition) among transects (2D stress = 0.16). Greenline and upslope transects are distinguished by solid and hollow points, respectively; streams are distinguished by different shapes. "Bal" = Ballston Creek; "Ind" = Indian Creek; "Kay" = Kayaderosseras Creek; "Gl" = greenline; "Up" = upslope.

Chapter 4: The role of large-scale abiotic factors in structuring local diversity, species distribution and species coexistence in riparian plant communities

Introduction

Riparian plant communities are often described as highly species-rich in comparison to nearby upland communities (Gregory et al. 1991, Naiman et al. 1993, Naiman and Décamps 1997, Goebel et al. 2003). There is a great deal of interest in characterizing the composition of riparian plant communities as well as identifying any links between this vegetation and underlying environmental conditions. Characteristics of riparian plant communities are often attributed to the hydrological and geomorphological characteristics of the riparian zone (Gregory et al. 1991, Auble et al. 1994, Bendix 1994, Toner and Keddy 1997). Physical conditions (e.g., water volume, flow and flood regime) change along the gradient from headwater or low-order to higher-order channels. Disturbance processes and associated habitat characteristics differ along this gradient (Montgomery 1999). The riparian zones of small streams are understudied relative to floodplains of larger rivers, and may differ in the characteristics of their plant communities.

Spatial patterns in the species composition of riparian plant communities may also be influenced by other environmental gradients outside of the direct role of flooding, such as regional climate, anthropogenic influences, or soil characteristics. Climate and environmental variables, and regional variation in these, have long been used as predictors of plant distribution, particularly in describing global patterns in the distribution of broad vegetation types, but also at other spatial scales (e.g., Woodward and Williams 1987, Franklin 1995, Hayden 1998, Stephenson 1998). Climate and topography affect soil development, moisture regime, and temperature regime of a habitat, which together determine which species may or may not succeed in that location (Franklin 1995). From that potential species pool, processes within a habitat (e.g., disturbance, competition) will influence which species are actually found in a local plant community. Micro-scale factors such as the slope, aspect, and other conditions of the terrain will also influence species composition at the local scale. In the northern reaches of the watershed of the Hudson River in New York State (hereafter called the Upper Hudson), riparian vegetation has been observed to have higher species turnover among localities within the region than upland vegetation at the same scale (Chapter 3). While microclimate variation within and among riparian zones is likely to contribute to this variation, some variation might also be attributable to regional environmental variation. At the regional scale, factors such as climate, topography and geology will influence the type of community that develops (Vannote et al. 1980, Montgomery 1999). These factors can determine the large-scale environment upon which more local controls of vegetation are superimposed. Variation in environmental characteristics across the landscape may be one way to explain species turnover among communities across a region. It is also possible that variation in dispersal rate among sites influences their compositional similarity. If dispersal of propagules is more common between sites in close proximity to one another than between distant sites, as is likely true for the majority of plants, compositional similarity may largely be explained by proximity (spatial autocorrelation) rather than variation in environmental conditions.

This study examined potential determinants of regional community composition and species turnover among riparian plant communities in the Upper Hudson watershed. The specific objectives of this study were to: (1) evaluate associations between local riparian plant community composition and large-scale environmental conditions, (2) determine if different groups of plants (i.e., annuals versus perennials and native versus introduced species) were distributed differently across the same suite of environmental conditions; and (3) assess spatial autocorrelation in community composition and environmental conditions.

Methods

Study area

This study was conducted in the riparian zones of small streams throughout the Upper Hudson watershed (NY, USA). Fifty-three riparian plant communities along second- and third-order streams were surveyed. To minimize selection bias, the sites were chosen using a random sampling approach across the landscape without stratification. Five hundred potential points were randomly selected using ArcGIS along second- and third-order streams in the Upper Hudson Watershed via the National Hydrography Dataset Plus (http://www.horizon-systems.com/nhdplus). These potential points were assessed for plausibility of sampling, based on the ability to obtain land access permissions and the physical accessibility and safety of the site. Inaccessible sites were discarded from further consideration, as were points that fell on developed land (e.g., paved areas or lawns). Of the suitable sites, 50 were selected to be used in this vegetation sampling. These fifty sites were selected in a haphazard fashion to be approximately evenly distributed across the eight sub-basins in the Upper Hudson watershed. Two of these sub-basins (Rondout and Hudson-Wappinger) were relatively under-sampled due to substantial amounts of development in these areas; they contained few suitable sites. Additionally, three sites surveyed earlier (Chapter 3) were re-surveyed for inclusion this study, for a total of 53 communities (Figure 4-1). Geographic coordinates of sites are given in Appendix D (Table D-1).

Vegetation sampling

I used a timed meander method of vegetation sampling (Goff et al. 1982). The timed meander method has been shown to be an effective and rapid method of documenting plant species richness (Goff et al. 1982, Huebner 2007) and has previously been used to describe riparian vegetation along the shores of the Hudson River (Strayer et al. 2012). Timed meander methods provide data only on species presences, rather than more detailed descriptions of the plant community (e.g., species abundances or vegetative cover), but are advantageous when more intensive methods (e.g., Peet et al. 1998) are too time-intensive and costly to adequately sample the desired area. Therefore, all analyses were conducted on presence/absence data. At each site, I followed a systematic procedure to delineate the search area, providing consistency necessary to use timed meander data in comparative studies of these communities. I outlined a 1 m x 50 m sampling area parallel to the river channel and located directly above the greenline. The greenline is defined as a clear linear area along the edge of a stream with at least 25% vegetation cover, and is a standard location for sampling riparian vegetation (Winward 2000; Figure 4-2). Transects included a 1 m band of greenline vegetation, and did not overlap into areas of the riverbank closer to the water than the greenline, where little vegetation establishes. I recorded the presence of all species observed in this search area within a 30 minute observation period.

Environmental characteristics

Environmental variables expected to affect the spatial distribution of riparian vegetation at a landscape scale were derived from various online databases, and were incorporated into a geodatabase using ArcGIS. Variables are listed in Table 4-1. The resolution of all climate and land cover layers was smaller than the distance between the closest pair of sites, which was 2 km. Elevation and latitude were initially used as explanatory environmental variables, but were found to be highly correlated with annual mean temperature, and so were removed from environmental analyses. Bioclimatic variables (annual mean temperature and annual precipitation, 800 m resolution) were obtained from the PRISM climate group (http://www.prism.oregonstate.edu/). Land cover variables (30 m resolution) were obtained from the 2006 National Land Cover Database (NLCD, http://www.mrlc.gov/). This database contains 20 land cover types that fall under 8 broader categories as defined by the NLCD classification system: water, developed, barren, forest, shrubland, herbaceous, cultivated, and wetlands. Developed areas are largely those that are anthropogenically modified and contain impervious surfaces, but can also include lawns and golf courses. Cultivated areas are those used either for livestock grazing pasture or the production of annual crops. I used the broader categories of developed, forest, cultivated, and wetland areas for analysis. Soil data were derived directly from field samples taken at each field site and analyzed in the lab. At each site, 10 cm deep soil cores were taken at six points evenly spaced along the transect (every 10 meters from 0 to 50 meters). All samples were air-dried, pulverized and sieved though a 2 mm mesh prior to analysis to exclude gravel and larger particles (Hoskins and Ross 2011). Soil pH was measured using an Oakton pH 700 benchtop pH meter following calibration with buffer solutions (pH of 4, 7 and 10). Sand content was determined using sedimentation rate by measuring the proportion of the soil sample that settled out of suspension in water after 60 seconds (Kilmer and Alexander 1949, Bohn and Gebhardt 1989). Soil organic matter was determined by loss-on-ignition. Samples were first oven-dried at 110°C for 24 hours to ensure that all residual moisture was removed from the soil samples and then weighed using a Sartorius ED323S-CW scale (precision 1 mg). Samples were then combusted in a muffle furnace at 360°C for 2 hours (Schulte and Hoskins 2009, Salehi et al. 2011) and reweighed with the same scale (precision 1 mg). Correlations among environmental variables and summary statistics for each are given in Table 4-2.

Statistical analysis

I identified relationships between environmental conditions (standardized to unit variance) and community composition via constrained correspondence analysis (CCA; Ter Braak 1987), a direct gradient analysis ordination approach, using the R statistical software (version 3.1.1) package *vegan* (Oksanen et al. 2013). Direct gradient analysis is used to directly relate species presence or species abundance to particular environmental characteristics, by maximizing correlations between variables in those two datasets. I performed a permutation test for significance (n = 999 permutations) of the environmental constraints in the CCA using the *vegan* function ‘anova.cca’. The CCA axes are related to environmental characteristics, and the strength of the relationship of any one variable is indicated by the length and direction of the vector. I also used the “BIOENV” approach first outlined by Clarke and Ainsworth (1993), as implemented in *vegan*, to identify the best subset of three environmental variables that maximizes correlation with dissimilarities in species composition among communities. This analysis used Mahalanobis distance to describe dissimilarities in site environmental characteristics. Mahalanobis distance scales the environmental factors to unit variance and forces orthogonality of explanatory variables in the matrix.

I looked for associations among these three dissimilarity-maximizing variables and particular groupings of plants (lifespan: annual versus perennial; species origin: native versus introduced). I used the *ade4* package (Dray and Dufour 2007) in R to perform an RLQ analysis to identify associations between these groups of plants and the selected environmental conditions (Legendre et al. 1997, Dray and Legendre 2008). While CCA models relationships between species composition and environmental conditions, RLQ partitions the variation in species composition among communities into groups of interest (usually defined by functional traits, although this is not required) to examine correlations between environmental conditions and those groups. In this method, three data matrices are used: site by environment (R), site by species (L), and species by trait/characteristic (Q). The site by species table is used to link the other two tables, to produce an environment by trait matrix. Correlations between environmental characteristics and traits (or other plant characteristics or groupings) are then derived from that matrix. I used RLQ fourth-corner analysis (Dray et al. 2014) to test the relationships between environmental conditions and annual versus perennial plants, as well as relationships between environment and native species versus those introduced to the United States. In the RLQ fourth-corner method, significance is tested by a permutation procedure. Most permutation models for this analysis have an inflated Type I error (Legendre et al. 1997). To avoid this, I used a model 6 permutation, which combines the outputs of a permutation model that permutes the values of each site (i.e., permutes rows) and a model that permutes the values of each species (i.e., permutes columns) as recommended by Dray and Legendre (2008) and ter Braak et al. (2012). I used the FDR (false discovery rate) method of correcting for multiple comparisons in the analysis (Benjamini and Hochberg 1995).

Finally, I used a Mantel test implemented in *vegan* to assess spatial autocorrelation by comparing spatial variance in plant community composition to spatial variance in environmental factors. I then performed a multiple regression of distance matrices (MRM; Lichstein 2007) using the *ecodist* package (Goslee and Urban 2007) in R to determine if environmental factors remained a significant explanatory factor for variation in community composition when spatial distance between communities was taken into account.

Results

The average species richness of the surveyed riparian plant communities was 30.5 ± 1.2 SE within a 50 m^2 transect. Across all sites, I identified a total of 287 plant species (Appendix D, Table D-2). Almost one-quarter (22.7%) of the variation in species composition among sites was explained by the eleven environmental variables considered (CCA, Table 4-3, Figure 4-3). Taken together, the explanatory power of environmental variables was statistically significant ($F = 1.096$, $p = 0.001$). Annual mean temperature showed a strong loading on CCA Axis 1, and the abundance of wetlands in the 1 km^2 surrounding the site showed a strong loading on CCA Axis 2 (Figure 4-3).

The three environmental variables with the best correlation to variation in community composition as shown by the BIOENV analysis were annual mean temperature, percent sandiness of the soil, and percent coverage of wetlands in the surrounding 1 km ($R^2 = 0.166$). I found a significant, positive correlation between annual plant richness and annual mean temperature (RLQ, $p_{adj} = 0.027$), but no significant correlation between native or introduced species richness and any environmental conditions (Table 4-4, Figure 4-4).

Species composition was significantly positively correlated between pairs of sites closer than 20 km (Mantel test, $r_m = 0.143$, $p = 0.003$; Table 4-5, Figure 4-5), and marginally positively correlated between pairs of sites separated by 20 to 40 km (Mantel test, $r_m = 0.063$, $p = 0.051$; Table 4-5, Figure 4-5). Species composition was significantly negatively correlated between pairs of sites separated by more than 70 km (Table 4-5, Figure 4-5). Similarity in environmental characteristics between pairs of sites was also significantly spatially autocorrelated ($r_m = 0.185$, $p = 0.017$), although this appears to largely be driven by high similarity between the closest pairs of sites (Figure 4-6). When spatial autocorrelation of community composition was taken into account, the association between community composition and environmental conditions was no longer significant (MRM, Table 4-6).

Discussion

The eleven environmental variables considered in this study explained slightly less than one quarter of the variation in species composition among the 53 riparian plant communities considered. Annual mean temperature, abundance of wetlands in the surrounding 1 km, and soil sandiness were the three strongest predictors of variation in species composition. When spatial autocorrelation was taken into consideration, environmental gradients were no longer a significant explanatory factor in the variation of species composition among these communities.

The number of introduced species present in a community was not correlated with annual mean temperature, local wetland abundance, or soil sandiness. While these conditions might favor particular introduced species, it appears that they do not influence the overall number of introduced species present in a location. However, the number of annual plant species in a community was positively correlated with annual mean temperature. Annual mean temperature at the sites included in this study varied from 4.7°C to 9.8°C. This likely reflects an underlying correlation between annual mean temperature and seasonality or length of the growing season in a given location. It is possible that annual plant species may be more abundant in warmer areas where they are able to grow and reproduce over a longer warm season, while in the cooler areas of this study region (e.g., the Adirondack Mountains), shorter growing seasons may instead favor perennial plants, if they are so short that annual plants cannot reliably reach reproductive age. Warmer summers might also result in greater growth and reproduction as compared to areas with cooler summers.

It is possible that additional environmental variables might be able to explain more of the variation in species composition. Notably, my analyses did not directly consider the influence of flooding on these plant communities, as the focus was to understand potential environmental gradients outside of variation in flooding that might explain regional variation in riparian plant community composition. Like the climate and land cover variables, the two hydrological variables included in this study were much broader than the scale at which vegetation patterns were described. Stream order is a measure of the position of a channel in the river network (Horton 1945, Strahler 1957) and a rough proxy of the size and discharge of the stream. Drainage area is a large-scale variable, and more local variables such as slope, aspect, and terrain shape are likely to drive patterns of water availability at local scales. This study focused on small streams; large-scale drainage patterns may affect large rivers differently. The riparian zone is characterized by strong hydrological processes caused by proximity to flowing water and consequent flood events (Junk et al. 1989, Naiman et al. 2005), and plant distributions in the riparian zone are likely controlled at least to some degree by the frequency of inundation and the susceptibility of plants to flood damage (Bendix and Hupp 2000). Considering smaller-scale flood-related variables directly might add substantial explanatory power to a model of variation in species composition among these communities.

Another possibility is that community composition in the riparian zone of small streams is largely determined by lottery-type processes (Chesson and Warner 1990, Chesson and Huntly 1997) in which fluctuations in environmental conditions favor species coexistence if those fluctuations open colonization or niche opportunities. For lottery-type processes, available space in the community is randomly allocated to species, and fluctuations open space for new colonizers, maintaining some level of diversity. In this case, the species composition of communities at any one time would reflect a more random assemblage of species that were able to colonize when opportunities arose, and may not show correlation to particular environmental variables. The same would be true for neutral community assembly (e.g., Hubbell 2001). If community assembly in riparian zone largely reflects lottery or neutral processes, different or additional environmental correlates would not help to explain inter-community variation in species composition.

The species composition of plant communities in this study was found to be significantly spatially autocorrelated, and environmental conditions were not significantly correlated with species composition in a model that included spatial autocorrelation. This suggests that similarity among communities may be driven by species dispersal, rather than by large-scale abiotic conditions. Environmental characteristics of sites were also spatially autocorrelated, although this was primarily driven by the closest pairs of sites (< 20 km). It is therefore unclear from this study whether similarity of communities is driven by more regular dispersal between nearby locations, by the regional environmental conditions that follow a similar spatial pattern, or both. Microscale variation in the environment, which was largely not measured here (with the exception of some soil characteristics), may also contribute to variation in community composition.

Spatial autocorrelation in this study was assessed using Euclidean distances between pairs of sites, rather than accounting for structure in the river network, which might influence the degree of spatial autocorrelation seen. For the riparian zones of small streams, connectivity of plant communities may not be substantially enhanced by the river network, as downstream flow does not connect small tributaries. Only two of the fifty-three sites in this study are located downstream of another site, such that they are connected by the unidirectional flow of the river network. All other connections between sites via the river network would require upstream as well as downstream movement. In these cases, directionality of water flow would work against connectivity of these sites via hydrochory. However, if the river network also acts as a terrestrial dispersal network (i.e., if it is easier for riparian species to disperse via riparian zones than along other terrestrial paths), the effective distance among the plant communities would reflect that variation in ease of dispersal. Ease of various dispersal paths is highly likely to differ among species (e.g., whether or not a propagule is water-dispersed). The connectivity between two riparian plant communities will depend on the dispersal ability of the members of those communities. The true spatial autocorrelation of these communities, accounting for potential network effects and dispersal abilities, bears further investigation.

The flow regime and dynamics of the riparian system are undoubtedly major structuring influences in the composition of riparian plant communities, but are unlikely to be the sole factors. Here, characteristics of climate, soil, and surrounding land use show some promise in explaining a part of the variation in composition of riparian plant communities, although much of the variation in both species composition and these environmental characteristics are explainable by spatial autocorrelation. Additional research into dispersal and a more accurate characterization of the connectivity among these communities, as well as measurement of micro-scale abiotic conditions rather than broad-scale factors, may help to further clarify the factors driving spatial variation in community composition.

Tables

Table 4-1 Environmental variables used in the analysis and data sources for each variable.

Category	Environmental Variable	Abbreviation	Data Source	Resolution
Soil	pH	pH	Field soil samples	.
	% organic matter	OM	Field soil samples	.
	% sand content	sand	Field soil samples	.
Hydrology	Stream order	SO	National Hydrology Dataset Plus	.
	Drainage area	DA	National Hydrology Dataset Plus	.
Land Cover	% wetland within 1 km radius	%WL	National Land Cover Database (NLCD 2006)	30 m
	% forested within 1 km radius	%FR	National Land Cover Database (NLCD 2006)	30 m
	% cultivated within 1 km radius	%CL	National Land Cover Database (NLCD 2006)	30 m
	% developed within 1 km radius	%DV	National Land Cover Database (NLCD 2006)	30 m
Climate	Annual mean temperature	AMT	PRISM Climate Group	800 m
	Annual precipitation	AP	PRISM Climate Group	800 m

Table 4-2 Correlations among environmental variables used in analysis, and summary statistics for each. Abbreviations for the environmental variables are defined in Table 1. AP = annual precipitation; AMT = annual mean temperature; SO = stream order; DA = stream drainage area; Sand = % sand in soil by volume; OM = soil % organic matter, measured by percent mass loss on ignition (%LOI); %DV = % of land within a 1 km radius that is developed; % FR = % land in 1 km radius that is forested; %CL = % land within 1 km radius that is cultivated; %WL = % land within 1 km radius that is wetland.

Variable	**AP**	**AMT**	**SO**	**DA**	**pH**	**Sand**	**OM**	**%DV**	**%FR**	**%CL**	**%WL**
AP											
AMT	-0.3472										
SO	0.0568	0.0938									
DA	-0.2304	0.2271	0.6527								
pH	-0.1056	0.1607	-0.0643	0.0238							
Sand	0.0077	-0.1441	-0.0066	0.0550	0.1751						
OM	0.1377	-0.0551	0.3085	0.0606	-0.4644	-0.1784					
%DV	-0.3294	0.6490	0.0323	0.1504	0.1416	0.03780	-0.1027				
%FR	0.4556	-0.5981	-0.1706	-0.2522	-0.1004	-0.1264	0.0262	-0.6416			
%CL	-0.4141	0.4963	0.1623	0.2176	0.2330	-0.0154	-0.0663	0.2550	-0.7118		
%WL	-0.0443	-0.1673	0.0357	0.0777	-0.3841	0.2232	0.1098	-0.1482	-0.2944	-0.1719	
Units	*mm*	*°C*	*order*	*sq km*	*pH*	*%*	*% LOI*	*%*	*%*	*%*	*%*
Mean	1081	7.5	.	238.5	6.3	0.76	0.033	0.115	0.567	0.1291	0.146
Median	1074	7.2	2	143.0	6.2	0.87	0.025	0.061	0.564	0.0730	0.125
Low	956	4.7	1	14.0	4.2	0.09	0.003	0.002	0.092	0.000	0.002
High	1294	9.8	4	1058.3	8.4	0.99	0.103	0.540	0.970	0.5210	0.474

Table 4-3 Partitioning of the mean squared contingency coefficient in constrained correspondence analysis.

	Inertia	**Proportion**
Total	4.966	1.000
Constrained	1.129	0.227
Unconstrained	3.837	0.773

Table 4-4 Fourth-corner test for significant interactions between three environmental variables (annual mean temperature, soil sand content, and abundance of wetlands in the surrounding 1 km radius) and two broad groupings of plant types (annuals vs. perennials and native vs. introduced to the United States). P-values were adjusted using the FDR method. Significant p-values are shown with an asterisk (*).

Test	**Stat**	**Observed**	**Std. Obs**	**p**	**p_{adj}**
AMT/Lifespan	F	35.017	5.993	0.001	0.006*
Sand/Lifespan	F	0.0047	-0.766	0.943	0.943
%WL/Lifespan	F	0.0636	-0.739	0.842	0.943
AMT/Origin	F	12.910	1.715	0.051	0.102
Sand/Origin	F	1.3676	-0.298	0.442	0.663
%WL/Origin	F	6.0729	1.160	0.105	0.210

Table 4-5 Mantel test of autocorrelation (n = 999 permutations). Adjusted p-values were calculated using the Holm correction method. Significant p-values are shown with an asterisk (*), and marginally significant values with †.

Distance class	Class index	N	Mantel r (r_m)	p	p_{adj}
1	12.3	282	0.249	0.001	0.001*
2	32.5	620	0.063	0.051	0.051†
3	52.8	638	0.010	0.371	0.371
4	73.1	420	-0.169	0.001	0.004*
5	93.3	266	-0.087	0.004	0.012*
6	113.5	188	-0.082	0.005	0.016*

Table 4-6 Summary of coefficients from MRM showing the relative effects of spatial distance and environmental distance on differences in species composition (overall test R^2 = 0.0265, p = 0.006). Differences in species composition are represented in Bray-Curtis dissimilarity; distances in space and in environmental conditions are both Euclidean.

	Dissimilarity	**p**
Intercept	0.7620	0.997
Spatial distance	0.0003	0.018*
Environmental distance	0.0001	0.163

Figures

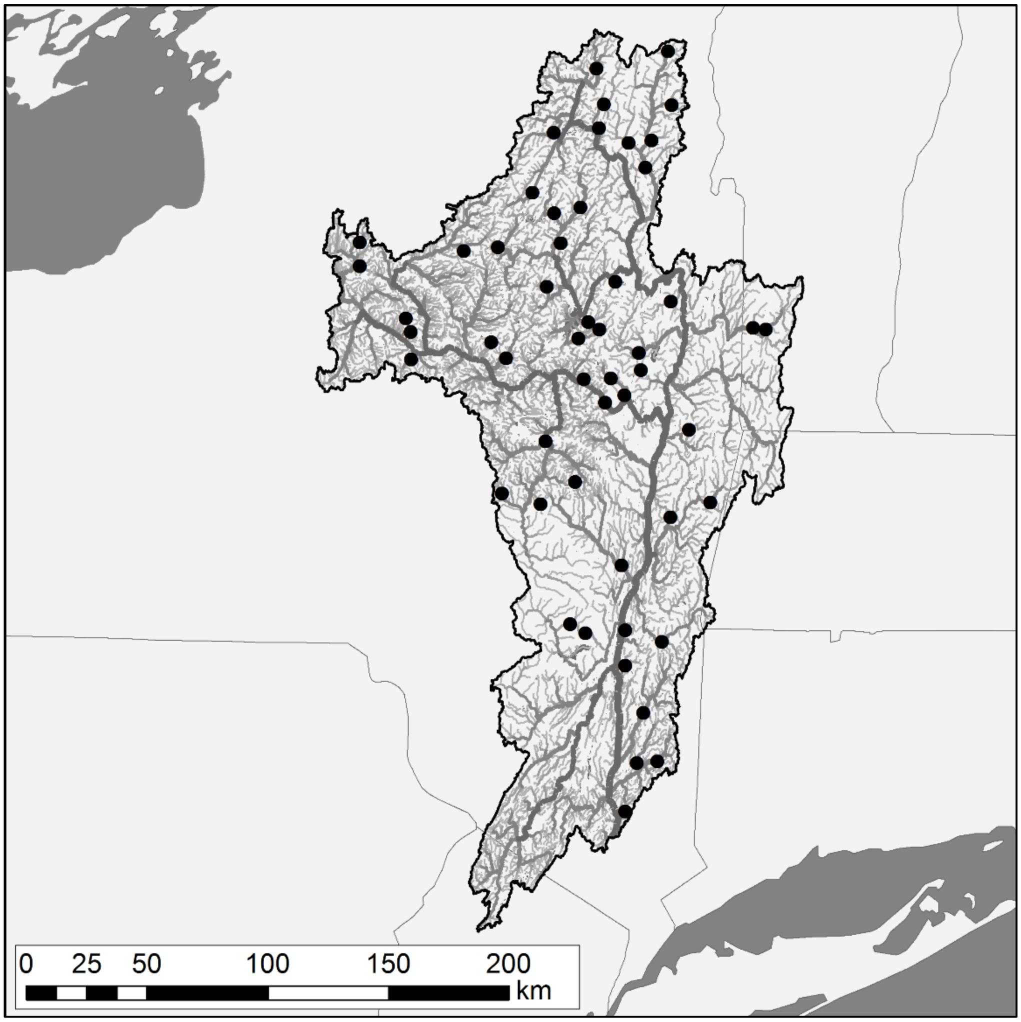


Figure 4-1 Map of the study area. The Upper Hudson Watershed is outlined in black. Field sites are indicated by the black circles. Latitudes and longitudes of each site are provided in Appendix D (Table D-1).

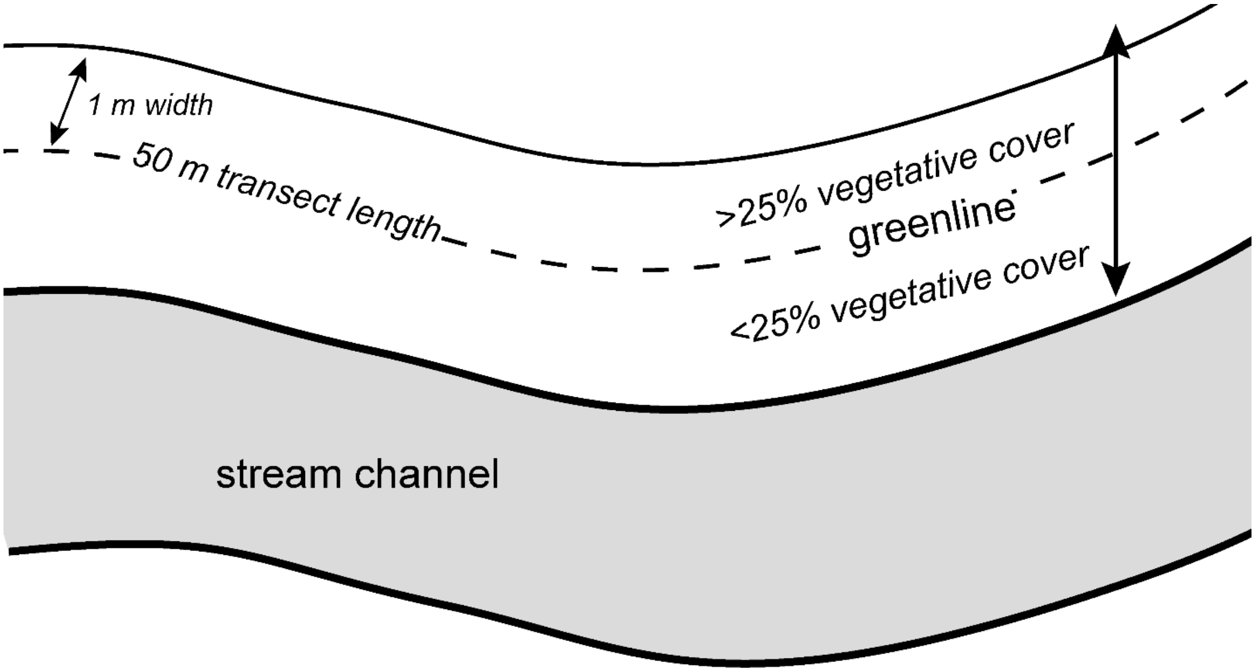


Figure 4-2 Diagram of transect placement and location of the greenline.

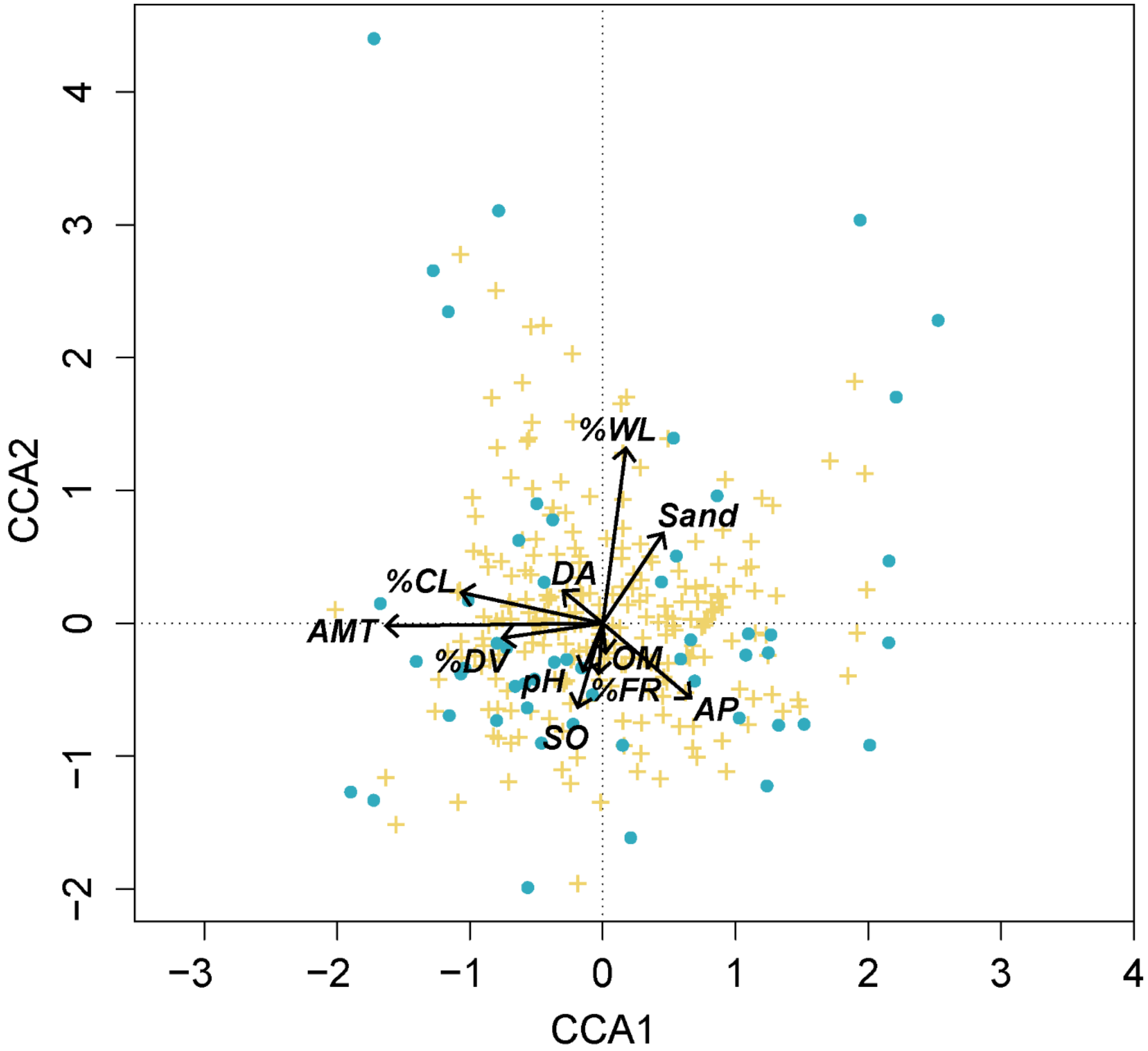


Figure 4-3 CCA ordination of 53 sites and 287 species with 11 environmental variables characterizing the composition of riparian plant communities in the Upper Hudson Watershed. Each sampled species is indicated by a yellow cross; field sites are represented by blue circles, and the environmental variables are indicated by the arrows. Abbreviations for environmental correlates are defined in Table 4-1.

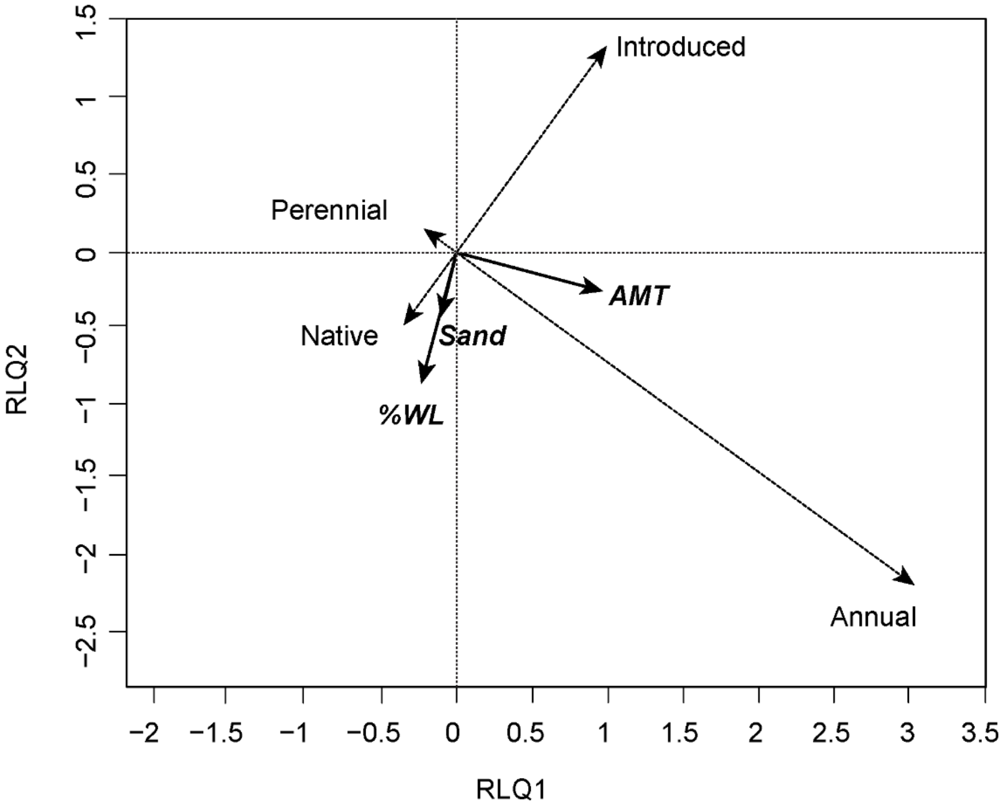


Figure 4-4 RLQ analysis showing associations of three environmental variables and two major groupings of plants. The three best environmental predictor variables were annual mean temperature (AMT), soil sand content (Sand), and abundance of wetlands in the surrounding kilometer radius (%WL). The two groupings of plant species were by lifespan (annuals and perennials) and by species origin relative to the United States (native or introduced). Length and direction of arrows shows strength of association with the RLQ axis.

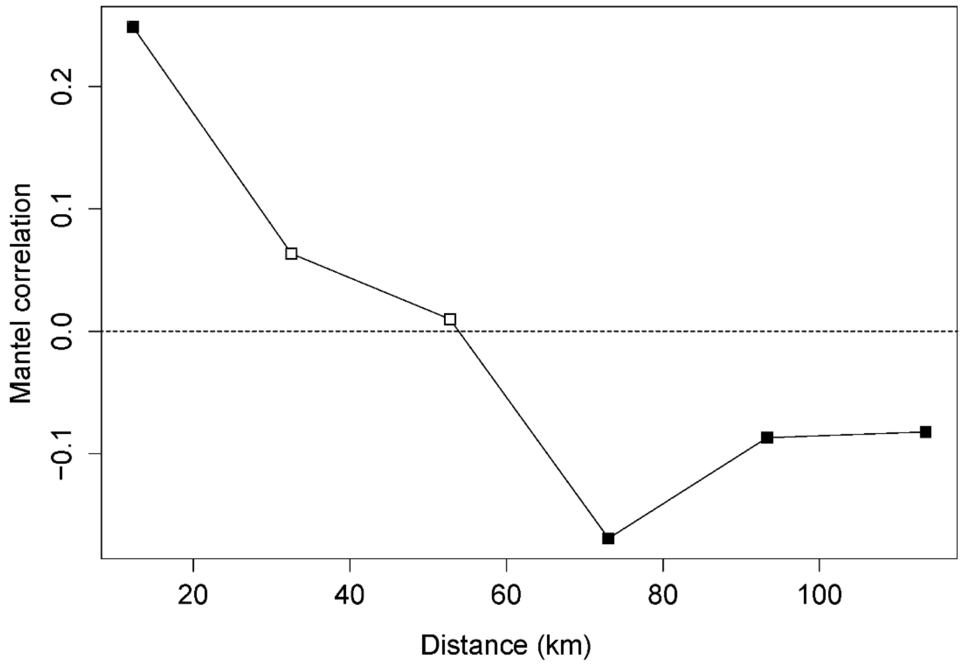


Figure 4-5 Mantel correlogram of correlation of species composition between pairs of sites for species composition. Positive spatial autocorrelation is shown above the 0.0 dotted horizontal line, and negative spatial autocorrelation is shown below the line. Significant spatial autocorrelation is shown in filled squares; non-significance in open squares. Species composition was significantly positively correlated for sites closer than 20 km to one another, and significantly negatively correlated for sites separated by greater than 70 km. Species composition was marginally positively correlated ($r_m = 0.063$, $p_{adj} = 0.051$; Table 4-5) for sites separated by 20 to 40 km.

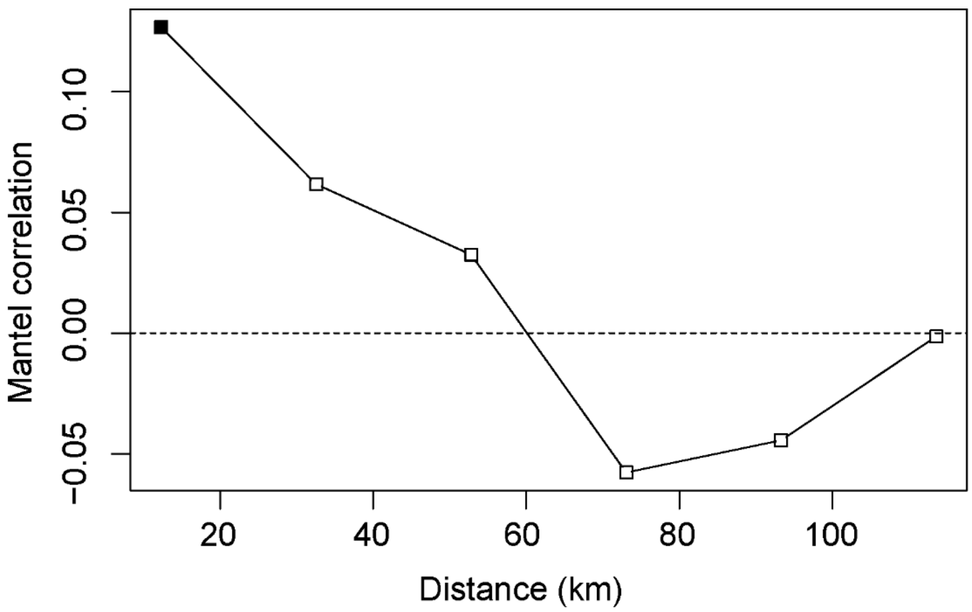


Figure 4-6 Mantel correlogram of correlation between pairs of sites for environmental conditions. Significant spatial autocorrelation is shown in filled squares; non-significance in open squares.

Chapter 5: Partitioning multiple influences of flooding on riparian and non-riparian plant species

Introduction

Riparian plant communities are strongly influenced by adjacent streams and rivers. While factors such as regional climate conditions may also influence patterns in riparian vegetation (Yang et al. 2011), the influence of these factors on vegetation operates within the hydrological and geomorphic context of the riparian zone (Tabacchi et al. 1998). Floods are undoubtedly an important structuring feature in riparian plant communities, and flood frequency is a common explanation for levels of plant diversity in the riparian zone (Pollock et al. 1998, Brown and Peet 2003, Violle et al. 2010), as well the abundance of particular species (Hupp and Osterkamp 1996, Scott et al. 1997, Yang et al. 2011).

The species composition of riparian zones is likely to be in part a reflection of differential tolerance to flooding events of the species found in the broader region, both in connected riparian zones and nearby uplands (i.e., the potential species pool). There is evidence to suggest that flood pulsing can exclude some species from the riparian zone (Vandersande 2001). Species less able to tolerate submergence under water or burial under sediments are less likely to establish in a riparian plant community, while common riparian species are likely to either be tolerant of these conditions or possibly even thrive under them (White 1979, Ewing 1996, Fenster 1997).

Floods can have several simultaneous effects on the riparian zone and its vegetation. Physiological stress caused by underwater submergence may place a plant at a competitive disadvantage against individuals or species better able to tolerate the physical effects of inundation (Palik et al. 1998, Bendix and Hupp 2000). In addition to the direct effects of submergence, receding floodwaters can leave behind sediments that bury riparian vegetation, which may inhibit seedling establishment or growth (Dittmar and Neely 1999) and may adversely affect photosynthetic rates in larger plants (Ewing 1996). A potential benefit of sediment deposition is the associated input of nutrients to the substrate (Vought et al. 1994, Morse et al. 2004, Noe and Hupp 2009). Flood events may also affect organisms that interact with vegetation, including soil microbes, parasites, and pathogens. Each of these consequences of a flood event may affect vegetation differently, but it is difficult to disentangle the relative contributions of each consequence from field observations alone. However, these effects can be applied separately as treatments in an experimental setting. Understanding the effects of flood events at a finer level may provide a greater understanding of mechanisms in riparian community assembly, and an explanation for the apparent exclusion of some regional species from the riparian zone.

The objective of this study was to measure the responses of plants to three consequences of a flood event: submergence under water, burial under deposited sediments, and addition of nutrients. Because survival and plant growth are sensitive to environmental stresses (Ewing 1996), these were used to assess the response of plants to the experimental treatments in the study. I used a greenhouse experiment to independently test the effects of three flood consequences on six herbaceous plant species common in the Upper Hudson watershed: three species commonly found in riparian zones, and three that are rarely observed in riparian zones. This experiment tested the effects of submergence under water, burial under sediments, and nutrient addition on plant survival and growth. I compared the performance of the riparian and non-riparian plants under these three conditions and a control, to determine if the riparian species perform better under various flooding conditions than the non-riparian species, and whether the three individual consequences of floods had different effects on plant survival and growth.

Methods

Species

This experiment included six herbaceous plant species found in the Upper Hudson watershed (Chapter 3). Three of these species (*Bidens frondosa* L., *Polygonum pensylvanicum* L., and *Prunella vulgaris* L.) are common in riparian zones, and three are primarily observed in upland areas outside of the area of regular flooding (*Solidago flexicaulis* L., *Polygonum virginianum* L., and *Marrubium vulgare* L.). These six species, all ruderals as classified by Grime (1974), and represent pairs from three plant families – Asteraceae, Polygonaceae, and Lamiaceae (Table 5-1). The selection criteria for species used in this experiment were: (1) The species was observed frequently during fieldwork (Chapters 3 and 4) in either the riparian zone or upland areas, but not both; (2) Seeds of the species could be obtained; and (3) A second species in the same plant family met Criteria 1 and 2 for the alternate habitat, such that both a riparian and an upland plant within the same family would be represented in the experiment.

Experiment

Seeds of the six species were sown in flats containing commercial potting mix (Sunshine Mix #1, SunGro Horticulture) and allowed to grow for two weeks under standard growth conditions (i.e., not under any experimental treatment). Seedlings were then transplanted into individual pots for the duration of the experiment. The potting mix into which the seedlings were transplanted consisted of 40% sand and 60% peat by volume, reflecting the average sand content of the soils in the riparian sites where they are found (Chapter 3). Lime was also added incrementally to the mix, to neutralize the acidity of the peat; pH was tested with each addition until a neutral pH of 7 was achieved. After transplanting (one plant per pot), the plants were allowed to acclimate for one week before the initiation of experimental treatments. There were

48 individuals of each species except *Solidago flexicaulis* (n = 19) and *Polygonum pensylvanicum* (n = 16), which had poor germination rates.

Plants were given one of four experimental treatments: (1) submergence under water; (2) burial under substrate; (3) nutrient addition; and (4) a control. The appropriate duration of submergence was determined through examination of USGS stream gage data for small streams in the Upper Hudson watershed; two days was the modal duration of events where the gage height was ≥ 10 cm higher than average flow. The submergence treatment consisted of the addition of water to 5 cm above the soil surface, maintained at that level for 2 days of every week. To maintain the water levels, each plastic pot was placed in a larger, clear, plastic pot that did not have drainage holes; submerged plants were manually drained at the end of each submergence period. Plants in all other treatments were also placed in clear plastic pots identical to those in the submergence treatment except for the presence of drainage holes. The burial treatment consisted of the weekly addition of a layer of the custom potting mix (which lacked additional fertilizer) approximately 0.1 cm deep, such that the total accumulation of additional substrate at the conclusion of the experiment represented an intermediate condition between the sedimentation rates tested in Dittmar and Neely (1999), who reported effects of sediment deposition on several congeners of the species used in this experiment (*Bidens coronata* and several *Polygonum* species). The nutrient addition treatment consisted of the once-weekly addition of 16:16:16 N:P:K fertilizer at a concentration of 20 mL per L of water. All plants were watered daily. The experiment lasted for 10 weeks, including one week of acclimation after potting and 9 weeks of treatment. In addition to natural light, grow lights were kept on a 12-hour light:dark cycle throughout the experiment, to normalize the photoperiod throughout the experiment. Survivorship (i.e., number of individuals still alive within each species) was recorded on a weekly basis. Number of leaves and stem height (cm) were recorded at the conclusion of the experiment.

The pots were arranged in three clusters (Figure 5-1). Within each cluster, plants were assigned to six squares, and within each square, assigned to spatial placement following a Latin Square arrangement rather than random assignment, to avoid bias due to potential spatial autocorrelation. The arrangement of the plants within the squares was not explicitly included in the statistical models because their inclusion would remove any replication and make the model impossible to analyze. The spatial arrangement of replicates of each treatment was used to account for expected environmental heterogeneity within the greenhouse (e.g., caused by variable distance from fans or sunlight intensities during the day). Each cluster contained one square for each species, and each square initially contained 4 replicates of each treatment for that species. Species were replicated across the three clusters and located in different positions in each cluster. There were 48 individuals per species, with 12 in each treatment (grouped into three separate clusters), except for two species (*S. flexicaulis* and *P. pensylvanicum*). In these species, low germination rates precluded the establishment of 48 plants. For these two species, individuals were distributed evenly throughout the three clusters and within each square, such that the species still received each treatment within each cluster (Figure 1). Empty pots were placed in the remaining positions of these squares so that the physical layout of the experiment and the number of neighboring pots did not differ among species.

Statistical analysis

All statistical analyses were first done at the species level for each experimental factor, comparing the effects of each experimental treatment to the control conditions. Response ratios were then calculated for each species under each treatment, again relative to the control. Riparian and upland species were compared statistically by comparing their response ratios. The use of response ratios rather than raw response variables (e.g., final height) allows comparison of the two communities without introducing variance caused by inherent differences among species into the comparison of the riparian and upland groups.

Survivorship was assessed for each species using a Cox Proportional Hazards (CPH) regression model stratified by cluster, implemented in the *survival* package (Therneau 2015) in R. The CPH model fits survival at each time step of the experiment (week) as a function of each experimental treatment as follows:

$$h(t,X) = h_o(t)^{\sum_{i=1}^{p} \beta_i X_i}$$

where h is the hazard (risk of death per unit time), t is the time step, X is the experimental treatment, and β is the regression parameter for each treatment. The CPH regression model assumes proportional hazards (meaning that the relative baseline hazard h_0 is constant), but allows stratification among groups that may have a different baseline hazard. When stratified by cluster, the proportional hazards assumption of the CPH regression was met (Appendix E, Table E-1). The hazard ratio (HR) was then calculated for each treatment for each species contrasted against the control:

$$HR(X^*:X) = \frac{e^{\beta X^*}}{e^{\beta X}}$$

where X^* is the experimental treatment, X is the control treatment, and β is the regression parameter for each treatment. Two species, *Prunella vulgaris* and *Solidago flexicaulis,* experienced no mortality under the submergence treatment. When there was no mortality, the hazard estimate for that treatment converges to infinity (in effect representing zero risk of death at any time step). Therefore, to assess the effects of submergence on these species, the data were modified to add one mortality event for each species in the final week. For species that otherwise had no mortality events, this allowed a non-infinite hazard ratio estimate to be calculated. Estimates of hazard ratios did not differ qualitatively between the modified and unmodified CPH models. Therefore, the modified CPH models are reported for these two species to allow the description of the effects of submergence. The unmodified CPH results are reported in Appendix E (Table E-2).

Reponses of the riparian and the upland species to each experimental treatment were compared using log hazard ratios. These were compared using a linear mixed-effects model fit by restricted maximum likelihood (REML) in the R package *metafor* (Viechtbauer 2010) in R statistical software version 3.2.2 (R Core Team 2015).

Growth variables (height and number of leaves) were analyzed for individuals surviving to the conclusion of the experiment. Treatment effects on each individual species were analyzed using a linear mixed-effects model fit by REML for each species, including treatment as a fixed effect and cluster as a random effect:

$$G_{ij} \sim N(E[G_{ij}], \sigma^2)$$

$$1: E[G_{ij}] = \mu + x_{ij}\beta + u_{ij}b_i$$

$$i = 1, \dots, m; j = 1, \dots, n_i$$

where m is the number of treatments (4), n_i is the number of individuals within each treatment for that species, β is the fixed effect parameter for treatment, and b is the random effect parameter for cluster.

To compare the overall growth responses of riparian and upland species to each treatment, log response ratios (LRR) of each treatment versus control were analyzed using a linear mixed-effects model fit by REML in *metafor*:

$$LRR \sim N(E[LRR], \sigma^2)$$

$$1{:}\ E[LRR] = \mu + x_{ij}\beta + u_{ij}b$$

$$i = 1,2\ (riparian\ or\ upland);\ j = 1,2,3\ (cluster)$$

where β is the fixed effect of the riparian-upland contrast and b is the random effect of cluster.

As the primary goal of this study was to examine differences between riparian and upland species in response to flooding treatments, the majority of the analyses described below include the riparian and upland effect and exclude plant family from the model. It was not possible to include effects both of plant family and of riparian/upland species in the same model, as there was no replication (i.e., there was only one riparian species and one upland species per plant family in the experiment). However, I performed a separate analysis to examine differences among the plant families in survival or growth.

Results

Survival

Riparian and upland species did not differ in survival rate under any of the three experimental treatments (submergence, burial, or nutrient addition) (Table 5-2). However, survival of some species differed among the three treatments (Table 5-3). Survival differed among treatments in *B. frondosa* (p = 0.0193, Table 5-3), although post hoc tests found no individual treatment was significantly different in mortality from the control treatment for this species (Figure 5-2, Table 5-3). Although the submergence treatment did not differ significantly from the control, it may drive the significance of the overall model for *B. frondosa* (Table 5-3). Only two individuals of this species died under the submergence treatment, while five died in the nutrient addition treatment, ten died in burial, and six died in the control. Mortality in this species was not spatially clustered in the experiment.

Both the nutrient addition (hazard ratio = 0.275, p = 0.019) and submergence treatments (hazard ratio = 0.045, p = 0.003) reduced mortality in *Polygonum virginianum* (Table 5-4, Figure 5-2). Reduction of mortality was also seen in *Prunella vulgaris* for both nutrient addition (hazard ratio = 0.255, p = 0.043) and submergence (hazard ratio = 0.043, p = 0.005) (Table 5-4, Figure 5-2). However, the nutrient addition effect was not significant for *P. vulgaris* in the unmodified CPH model (hazard ratio = 0.0284, p = 0.061), although the hazard ratios in the two models are similar (Appendix E, Table E-2). Burial appeared to increase mortality in *Marrubium vulgare* (upland; hazard ratio = 2.94, p = 0.039; Table 5-4, Figure 5-2), although the overall CPH regression for *M. vulgare* was not significant (Table 5-3).

Growth

Burial significantly reduced the final height of upland, but not riparian, plants (z = -2.09, p = 0.038, Table 5-5) in comparison to controls. Submergence and nutrient addition did not affect riparian and upland plants differently (Table 5-5).

Individual species differed in their responses to the three experimental treatments. Nutrient addition increased plant height in *S. flexicaulis* (t = 4.10, p = 0.009; Tables 5-6 and 5-7, Figure 5-3) and increased the number of leaves in *P. virginianum* (t = 2.91, p = 0.010; Tables 5-6 and 5-7, Figure 5-4). Nutrient addition did not have a significant effect on plant growth measures in any of the other species (Table 5-7). Burial significantly reduced final height in *M. vulgare* (t = -4.80, p = 0.003; Table 5-7, Figure 5-3). While the overall model found a significant effect of treatment on the number of leaves produced by *P. vulgaris*, individual treatment contrasts did not have sufficient power to detect which treatments were significantly different from the control. The number of leaves produced by *P. vulgaris* tended to be lower in burial treatments (t = -2.03, p = 0.053) and higher under nutrient addition (t = 1.88, p = 0.072), but neither difference was significant (Table 5-7, Figure 5-3). No other treatments significantly affected growth measurements in surviving plants in any species (Table 5-7).

Differences among plant families

Differences among plant families in their survival rate were not significant (df = 2, p = 0.075). Final height and number of leaves both differed among families (height: $\chi^2 = 23.1$, df = 3, $p < 0.0001$; leaves: $\chi^2 = 39.9$, df = 3, $p < 0.0001$).

Alternative analysis designs

Performing the analyses described above with three clusters containing two columns of squares each (Figure 5-5), rather than the three horizontal rows in the individual design (Figure 5-1), produced results that did not differ in significance from those described above (Appendix E, Tables E-3 and E-4). Analyses with no blocking included in the model also produced results that did not differ in significance from those obtained in the analyses above.

Discussion

Flood events are often implicated in the structure and composition of riparian plant communities. Many studies have examined the effects of flooding on riparian plant community composition and on the success of individual species. Some focus on multiple effects of submergence, such as examining the consequences of the depth, duration and frequency of submergence (Casanova and Brock 2000, Warwick and Brock 2003). Here, I separated the effects of submergence, sediment deposition and nutrient addition to understand how each of these aspects of a flood event influenced survival and growth of vegetation, and whether these effects differed among three common riparian species and three common upland species of the Upper Hudson watershed in New York State.

Survival did not differ overall between riparian and upland species under any of the three experimental treatments. Overall, riparian and upland species did not differ in growth responses to submergence or nutrient addition, but did differ in response to burial. Additionally, for both riparian and upland species, individual species differed in response to some of the different treatments.

Submergence reduced mortality in one riparian (*Prunella vulgaris*) and one upland species (*Polygonum virginianum*), which are in different families. Some species are known to thrive under submerged conditions. For instance, two species of *Polygonum*, congeners to two of the species in this study, have been shown to grow better under flooded than drained conditions (Carter and Grace 1990). While some species do grow best under flooded conditions, it is also possible that in this experiment the benefit from submergence reflects an overall benefit of additional water in a greenhouse setting where plants might dry out quickly in small pots, even if watered daily, rather than a true benefit from flooding conditions. Future experiments conducted using a standing water table rather than daily watering treatments are needed test this aspect of the effect of submergence on survival.

This study included one riparian and one upland species from each of three plant families and all selected species were ruderals (Grime 1974). This design was intented to minimize differences that might arize from comparing plants that are too distantly related or have different life strategies. Because the study only included one riparian and one upland species from each family, analyses were not able to include the family effect, treatment effects, and the riparian/upland effect simultaneously. However, when comparing the responses of plants among families, there was a difference in growth (final height and number of leaves). Families did not differ significantly in survival rate.

The three experimental conditions (submergence, burial under sediment, and nutrient addition) did not significantly improve or hinder the growth of riparian species. These results suggest that the three riparian species in this study do not especially thrive under flooding conditions, but are largely capable of tolerating them. Interestingly, nutrient addition did not significantly benefit the three riparian species, while it was found to increase growth in two upland species and reduce mortality in one. Burial and submergence did not adversely affect upland species, with the exception of *Marrubium vulgare*, which showed increased mortality and reduced height under the burial treatment. This suggests that flooding may be the mechanism by which *M. vulgare* is excluded from riparian plant communities in the Upper Hudson watershed. In contrast, it does not appear that the effects of flooding tested in this study are a primary mechanism in excluding the other two upland species from the riparian zone.

It is possible that these upland species, while able to tolerate the effects of flooding when grown in isolation, are poor competitors under these conditions. This was observed in a comparison of competitive ability in native riparian plants of the southeastern US and the introduced species *Tamarix ramosissima* (Vandersande 2001). Under flooded conditions, the native riparian species outperformed *T. ramosissima*, suggesting that natural flood pulse regimes reduced the competitive advantage that the introduced species has under altered flooding regimes. A study of three herbaceous *Polygonum* species found a trade-off between flood tolerance and competitive ability (Carter and Grace 1990). Similar competitive interactions may play a role in the exclusion of the three upland species in this study from the riparian zone, although competition was not examined in this experiment. Flood events may also affect a different life history stage than was tested in this study, such as seed survival or germination.

Another possibility is that species not found in the riparian zone are excluded not because of regular, small flood events, but instead by rarer and more extreme ones.

Other factors not examined here, including indirect effects of parasites and mutualists, may also play a role in species distributions. Pathogens, mutualists, and parasites may be tolerant or intolerant of drought or excess moisture, and plants may vary in their ability to resist these pathogens. Soil microbial communities also differ between wet and dry soils, a factor not addressed in this experiment. Riparian soils are younger than upland soils, and older upland soils potentially have more microbial interactions that affect plant growth. While soil was mixed to represent the soil chemistry of field sites where these plant species were observed (Chapter 3), I did not attempt to replicate the microbial characteristics of these soils. The effects of soil microbial communities and plant-soil feedbacks are known to greatly influence plant community composition (Klironomos 2002, Ehrenfeld et al. 2005, Kardol et al. 2006, 2007, Kulmatiski et al. 2008, Schnitzer et al. 2011). Soil characteristics may potentially have affected the results of this experiment. Upland species consistently were lower in height than riparian species (Figure 5-3), even under control conditions, suggesting that they may have been more successful in the experimental soil conditions, while upland species may have required a more developed microbial community in the substrate to thrive.

I found that species' responses to particular aspects of flooding were individualistic. No single species responded universally positively or negatively, in terms of survival and growth, to all treatments. This suggests that the mechanisms excluding species from the riparian zone are likely to be variable and dependent on the characteristics of individual species. Here, *M. vulgare* performed poorly under burial conditions, while the two other upland species in the experiment did not. Not all riparian species responded in the same way to a given treatment, nor did all upland species. Except for the difference in plant height between riparian and upland plants in response to burial, no particular response trends distinguish these two groups. It is clear that the responses of vegetation to flood events are complex. The results of this experiment demonstrate that plant responses to a flood depend on the species in question and the specific consequences of the flood event. Riparian plant community composition may represent a mosaic of such individualistic responses of species to multiple, simultaneous consequences of flood events.

Tables

Table 5-1 Species used in the experiment. Three species representative of riparian plant communities, and three representative of upland plant communities were included. The species were paired by family. N indicates the number of plant across all treatments at the start of the experiment, and N (End) indicates the number of individuals remaining alive at the conclusion of the experiment.

	Riparian	**N**	**N (End)**	**Upland**	**N**	**N (End)**
Asteraceae	*Bidens frondosa* L.	48	25	*Solidago flexicaulis* L.	19	11
Polygonaceae	*Polygonum pensylvanicum* L.	16	8	*Polygonum virginianum* L.	48	22
Lamiaceae	*Prunella vulgaris* L.	48	29	*Marrubium vulgare* L.	48	11

Table 5-2 Results of a linear mixed-effects model comparing the survival of riparian and upland species in each treatment. Treatment effects are given as the log hazard ratio contrasted with the control. Significant p-values are represented with an asterisk (*).

	Est.	**95% CI (Lower)**	**95% CI (Upper)**	**SE**	**z**	**p**
Submergence						
Intercept	-2.0420	-4.0561	-0.0278	1.0276	0.0469	0.0469*
Habitat (Upland)	0.7785	-2.0176	3.5746	1.4266	0.5457	0.5853
Burial						
Intercept	0.0476	-1.0533	1.1485	0.5617	0.0847	0.9325
Habitat (Upland)	0.0373	-1.4833	1.5579	0.7758	0.0481	0.9616
Nutrient addition						
Intercept	-0.3532	-1.4711	-0.7648	0.5704	-0.6192	0.5358
Habitat (Upland)	-0.2829	-1.8025	1.2367	0.7753	-0.3649	0.7152

Table 5-3 Overall model fit of Cox Proportional Hazards (CPH) regression on the survival of each of the six species. Significant p-values are represented with an asterisk (*).

	Concordance	**SE**	**R^2**	**LR**	**p**
Bidens frondosa	0.680	0.124	0.187	9.91	0.0193*
Solidago flexicaulis	0.750	0.259	0.215	4.60	0.2040
Polygonum pensylvanicum	0.750	0.208	0.228	4.14	0.2467
Polygonum virginianum	0.756	0.117	0.355	21.04	0.0001*
Prunella vulgaris	0.733	0.126	0.269	15.03	0.0018*
Marrubium vulgare	0.652	0.124	0.117	5.98	0.1125

Table 5-4 Treatment coefficients from Cox Proportional Hazards regression on the survival of each species, contrasted against the control treatment. A hazard ratio greater than 1 represents an increase in hazard (i.e., lower survival) as compared to the control; a hazard ratio lower than 1 represents higher survival. Significant p-values are represented with an asterisk (*).

	Coef.	**SE**	**Hazard Ratio**	**95% CI (lower)**	**95% CI (upper)**	**z**	**p**
Bidens frondosa (Asteraceae; riparian)							
Burial	0.7072	0.5363	2.0283	0.709	5.803	1.319	0.1873
Nutrient addition	-0.0756	0.5957	0.9272	0.288	2.980	-0.127	0.8991
Submergence	-1.4184	0.8245	0.2421	0.048	1.218	-1.720	0.0854
Solidago flexicaulis (Asteraceae; upland)							
Burial	-0.9780	0.9562	0.3761	0.058	2.450	-1.023	0.3064
Nutrient addition	-0.8938	0.9479	0.4091	0.064	2.622	-0.943	0.3457
Submergence	-2.2466	1.2112	0.1058	0.010	1.136	-1.855	0.0636
Polygonum pensylvanicum (Polygonaceae; riparian)							
Burial	0.2264	1.0859	1.2541	0.149	10.530	0.209	0.8350
Nutrient addition	0.9850	1.1211	2.6777	0.298	24.100	0.879	0.3800
Submergence	-1.6773	1.1833	0.1869	0.018	1.900	-1.417	0.1560
Polygonum virginianum (Polygonaceae; upland)							
Burial	-0.2977	0.4773	0.7426	0.291	1.892	-0.624	0.5329
Nutrient addition	-1.2909	0.5522	0.2750	0.093	0.812	-2.338	0.0194*
Submergence	-3.1051	1.0535	0.0448	0.006	0.3534	-2.947	0.0032*
Prunella vulgaris (Lamiaceae; riparian)							
Burial	-0.7176	0.5579	0.4879	0.164	1.456	-1.286	0.1983
Nutrient addition	-1.3651	0.6778	0.2553	0.068	0.964	-2.014	0.0434*
Submergence	-3.1331	1.1052	0.0436	0.005	0.380	-2.835	0.0046*
Marrubium vulgare (Lamiaceae; upland)							
Burial	1.0421	0.5047	2.8351	1.054	7.623	2.065	0.0389*
Nutrient addition	0.1356	0.5328	1.1452	0.403	3.254	0.254	0.7992
Submergence	0.7171	0.4819	2.0485	0.797	5.268	1.488	0.1367

Table 5-5 Results of a generalized linear model comparing growth (final height and final number leaves) between riparian and upland species, as represented by log response ratios contrasting each experimental treatment to the control. Significant p-values are represented with an asterisk (*).

	Est.	95% CI (Lower)	95% CI (Upper)	SE	z	p
Submergence						
Height (cm)						
Intercept	-0.3306	-0.7164	0.0552	0.1968	-1.6797	0.0930
Habitat (Upland)	0.3718	-0.1982	0.9417	0.2908	1.2785	0.2011
Number of leaves						
Intercept	0.1153	-0.4365	0.6671	0.2815	0.4095	0.6822
Habitat (Upland)	-0.3622	-1.1931	0.4688	0.4240	-0.8542	0.3930
Burial						
Height (cm)						
Intercept	-0.0615	-0.5941	0.4712	0.2717	-0.2261	0.8211
Habitat (Upland)	-0.7449	-1.4468	-0.0429	0.3581	-2.0799	0.0375*
Number of leaves						
Intercept	0.2894	-0.8983	1.4772	0.6060	0.4776	0.6330
Habitat (Upland)	-0.7370	-2.4328	0.9589	0.8653	-0.8517	0.3944
Nutrient addition						
Height (cm)						
Intercept	0.2478	-0.2292	0.7249	0.2434	1.0181	0.3086
Habitat (Upland)	0.2933	-0.3667	0.9534	0.3368	0.8710	0.3837
Number of leaves						
Intercept	0.8664	0.0554	1.6774	0.4138	2.0939	0.0363*
Habitat (Upland)	-0.3068	-1.4412	0.8275	0.5788	-0.5302	0.5960

Table 5-6 Overall significance of the linear mixed-model tests of the effects of experimental treatments on growth in each species. Significant p-values are represented with an asterisk (*).

	num df	den df	F	p	
***Bidens frondosa* (Asteraceae; riparian)**					
Height (cm)					
Intercept	1	18	131.494	< 0.0001	*
Treatment	3	18	0.378	0.7698	
Number of leaves					
Intercept	1	18	62.548	< 0.0001	*
Treatment	3	18	0.243	0.8651	
***Solidago flexicaulis* (Asteraecae; upland)**					
Height (cm)					
Intercept	1	5	134.756	0.0001	*
Treatment	3	5	21.228	0.0028	*
Number of leaves					
Intercept	1	5	45.098	0.0011	*
Treatment	3	5	13.205	0.0082	*
***Polygonum pensylvanicum* (Polygonaceae; riparian)**					
Height (cm)					
Intercept	1	2	66.463	0.0147	*
Treatment	3	2	2.102	0.3385	
Number of leaves					
Intercept	1	2	46.762	0.0207	*
Treatment	3	2	7.182	0.1247	
***Polygonum virginianum* (Polygonaceae; upland)**					
Height (cm)					
Intercept	1	16	103.844	< 0.0001	*
Treatment	3	16	2.817	0.0724	
Number of leaves					
Intercept	1	16	59.361	< 0.0001	*
Treatment	3	16	13.330	< 0.0001	*
***Prunella vulgaris* (Lamiaceae; riparian)**					
Height (cm)					
Intercept	1	23	153.244	< 0.0001	*
Treatment	3	23	0.970	0.4240	
Number of leaves					
Intercept	1	23	127.383	< 0.0001	*
Treatment	3	23	7.165	0.0014	*

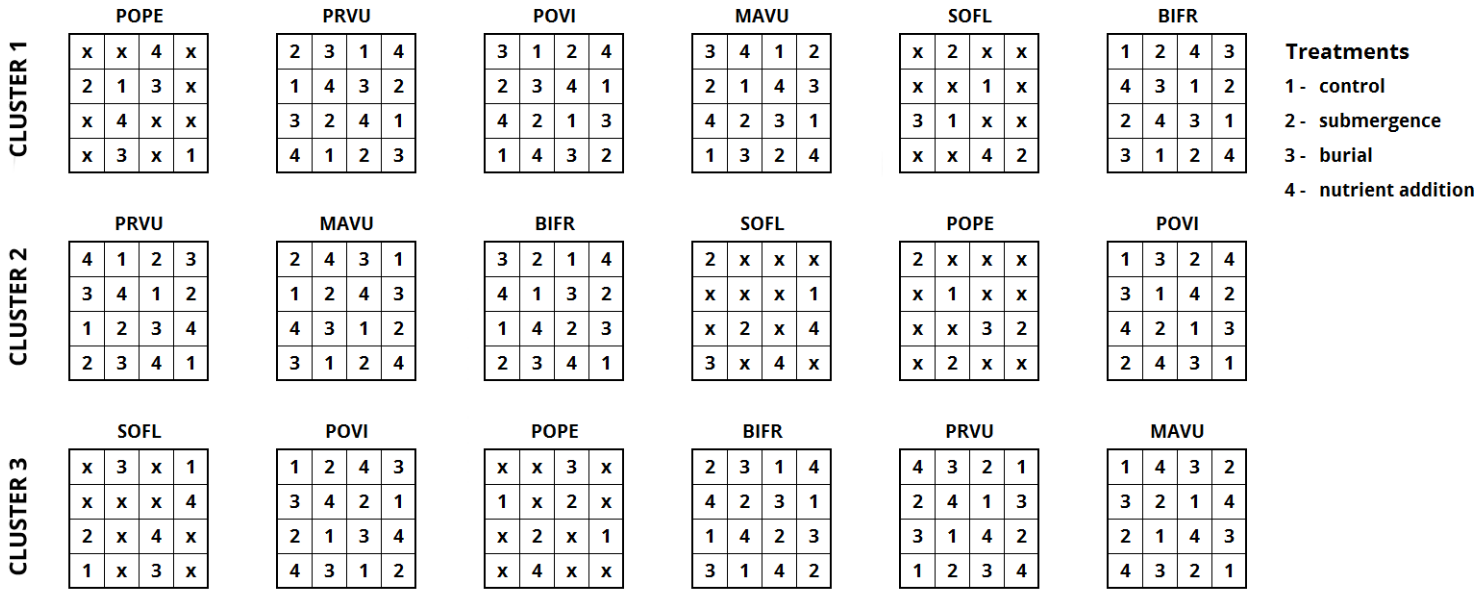
	num df	den df	F	p	
***Marrubium vulgare* (Lamiaceae; upland)**					
Height (cm)					
Intercept	1	6	252.654	< 0.0001	*
Treatment	2	6	14.669	0.0049	*
Number of leaves					
Intercept	1	6	17.109	0.0061	*
Treatment	2	6	2.512	0.1612	

Table 5-7 Results of linear mixed-effects models of plant growth in each species, as measured by height and number of leaves, with treatment effects contrasted against the control treatment. Model includes all surviving individuals at the conclusion of the experiment. The flooded treatment is not included for *Marrubium vulgare* as no individuals of that species in that treatment survived to the conclusion of the experiment. Significant p-values are represented with an asterisk (*).

	β	**SE**	**df**	**t**	**p**
Bidens frondosa **(Asteraceae; riparian)**					
Height (cm)					
Intercept	17.85	2.878	18	6.203	< 0.0001 *
Burial	-4.417	4.985	18	-0.886	0.387
Nutrient addition	0.033	4.070	18	0.008	0.994
Submergence	-2.150	3.715	18	-0.579	0.570
Number of leaves					
Intercept	19.83	4.982	18	3.981	0.001 *
Burial	4.167	8.629	18	0.483	0.635
Nutrient addition	0.967	7.045	18	0.137	0.892
Submergence	-2.389	6.432	18	-0.371	0.715
Solidago flexicaulis **(Asteraecae; upland)**					
Height (cm)					
Intercept	9.600	3.732	5	2.572	0.045 *
Burial	-6.400	4.571	5	-1.400	0.220
Nutrient addition	17.667	4.310	5	4.099	0.009 *
Submergence	-0.420	4.089	5	-0.103	0.922
Number of leaves					
Intercept	13.58	2.930	5	4.637	0.006 *
Burial	-6.000	2.953	5	-2.032	0.098
Nutrient addition	4.021	3.012	5	1.335	0.240
Submergence	-7.100	2.943	5	-2.413	0.060
Polygonum pensylvanicum **(Polygonaceae; riparian)**					
Height (cm)					
Intercept	18.8	6.392	2	2.941	0.099
Burial	3.4	7.829	2	0.434	0.706
Nutrient addition	11.2	9.040	2	1.239	0.341
Submergence	-5.25	7.147	2	-0.735	0.539
Number of leaves					
Intercept	4	4.757	2	0.841	0.489
Burial	15.5	5.826	2	2.661	0.117
Nutrient addition	21	6.727	2	3.122	0.089
Submergence	2	5.318	2	0.376	0.743

	β	**SE**	**df**	**t**	**p**	
***Polygonum virginianum* (Polygonaceae; upland)**						
Height (cm)						
Intercept	8.500	4.921	16	1.7274	0.1034	
Burial	-2.8333	5.682	16	-0.4987	0.6248	
Nutrient addition	6.2143	5.2605	16	1.1813	0.2547	
Submergence	1.200	5.1400	16	0.2335	0.8183	
Number of leaves						
Intercept	5.0832	2.0581	16	2.4699	0.0252	*
Burial	2.9383	2.2711	16	1.2937	0.2141	
Nutrient addition	5.6725	1.9518	16	2.9062	0.0103	*
Submergence	0.3637	1.9432	16	0.1872	0.8539	
***Prunella vulgaris* (Lamiaceae; riparian)**						
Height (cm)						
Intercept	7.2912	1.5938	23	4.5747	0.0001	*
Burial	-0.1568	2.0064	23	-0.0782	0.9384	
Nutrient addition	2.0254	1.8230	23	1.1110	0.2781	
Submergence	1.8588	1.7521	23	1.0609	0.2997	
Number of leaves						
Intercept	35.00	8.0702	23	4.3370	0.0002	*
Burial	-22.00	10.8273	23	-2.0319	0.0539	
Nutrient addition	18.6250	9.8839	23	1.8844	0.0722	
Submergence	-6.0833	9.3186	23	-0.6528	0.5203	
***Marrubium vulgare* (Lamiaceae; upland)**						
Height (cm)						
Intercept	9.29058	0.7589	6	12.2419	<0.0001	*
Burial	-6.39207	1.33192	6	-4.7991	0.0030	*
Nutrient addition	0.8324	1.11387	6	0.7473	0.4831	
Number of leaves						
Intercept	16.4096	6.1229	6	2.6801	0.0365	*
Burial	-12.8848	9.8637	6	-1.3063	0.2393	
Nutrient addition	11.4003	8.7117	6	1.3086	0.2386	

Figures



CLUSTER 1

POPE

x	x	4	x
2	1	3	x
x	4	x	x
x	3	x	1

PRVU

2	3	1	4
1	4	3	2
3	2	4	1
4	1	2	3

POVI

3	1	2	4
2	3	4	1
4	2	1	3
1	4	3	2

MAVU

3	4	1	2
2	1	4	3
4	2	3	1
1	3	2	4

SOFL

x	2	x	x
x	x	1	x
3	1	x	x
x	x	4	2

BIFR

1	2	4	3
4	3	1	2
2	4	3	1
3	1	2	4

Treatments

1 - control
2 - submergence
3 - burial
4 - nutrient addition

CLUSTER 2

PRVU

4	1	2	3
3	4	1	2
1	2	3	4
2	3	4	1

MAVU

2	4	3	1
1	2	4	3
4	3	1	2
3	1	2	4

BIFR

3	2	1	4
4	1	3	2
1	4	2	3
2	3	4	1

SOFL

2	x	x	x
x	x	x	1
x	2	x	4
3	x	4	x

POPE

2	x	x	x
x	1	x	x
x	x	3	2
x	2	x	x

POVI

1	3	2	4
3	1	4	2
4	2	1	3
2	4	3	1

CLUSTER 3

SOFL

x	3	x	1
x	x	x	4
2	x	4	x
1	x	3	x

POVI

1	2	4	3
3	4	2	1
2	1	3	4
4	3	1	2

POPE

x	x	3	x
1	x	2	x
x	2	x	1
x	4	x	x

BIFR

2	3	1	4
4	2	3	1
1	4	2	3
3	1	4	2

PRVU

4	3	2	1
2	4	1	3
3	1	4	2
1	2	3	4

MAVU

1	4	3	2
3	2	1	4
2	1	4	3
4	3	2	1

Figure 5-1 Diagram of the spatial layout of the experimental arrangement within the greenhouse. Species were replicated in three clusters. Each cluster contained one Latin square for each species containing the four treatments. POPE = *Polygonum pensylvanicum*, PRVU= *Prunella vulgaris*, POVI = *Polygonum virginianum*, MAVU = *Marrubium vulgare*, SOFL = *Solidago flexicaulis*, BIFR = *Bidens frondosa*. Due to low germination rates in *P. pensylvanicum* and *S. flexicaulis*, some positions in the experimental grid remained empty because of lack of germination, and are indicated with an x. Within these species, samples were still arranged such that no treatments were repeated within rows or columns of a square, each square contained all four treatments, and sample sizes were as equal as possible across the four treatments. Clusters were taken into account in analyses to account for potential gradients in environmental conditions in the greenhouse.

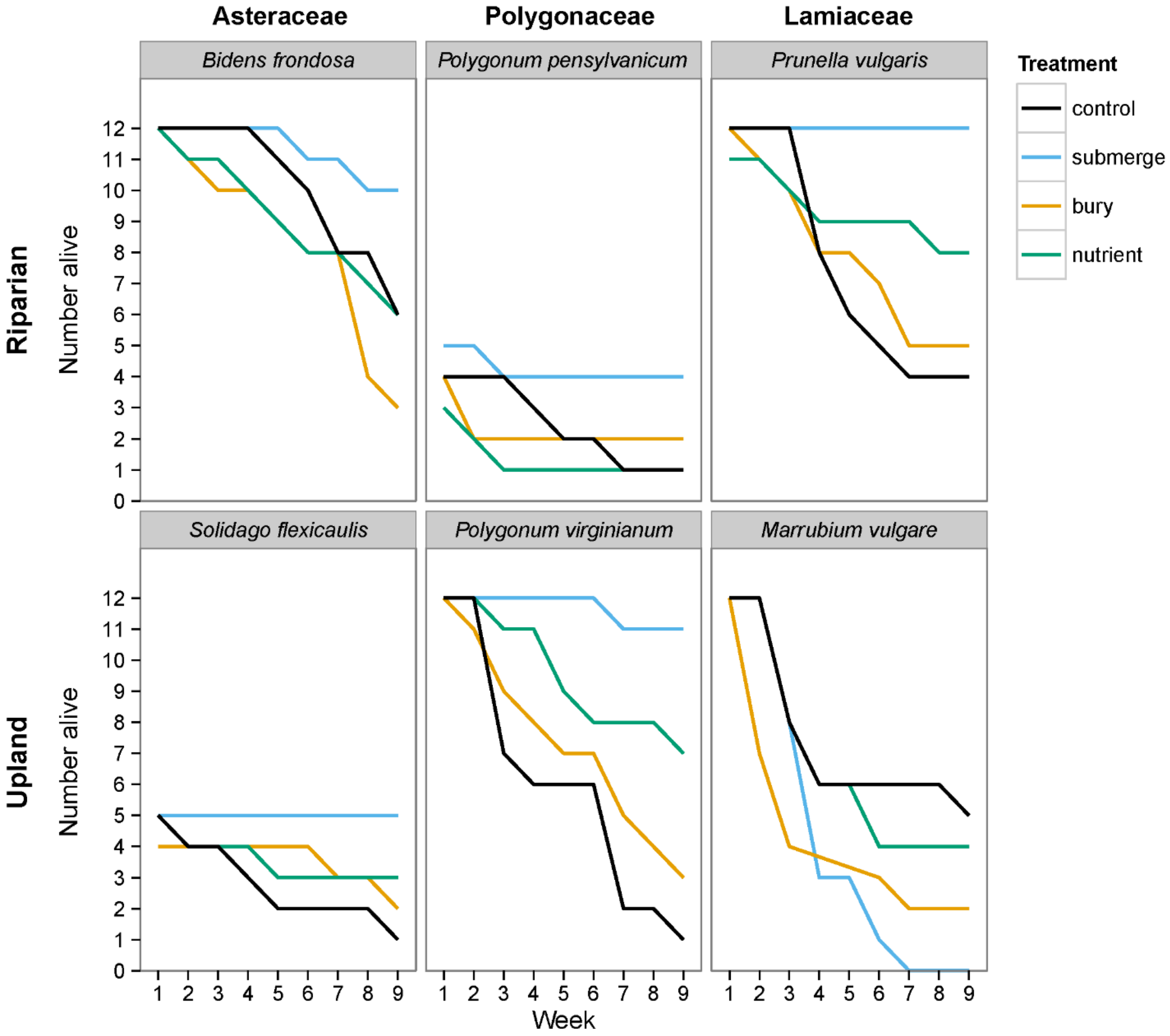


Figure 5-2 Survivorship of the six species in each of the four treatments. Control is shown in black; submerged treatment in blue; burial in brown; and nutrient addition in green. Riparian species are shown in the top row and upland species in the bottom row.

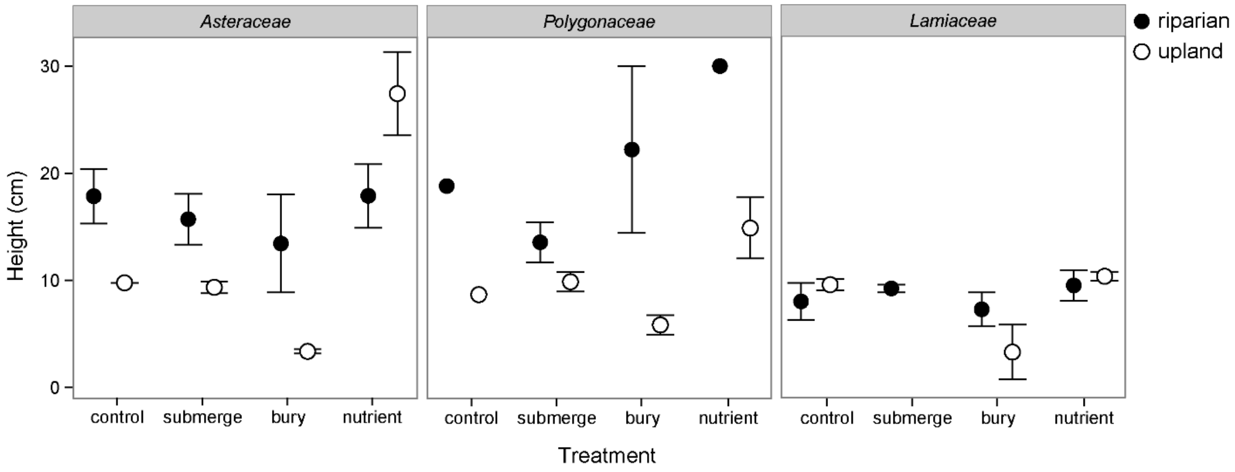


Figure 5-3 Mean height (± SE) of surviving plants at the conclusion of the experiment for each species (grouped by family) and treatment. Riparian species are shown in closed circles and upland species in open circles. Points with no error bars are for species with only one surviving individual at the end of the experiment. No point is shown for *M. vulgare* (Lamiaceae, upland) under the submergence treatment as no individuals survived to the conclusion of the experiment.

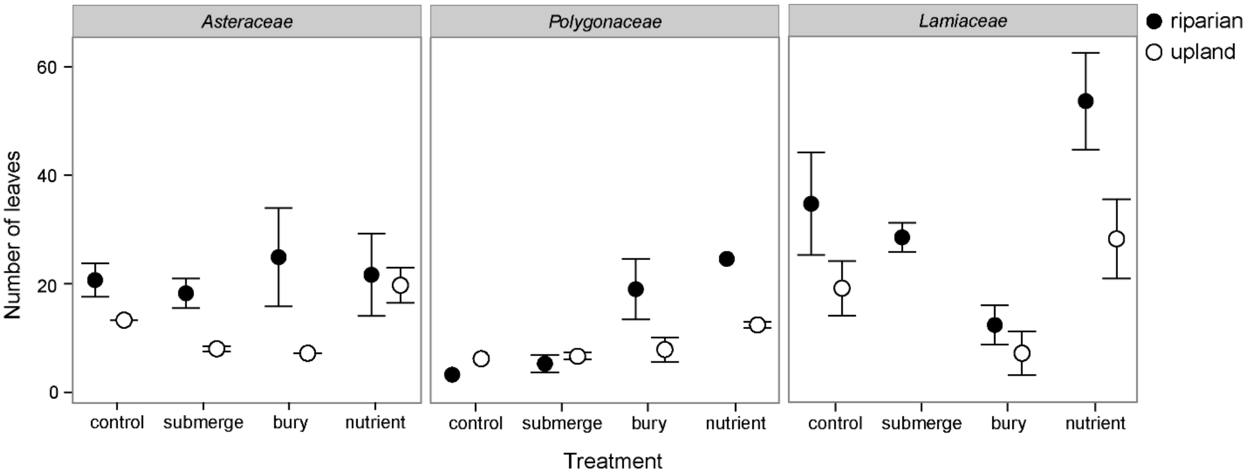
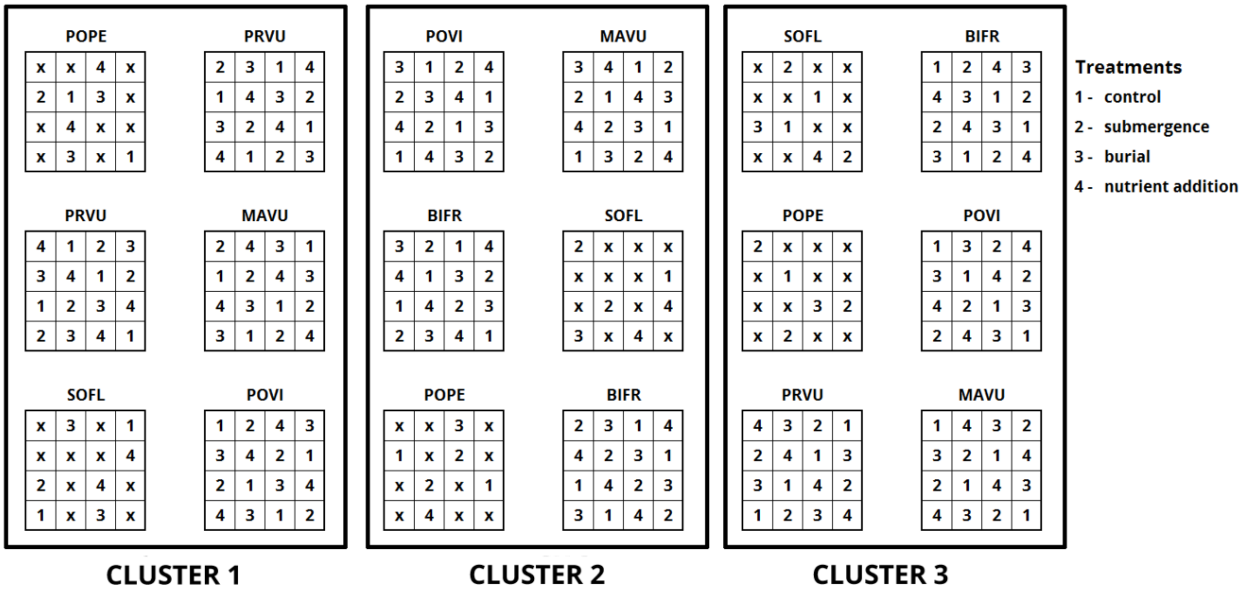


Figure 5-4 Mean number of leaves (± SE) surviving plants at the conclusion of the experiment for each species (grouped by family) and treatment. Riparian species are shown open circles and upland species in closed circles. Points with no error bars are for species with only one surviving individual at the end of the experiment. No point is shown for *M. vulgare* (Lamiaceae, upland) under the submergence treatment as no individuals survived to the conclusion of the experiment.



POPE

x	x	4	x
2	1	3	x
x	4	x	x
x	3	x	1

PRVU

2	3	1	4
1	4	3	2
3	2	4	1
4	1	2	3

PRVU

4	1	2	3
3	4	1	2
1	2	3	4
2	3	4	1

MAVU

2	4	3	1
1	2	4	3
4	3	1	2
3	1	2	4

SOFL

x	3	x	1
x	x	x	4
2	x	4	x
1	x	3	x

POVI

1	2	4	3
3	4	2	1
2	1	3	4
4	3	1	2

CLUSTER 1

POVI

3	1	2	4
2	3	4	1
4	2	1	3
1	4	3	2

MAVU

3	4	1	2
2	1	4	3
4	2	3	1
1	3	2	4

BIFR

3	2	1	4
4	1	3	2
1	4	2	3
2	3	4	1

SOFL

2	x	x	x
x	x	x	1
x	2	x	4
3	x	4	x

POPE

x	x	3	x
1	x	2	x
x	2	x	1
x	4	x	x

BIFR

2	3	1	4
4	2	3	1
1	4	2	3
3	1	4	2

CLUSTER 2

SOFL

x	2	x	x
x	x	1	x
3	1	x	x
x	x	4	2

BIFR

1	2	4	3
4	3	1	2
2	4	3	1
3	1	2	4

POPE

2	x	x	x
x	1	x	x
x	x	3	2
x	2	x	x

POVI

1	3	2	4
3	1	4	2
4	2	1	3
2	4	3	1

PRVU

4	3	2	1
2	4	1	3
3	1	4	2
1	2	3	4

MAVU

1	4	3	2
3	2	1	4
2	1	4	3
4	3	2	1

CLUSTER 3

Treatments
1 - control
2 - submergence
3 - burial
4 - nutrient addition

Figure 5-5 Alternative design for analysis, including three clusters of two columns each.

Chapter 6: Introduced plants have different suites of traits than native species in riparian plant communities

Introduction

Plant traits are characteristics of species measurable at the individual level, including morphological, anatomical, chemical, or physiological features (Violle et al. 2007). The size of leaves, leaf nitrogen content, seed size, and maximum rate of photosynthesis are examples of plant traits. Plant characteristics can also be considered as response or effect traits, where response traits determine a plant's response to environmental conditions, while effect traits determine how a plant affects neighboring plants, communities, and ecosystem services (Lavorel and Garnier 2002, Gross et al. 2008, Suding et al. 2008). Identifying the specific characteristics of species most likely to be relevant to an ecological factor of interest in a given study is important for determining if those traits directly impact ecological performance. Trait-based analytical approaches present a promising opportunity to make inferences about the relative importance of traits of organisms, rather than species identity, to community composition (Grime 2006, Ackerly and Cornwell 2007, Suding et al. 2008, Cornwell and Ackerly 2009, Messier et al. 2010, Andersen et al. 2012). For example, patterns in the response trait composition of a community may reflect the mechanisms governing the assembly of that community (Ackerly and Cornwell 2007, Cornwell and Ackerly 2009, Sutton-Grier et al. 2011, Andersen et al. 2012).

The potential predictive value of plant traits in explaining patterns within plant communities has made trait-based approaches effective for addressing many kinds of questions in community ecology, and for generating hypotheses about community structure (e.g., Wright et al. 2004, McGill et al. 2006, Grime 2006, Ackerly and Cornwell 2007, Kearney et al. 2010). For example, differences in trait composition may mediate species coexistence because species will be less likely to compete for the same resources (limiting similarity; MacArthur and Levins

1967). From the schools of plant geography and physiology, it has been observed that coexisting plant species often exhibit broad similarities in traits relevant to their life histories and morphologies, supporting the notion of environmental filtering (Tansley 1939, Chabot and Mooney 1985), and that shared characteristics (traits) are important for success in the environmental characteristics of a region. The suites of traits possessed by species in a community may therefore reflect either limiting similarity (dissimilar suites of traits among species, avoiding competition) or environmental filtering (similar suites of traits among species, necessary for success in that habitat).

A trait-based approach has potential to shed light on patterns of introduced plant invasions. Two major hypotheses for the success of invasive plants in novel environments provide clear alternative predictions regarding the trait composition that would be expected when introduced plants successfully invade native communities. The pre-adaptation hypothesis (Darwin 1859, Müller-Schärer and Steinger 2004, Whitney and Gabler 2008), which proposes that introduced species with traits that are similar to those of native species are more likely to succeed when introduced because they are already adapted to similar environments, is consistent with the environmental filtering hypothesis (Keddy 1992, Zobel 1997). Conversely, Darwin’s naturalization hypothesis and Elton’s hypothesis of biotic resistance (Darwin 1859, Elton 1958, Daehler 2001, Diez et al. 2008) suggest that similarity to native species might impede the establishment of novel species because of niche overlap and competition with native species, consistent with the principle of limiting similarity in species co-existence (Hardin 1960, MacArthur and Levins 1967). Support for these hypotheses within the species invasion literature is varied, with evidence in support of both the pre-adaptation (Duncan and Williams 2002) and

Darwin's naturalization hypotheses (Ricciardi and Atkinson 2004, Strauss et al. 2006, Diez et al. 2008).

In plant invasion ecology, Darwin's naturalization hypothesis and the pre-adaptation hypothesis are usually tested inferentially in the context of species introductions by seeking phylogenetic patterns of similarity between invaders and native communities, implicitly assuming that more closely related species are more similar in their traits (Diez et al. 2008, Hamilton et al. 2009, Jiang et al. 2010, Ness et al. 2011, Schaefer et al. 2011). The pre-adaptation hypothesis is supported when invaders in a community are observed to be phylogenetically similar to natives. Conversely, communities in which invaders are phylogenetically different from native species provide evidence for Darwin's naturalization hypothesis. Fewer studies have tested these two hypotheses using information on plant traits directly. Fargione et al. (2003) used a trait-based experimental test of plant introduction success in grasslands, and found support for Darwin's naturalization hypothesis. They found that established species were more effective at inhibiting introductions of species from within their own functional group, and that introduced species from other functional groups established more successfully. More studies in more systems are needed to determine if this is a generalizable pattern.

Riparian plant communities are an excellent system in which to test hypotheses of community assembly and the establishment of invasive species. Riparian plant communities are dynamic environments that often experience disturbances of various magnitudes in the form of flooding, which may change the dynamics of community assembly. Riparian plant communities often have high abundances of introduced species (Pyšek and Prach 1994, Brown and Peet 2003, Richardson et al. 2007), making them an interesting system in which to investigate the success of introduced species. In the riparian zones of small streams, neutral processes such as random colonization may be sufficient to produce both the overall species composition and the presence of introduced species, while direct species interactions may have a greater influence on community assembly in other habitats where competition is more important (Daleo et al. 2009). Alternatively, environmental filtering, based on tolerance to the hydrological environment, might be important in both the assembly and invasion of riparian plant communities.

I surveyed the species composition of riparian plant communities along 53 small streams of the Upper Hudson watershed (NY, USA) and used plant trait information obtained from the plant traits database TRY-DB and database contributors (Niinemets 1999, 2001, Kerkhoff et al. 2006, Kattge et al. 2011) to compare the trait composition of the native and introduced subsets of these communities. The traits I used (Table 6-1) were largely physiological and morphological traits related to the fundamental adaptations of these species. It is difficult to characterize these as either effect or response traits, although they have consequences for both plant responses and plant effects on their biotic and abiotic environments.

There are some caveats to the database approach to trait analysis, which relies on the open data contributions of many researchers. It is not possible to know that all contributed data were measured accurately, and in some cases the data are unclear as to the units or the method used to measure the trait. These uncertain data were excluded from analyses. It also cannot be known with certainty the degree to which means taken from database entries accurately represent the true trait mean of a species, or if the trait means vary among habitats or local environments. Many traits are highly variable both among and within species (Kattge et al. 2011), and the accuracy of inference using data from this database depends on the degree to which the contributed data encompass this variability without bias. The advantage of the database is that more data are available than would be possible to collect by a single researcher. This approach also allows a quantitative comparison of a greater number of plant traits than would likely be measurable in a single study. The database approach also facilitates broader study of plant characteristics that are expensive or laborious to measure, and would likely not be included in many individual studies for that reason.

Methods

The study sites were the same as those in Chapter 4, and all analyses used the field data on plant community composition collected as described in Chapter 4. These data included the community composition (presence/absence) of the riparian zones of 53 small streams throughout the Upper Hudson watershed. The plant species found and their native or invasive status are given in Appendix D, Table D-2. I selected 19 characteristics from the TRY-DB plant traits database that were likely to be related to plant responses to resource availability or other environmental conditions, or to their ability to persist through or re-establish after disturbances (Table 1). As such, these traits are all treated here as response traits (traits that determine how a plant responds to its environment) rather than effect traits (traits that determine how a plant effects its environment) (Lavorel and Garnier 2002, Suding et al. 2008). The traits used in this study were generally not strongly correlated (Appendix F, Table F-1). The highest correlation observed was between leaf carbon (mg/g dry leaf) and leaf nitrogen (mg/g dry leaf) (R = 0.72).

Due to the collaborative nature of the TRY traits database, which currently contains over 200 plant trait datasets contributed by nearly 2000 researchers (Boenisch and Kattge 2015), not all plant traits are represented equally in the database. Traits used in analyses here were selected in part based on those that had information for as many species in my dataset as possible; of those, traits considered most biologically relevant were included in analyses. When more than one measurement was available for a given trait for a species, trait measurements from the database were averaged for analysis. Data on photosynthetic rate were limited to light-saturated CO_2 assimilation rate (A_{max}) measurements standardized per leaf dry mass. For other traits, data were standardized to a given unit, and entries lacking units were not included in analyses. Data were not available for every trait for every species.

To calculate the community-level weighted mean of trait values (CWM; e.g., Lavorel et al. 2008), I used the *FD* package in R statistical software (version 3.1.1). I then used the R package *vegan* (Oksanen et al. 2013) to perform non-metric multidimensional scaling (NMDS) ordination on the CWM values, using the Gower measure of dissimilarity, which is robust to missing pairs of data (Pavoine et al. 2009). I used an analysis of similarity (ANOSIM, from the R package *vegan*) to test for significant differences in CWM between the introduced and native subsets of the plant communities, as well as to examine post-hoc differences between introduced and native plants in the average values of individual traits. I also evaluated whether categorical differences in growth form (1: herbaceous; 2: woody) and lifespan (1: annual; 2: biennial; 3: perennial) were correlated with trait differences between native and introduced species. For instance, if introduced species are more likely to be herbaceous than native species, observed differences in traits between introduced and native species might largely reflect differences between herbaceous and woody species. To evaluate these potential effects, I tested for differences in the relative numbers of introduced and native species with different growth forms and lifespans. I compared the number of herbaceous and woody species that were native versus introduced using a Quasi-Poisson model

$$Y_i = QuasiPois(E[Y_i]_, \phi)$$

where the expected number of species is modelled as a function of species origin, growth form, and their interaction:

$$1: E[Y_i] = \lambda \; + \; O_i + G_j + OG_{ij}$$

where O is species origin (native or introduced), G is growth form (herbaceous or woody) and ϕ is a parameter that compensates for overdispersion in the data.

I compared the numbers of annual, biennial and perennial species that were native or introduced using a Quasi-Poisson model

$$Y_i = QuasiPois(E[Y_i]_, \phi)$$

where the expected number of species is modelled as a function of species origin, growth form, and their interaction:

$$1: E[Y_i] = \lambda \; + \; O_i + L_j + OL_{ij}$$

where O is species origin (native or introduced), L is lifespan (annual, biennial or perennial) and ϕ is a parameter that compensates for overdispersion in the data.

A likelihood ratio test was used to determine which variables contributed significantly to each model (i.e., species origin, native or introduced, and growth form for the first model; species origin and lifespan for the second) and to test statistical differences in model fit. I then re-performed the ANOSIM analysis for each growth form and life history category (i.e., within annual plants, within perennial plants, within herbaceous plants, and within woody plants) to evaluate if any overall differences in traits between native and introduced species were maintained within these subgroups. All biennial species were introduced.

Results

The native and introduced subsets of the riparian plant communities differed significantly in community-weighted mean trait composition (ANOSIM, R = 0.507, p < 0.001; Table 2;

Figure 6-1). The native and introduced portions of the community also differed in the relative number of species with different growth forms ($\chi^2 = 392.0$, $p = 0.0019$) and lifespans ($\chi^2 = 439.9$, $p < 0.0001$) (Table 6-3). Fifteen of the 53 communities had no introduced woody species, and three had no introduced herbaceous species (Figure 6-2). None of the native species were biennial, but 9 of the introduced species were (Figure 6-2). Native and introduced species differed significantly in community-weighted mean trait composition (i.e., their overall suite of trait states) within both herbaceous (ANOSIM, $R = 0.430$, $p < 0.001$; Figure 6-3) and woody plants (ANOSIM, $R = 0.430$, $p < 0.001$; Figure 6.4) (Table 6-2). Community-weighted mean trait composition also differed between native and introduced species within annual plants (ANOSIM, $R = 0.400$, $p = 0.002$; Figure 6-5) and within perennial plants (ANOSIM, $R = 0.483$, $p = 0.001$; Figure 6-6) (Table 6-2).

When examined individually, many traits differed significantly between the introduced and native subsets of the community (Table 6-1; Figure 6-7). In particular, introduced species had an average leaf nitrogen content higher than that of native species (ANOSIM, $R = 0.0337$, $p < 0.001$, Table 6-1, Figure 6.7). Conversely, root nitrogen content was significantly lower (at a sequential-Bonferroni adjusted α) in introduced species than in natives ($R = 0.315$; $p < 0.001$, Table 6-1). Leaf carbon content (per g dry weight) was approximately twice as high on average in introduced than in native species ($R = 0.063$, $p = 0.005$; Table 6-1, Figure 6-8). Specific leaf area was more than twice as high in native plants than in introduced plants, although highly variable among species ($R = 0.032$, $p = 0.020$, Table 6-1, Figure 6-7). Light-saturated photosynthetic rate was significantly higher in introduced plants than in natives ($R = 0.148$, $p < 0.001$, Table 6-1, Figure 6-7). Introduced species had more seeds ($R = 0.124$, $p < 0.0001$) and smaller seeds (R = 0.398, P < 0.001) than native species. The means and SEs for all of the traits examined are shown in Figure 6-7.

Discussion

“What determines the success and invasiveness of introduced organisms?” is both a fundamentally interesting question ecologically as well as an important topic for land management and conservation. In this study, I found that traits of introduced species in riparian plant communities differed significantly from those of native species, and that these differences were maintained even when comparisons were limited to particular broad groups of plants (i.e., annual, perennial, herbaceous, or woody). These results are consistent with limiting similarity as a force driving the assembly of these communities. Under limiting similarity, introduced species need to differ sufficiently from the natives present in order to succeed. The differences between natives and invaders are also consistent with the empty niche hypothesis, where introduced species occupy a trait space that no native species occupy. Alternatively, introduced species in these communities may have outcompeted native species that share similar traits, leaving only dissimilar natives in the community.

The study of so-called “invasive traits” (e.g., Rejmánek and Richardson 1996; Whitney and Gabler 2008) has a long history, and many researchers have sought to contrast particular traits that are suspected to be associated with invasiveness, such as fitness or dispersal-related characteristics (Baker 1974) and seed mass (Rejmánek and Richardson 1996). This study took an alternate approach by examining the community-weighted means of quantitative rather than qualitative traits and by integrating many traits with multivariate analyses. Nevertheless, in this study, the patterns in trait values support the concept of an introduced species as ‘opportunistic’ or ‘weedy’ species. Native and introduced species differed strikingly in nitrogen allocation –

native species had more nitrogen in their roots than did introduced species, while introduced species had more leaf nitrogen than natives. Introduced species also tended to have higher photosynthetic and respiration rates. The leaf traits of introduced species tended to reflect the 'quick-return-on-investment' end of the leaf economic spectrum, as described by Wright et al. (2004) – high concentration of leaf nutrients and high photosynthetic and respiration rates – while the characteristics of natives were, on average, consistent with the slow-return end of that spectrum. Introduced species also tended to have more, smaller seeds than did native species. Small seeds are more easily dispersed by wind than large seeds, facilitating colonization. Previous studies of seed size in introduced species have had varying results, with introduced species sometimes having larger or smaller seeds than natives (Cadotte and Lovett-Doust 2001, Pyšek and Richardson 2008), although studies on disturbed habitats have found that introduced species have small seeds (Lake and Leishman 2004).

The quantitative, multivariate trait differences observed in this study may largely reflect previously understood plant strategies and trait syndromes. In terms of growth, natives may be allocating more energy to long-term storage, while introduced species tend to allocate energy to immediate growth. In dispersal, the smaller and more abundant seeds of introduced species may reflect an r-strategic or opportunistic strategy. Beyond individual traits, the multivariate trait difference between the native and introduced species is in itself biologically meaningful. Species do not generally interact by way of a single shared trait, but by the overall similarity or dissimilarity of the integrated phenotype. From this perspective, the strong dissimilarity between introduced and native species when considering the 19 traits included in this study together suggests an overall difference in phenotype.

The traits investigated in this study did not include those associated with early-establishment characteristics (e.g., germination rates, emergence rates, or growth traits of seedlings rather than larger plants), and dispersal traits were limited to three seed characteristics rather than dispersal modes or syndromes. This is a result of limitations of the currently-available trait data. Many traits of potential interest have yet to be measured for many of the species observed in this study. It is possible that early establishment characteristics might not differ between native and introduced species in these communities, if an environmental filtering effect favors species with particular early growth characteristics to establish in the riparian zone. While the only dispersal-related traits in this study were seed characteristics, other dispersal traits are likely of interest in studying biological invasions. For instance, Catford and Jansson (2014) found that plants invading riparian zones had more dispersal modes than introduced species that did not invade riparian ecosystems, suggesting that dispersal ability may be an important factor in governing the composition of riparian plant communities as well. It is possible that riparian plant community composition reflects an initial environmental filter on dispersal and early life stages, and a later influence of limiting similarity on established species.

Previous studies have demonstrated that introduced species differing in functional traits from the native community are more likely to succeed in that community. Introduced species in grasslands have been shown to differ both in morphology and phenology from the dominant natives (Pearson et al. 2012). The successful introduction of *Elaeagnus umbellata* in Michigan forests has been attributed to its differences in leaf traits from the native woody plant community (Brym et al. 2011). Leaf characteristics of *E. umbellata* were found to be characteristic of a fast-growing plant with high light demands, in contrast to the native woody plant community, which were largely shade-adapted. Additionally, native and introduced species have been found to consistently differ in functional traits across a gradient of nitrogen addition (Cleland et al. 2011). However, this pattern may not hold for all communities or all groups of plants. A recent meta-analysis found mixed evidence for limiting similarity in experimental manipulations of grasslands (Price and Pärtel 2013). While native communities containing forbs experience reduced invasion of other forbs, communities dominated by native grasses do not have reduced colonization of grass invaders.

It is possible that the strong trait differences observed between the native and introduced subsets of the communities in this study reflect phylogenetic differences between the native and introduced groups and intrinsically different suites of traits between different phylogenetic groups (Hamilton et al. 2009). While this study found that native and introduced species differed in many trait averages, there is also a great deal of variation in trait states within both groups and overlap between them. All introduced species in the region are not different from all native species. Because trait overlap exists between native and introduced species in the regional species pool, patterns of traits observed within a local community are likely to reflect community assembly processes in addition to any phylogenetic differences that may exist between native and introduced species.

Inferences that can be made from comparing introduced and native species within an introduced range are necessarily limited (van Kleunen et al. 2010). Some of the native species in this study likely have weedy or ruderal characteristics, and may themselves be or become introduced or invasive elsewhere in the world. While the average traits held by the introduced species did differ significantly from the native portion of the communities in this study, these traits and trait states ought not to be interpreted as “invasive traits”, but rather as supporting Darwin’s naturalization hypothesis, suggesting that species with traits different from those already present in a community are more likely to succeed in that community. My results suggest that moving beyond comparing broad groups of plants and taking a quantitative trait-based approach to addressing invasion biology is crucial for understanding community assembly in general and the success of introduced species in particular.

Tables

Table 6-1 Plant traits used in analyses. Traits were obtained from the TRY-DB Plant Traits Database. Means and standard errors of each trait used in analyses are shown for introduced and native species. The number of species for which data on a given trait were available is also given. Significant differences between native and introduced species (corrected for multiple comparisons using the sequential-Bonferroni method) are marked with an asterisk (*).

Category	Abbreviation	Trait	Native			Introduced			R	p
			N	Mean	SE	N	Mean	SE		
Leaf traits	Leaf C	C (mg/g dry leaf)	35	110.4	4.1	28	218.7	6.8	0.063	0.005*
	Leaf N	N (mg/g dry leaf)	99	6.5	0.1	36	13.2	0.3	0.337	< 0.001*
	Leaf P	P (mg/g dry leaf)	86	1499.0	11.7	31	574.9	28.9	0.320	< 0.001*
	Leaf K	K (mg/g dry leaf)	34	2.2	0.1	5	10.8	0.8	0.240	< 0.001*
	C:N	C:N	37	23.8	0.2	23	18.6	0.28	0.417	< 0.001*
	N:P	N:P	75	10.2	0.1	18	12.1	0.2	0.070	< 0.001*
	SLA	Specific leaf area (cm^2/g dry leaf)	112	619.2	25.8	51	258.2	12.9	0.032	0.020*
	LWR	Leaf weight ratio (% of plant)	35	11.6	0.5	25	13.4	0.8	0.041	0.006*
	Stomata cond.	Stomata conductance per leaf area	30	163.9	5.0	11	189.9	11.6	0.086	< 0.001*
Stem traits	SSD	Stem specific density (g/cm^3)	43	59.3	2.9	19	35.9	4.8	0.141	< 0.001*
	Woody mass	Wood dry mass (% of plant)	15	60.4	0.9	13	50.8	1.5	0.236	< 0.001*
Root traits	Root N	N (mg/g dry root mass)	19	9.3	0.4	11	1.8	0.1	0.315	< 0.001*
	Root depth	Rooting depth (cm)	117	18.2	0.1	19	10.9	0.3	0.179	< 0.001*
Seed traits	Seed number	Number of seeds per reproductive unit (tussock or individual plant)	35	8.8×10^6	1.4×10^7	47	2.1×10^5	2.1×10^4	0.124	< 0.001*
	Seed protein	Seed protein content per mass (%)	29	23.3	0.4	25	23.0	0.3	0.000	0.552
	Seed mass	Seed mass (g)	159	9.3×10^4	2191.1	58	4.3×10^4	5088.1	0.398	< 0.001*
Other	RGR	Relative growth rate (g/g/day)	34	0.2	0.002	22	0.2	0.003	0.239	< 0.001*
	Photosynthetic rate	Light-saturated photosynthetic rate (nmol CO_2/g dry leaf/s)	34	112.7	2.4	8	207.7	18.0	0.148	< 0.001*
	Leaf respiration	Leaf respiration (nmol CO_2/g dry leaf/s)	21	11.8	0.4	2	24.8	0.5	0.205	< 0.001*

Table 6-2 Results of ANOSIM analyses to assess the overall similarity of trait composition of the introduced and native subsets of the sampled riparian plant communities. Asterisks (*) denote significant dissimilarity between introduced and native species; these remain significant at the Bonferroni-adjusted $\alpha = 0.01$.

Comparison	**R**	**p**
All species	0.5069	< 0.001*
Woody species only	0.2111	< 0.001*
Herbaceous species only	0.4297	< 0.001*
Annual species only	0.3995	0.002*
Perennial species only	0.4828	0.001*

Table 6-3 Results of GLMs for (a) the number of herbaceous versus woody species within the introduced and native subsets of the sites; (b) the number of annual, biennial, or perennial species within the introduced and native subsets of the sites. Significant interactions were found between species origin and growth form, as well as between species origin and lifespan.

		df	**Deviance**	**Res. df**	**Residual Deviance**	**p**
Growth form	Null			211	1318.28	
	Origin	1	566.53	210	751.75	< 0.0001*
	Growth form	1	342.05	209	409.70	< 0.0001*
	Origin x Growth form	1	17.66	208	392.04	0.0019*
Lifespan	Null			317	3352.2	
	Origin	1	566.53	316	2785.7	< 0.0001*
	Lifespan	2	2226.98	314	558.7	< 0.0001*
	Origin x Lifespan	2	118.80	312	439.9	< 0.0001*

Figures

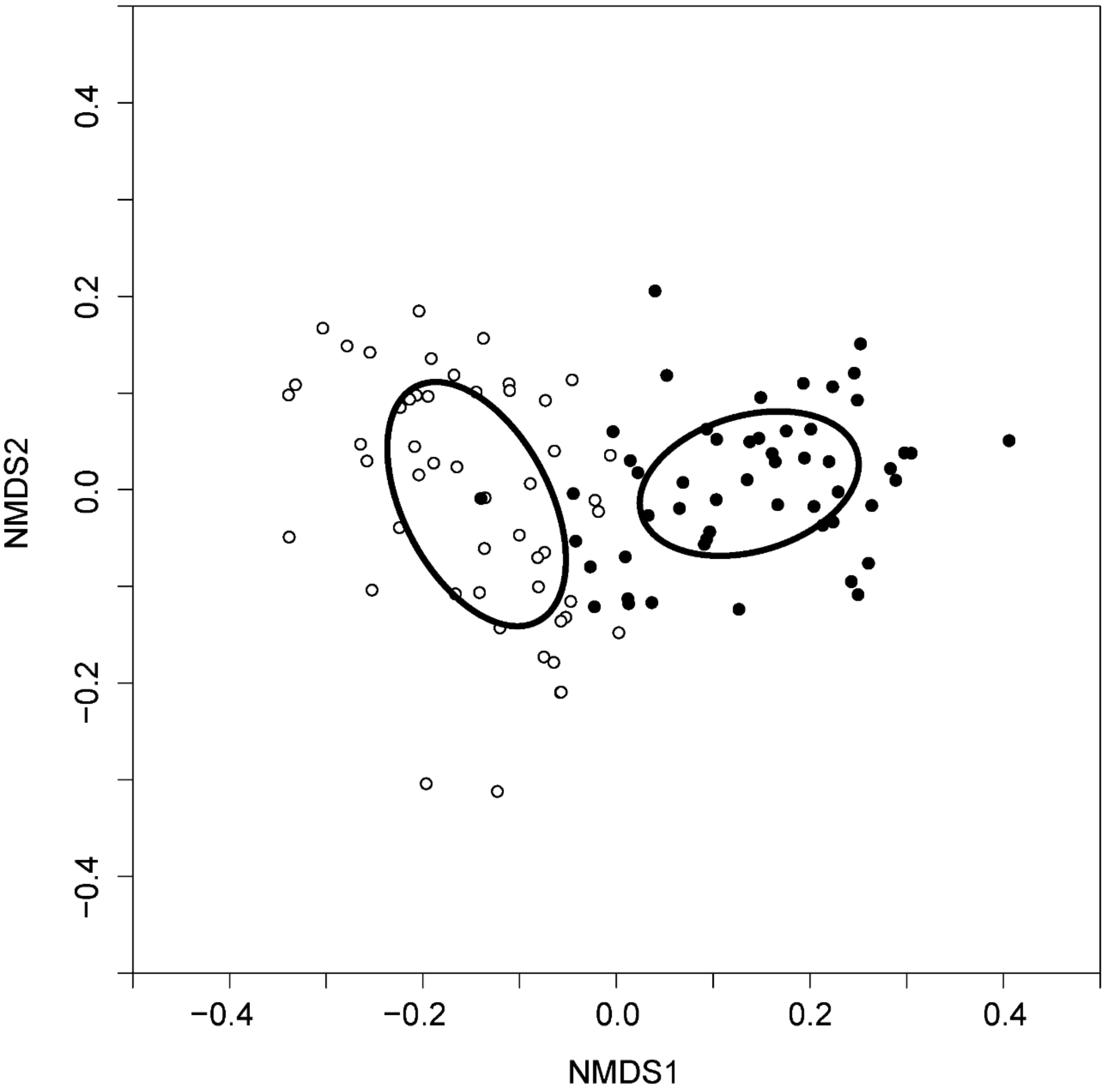


Figure 6-1 NMDS ordination (2D stress = 0.129) of community-weighted mean trait values. Native species are represented by closed points, and introduced species by open points. The black ovals represent one standard deviation around the centroid of each group.

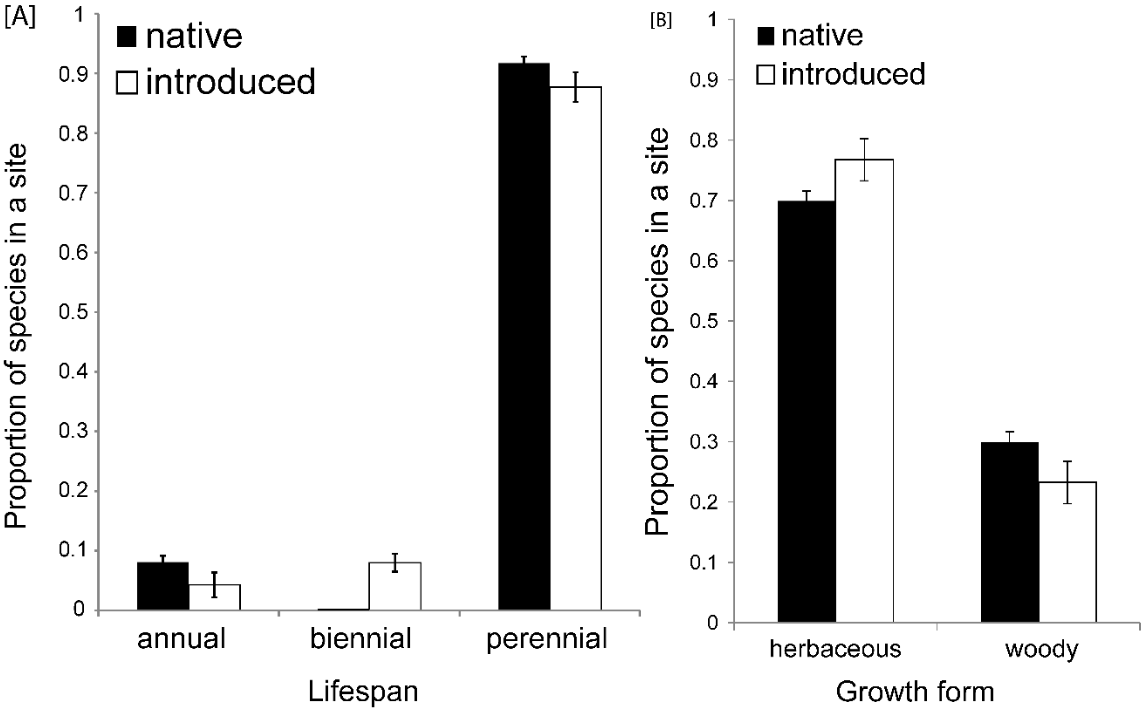


Figure 6-2 (A) The average proportion of native and introduced species within each site that were annual, biennial, or perennial species. Bars represent the average proportions, and whiskers show ± 1 SE. (B) The average proportion of native and introduced species within a site that were herbaceous and woody species.

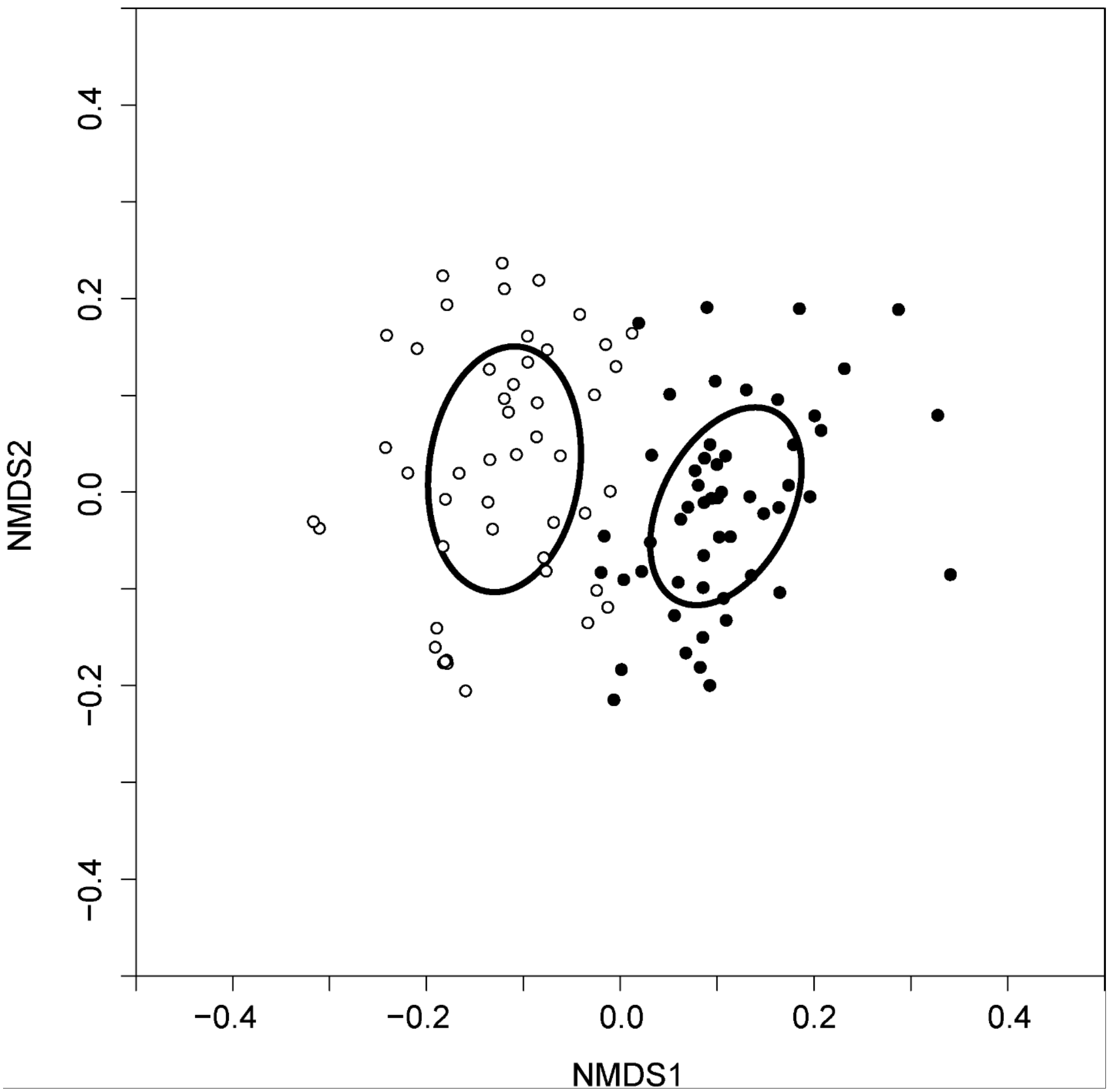


Figure 6-3 NMDS ordination (2D stress = 0.134) of community trait composition, limited to herbaceous species only. Native species are represented by closed points and introduced species by open points. The black ovals represent one standard deviation around the centroid.

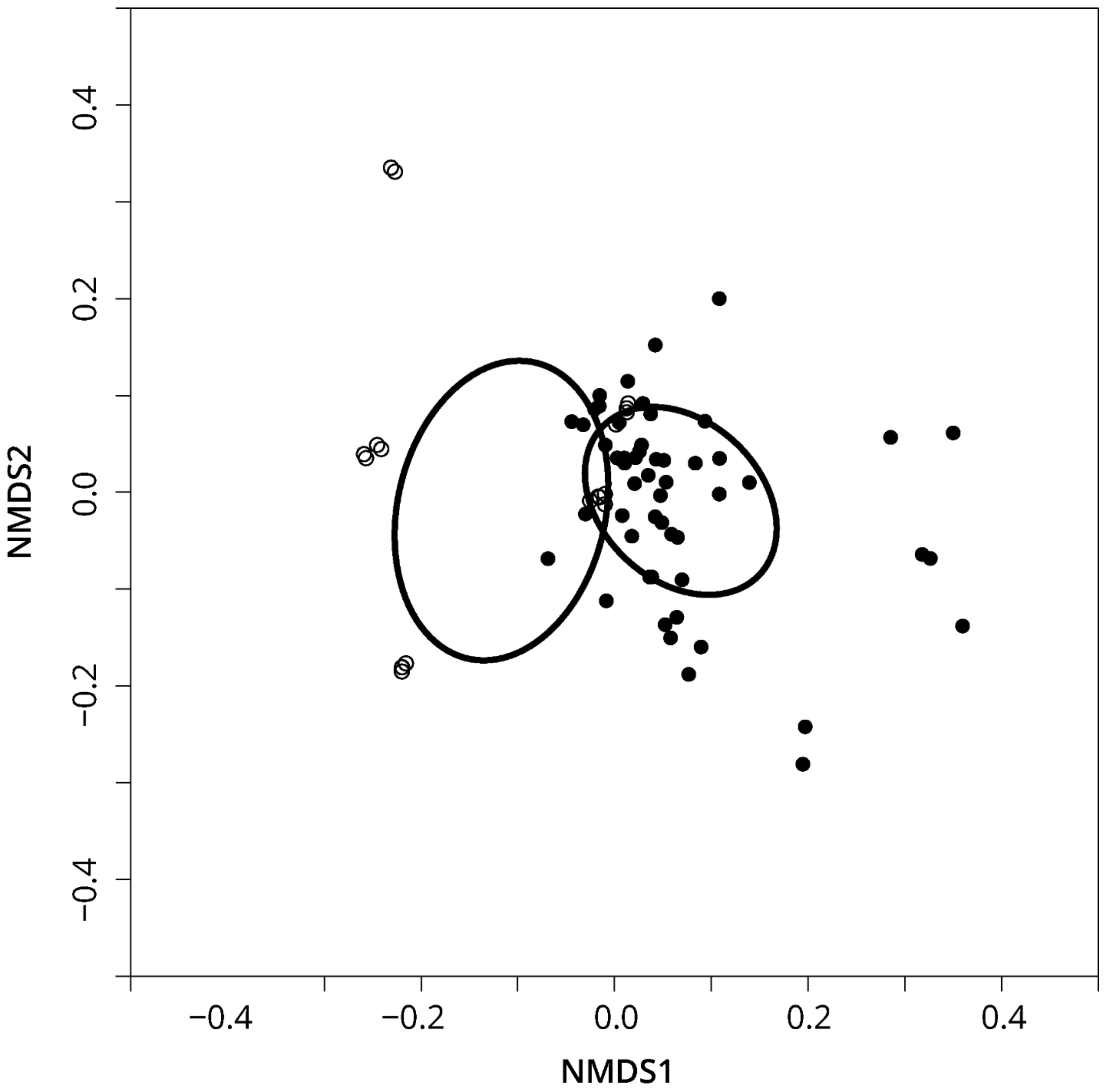


Figure 6-4 NMDS ordination (2D stress = 0.116) of community trait composition, limited to woody plants. Native species are represented by closed circles, and introduced species by open circles. The black ovals represent one standard deviation around the centroid of each group. The limited number of points representing introduced species is caused by the relatively small number of sites containing any woody introduced species. Several sites share 100% of their woody introduced species, leading to an identical trait composition for those sites; points have therefore been jittered slightly to allow visualization of overlapping points.

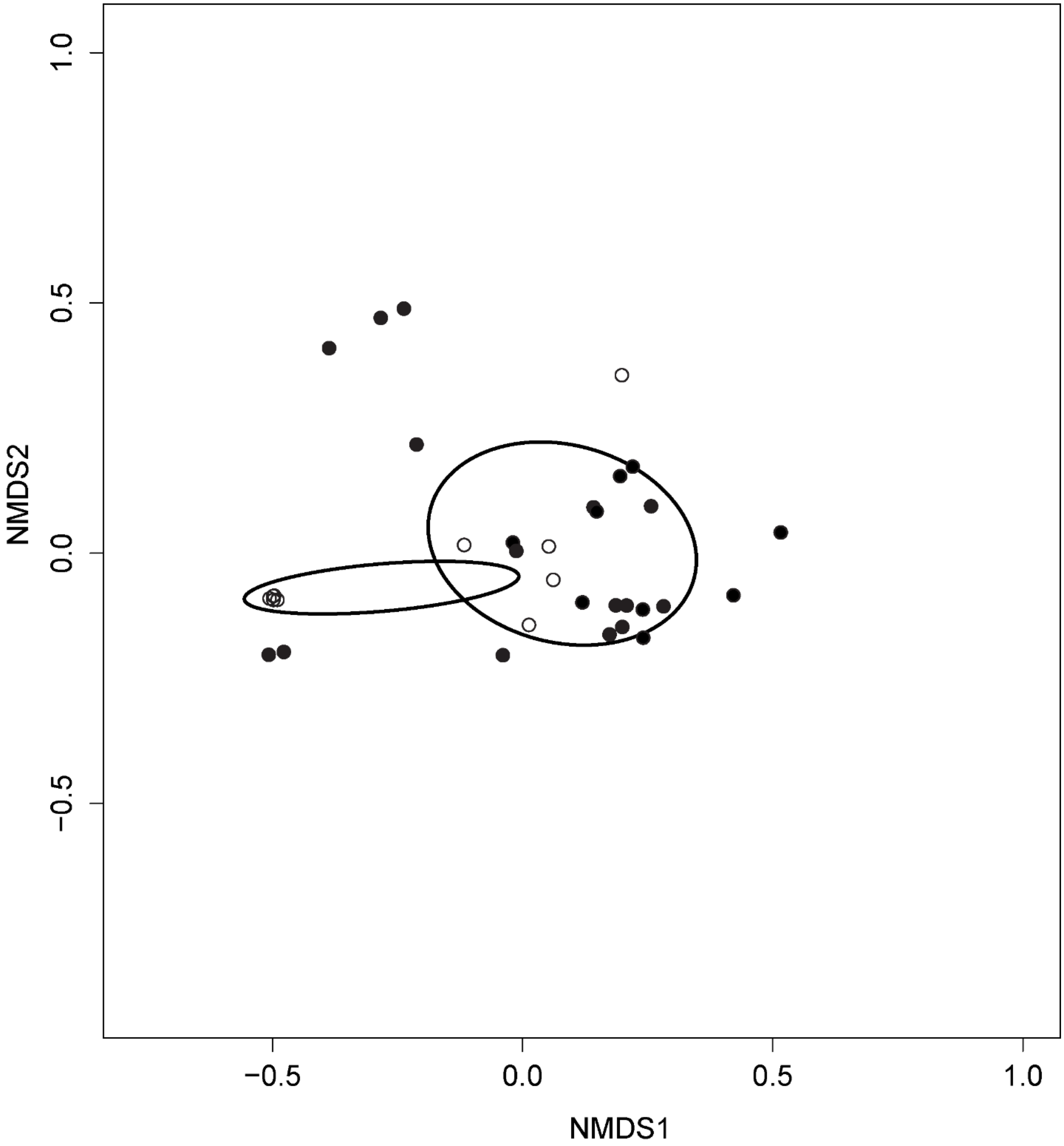


Figure 6-5 NMDS ordination (2D stress = 0.053) of community trait composition, limited to annual species only. Native species are represented by closed circles, and introduced species by open circles. The black ovals represent one standard deviation around the centroid of each group. Several sites share 100% of their annual introduced species, leading to an identical trait composition for those sites; points have therefore been jittered slightly to allow visualization of overlapping points.

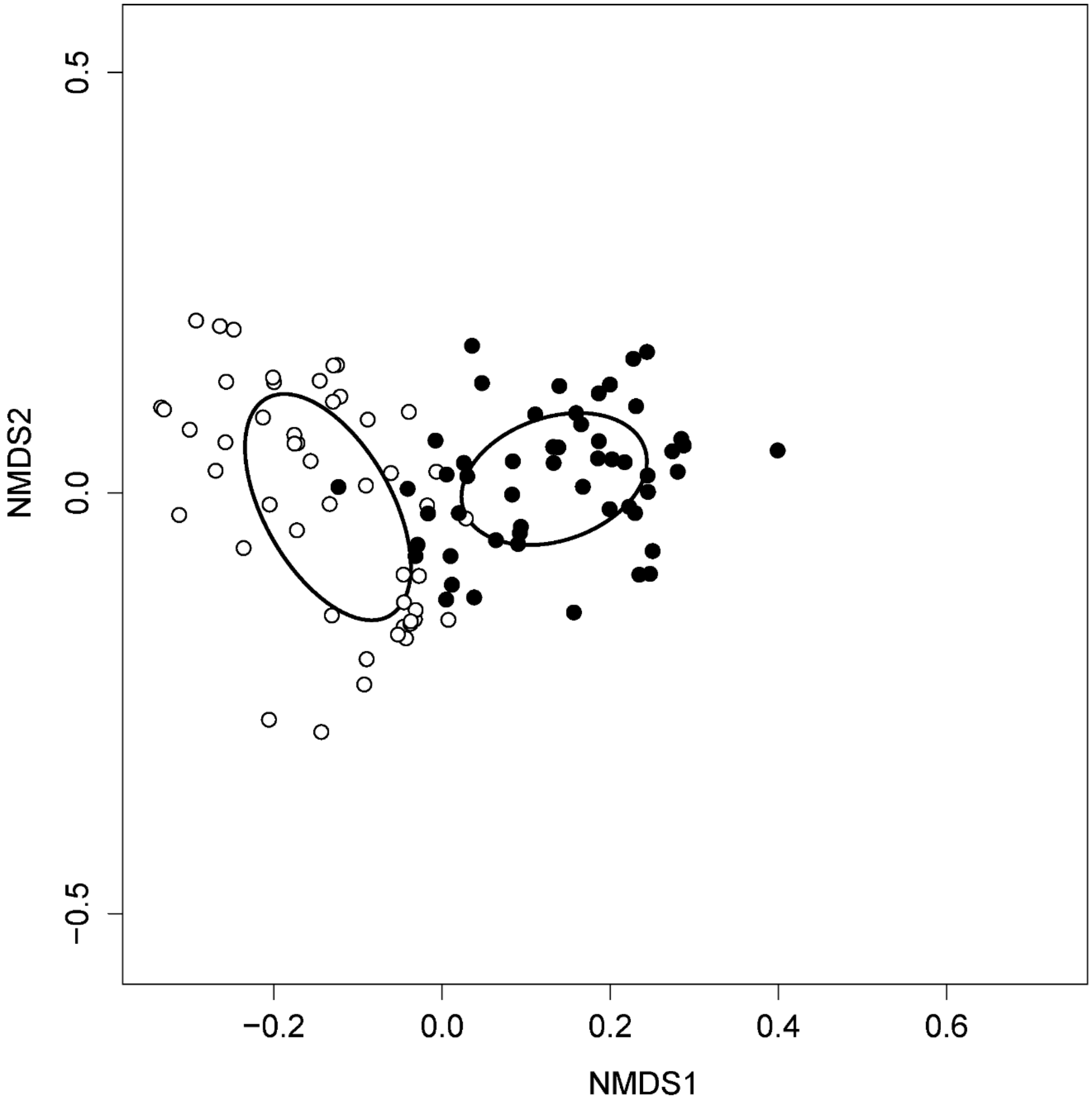


Figure 6-6 NMDS ordination (2D stress = 0.127) of community trait composition, limited to perennial species only. Native species are represented by closed circles, and introduced species by open circles. The black ovals represent one standard deviation around the centroid of each group.

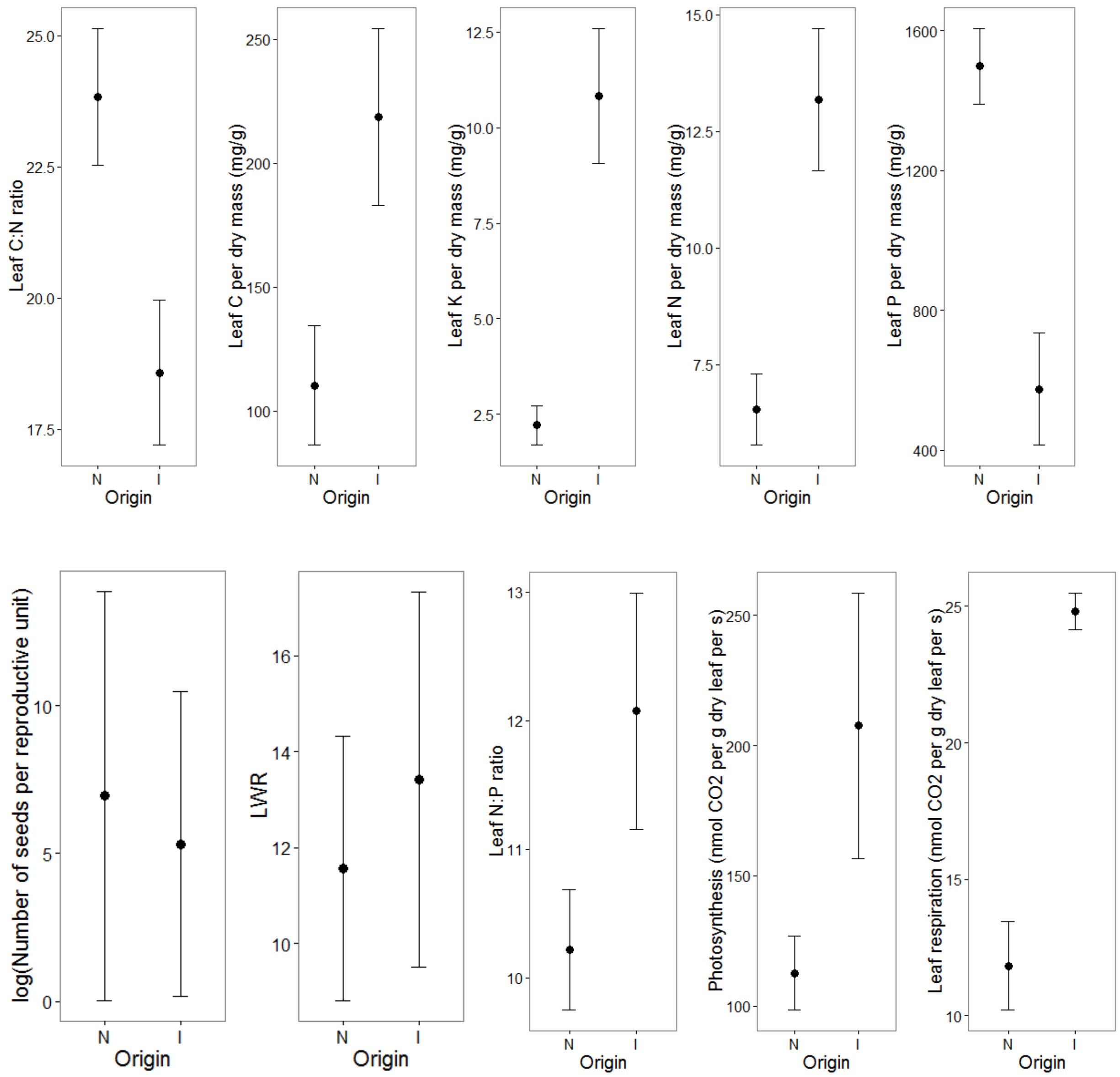


Figure 6-7 Means (dots) +/- 1 SE (whiskers) for the native (N) and introduced species (I) found across the 53 sites sampled, for each of the nineteen traits used in this study.

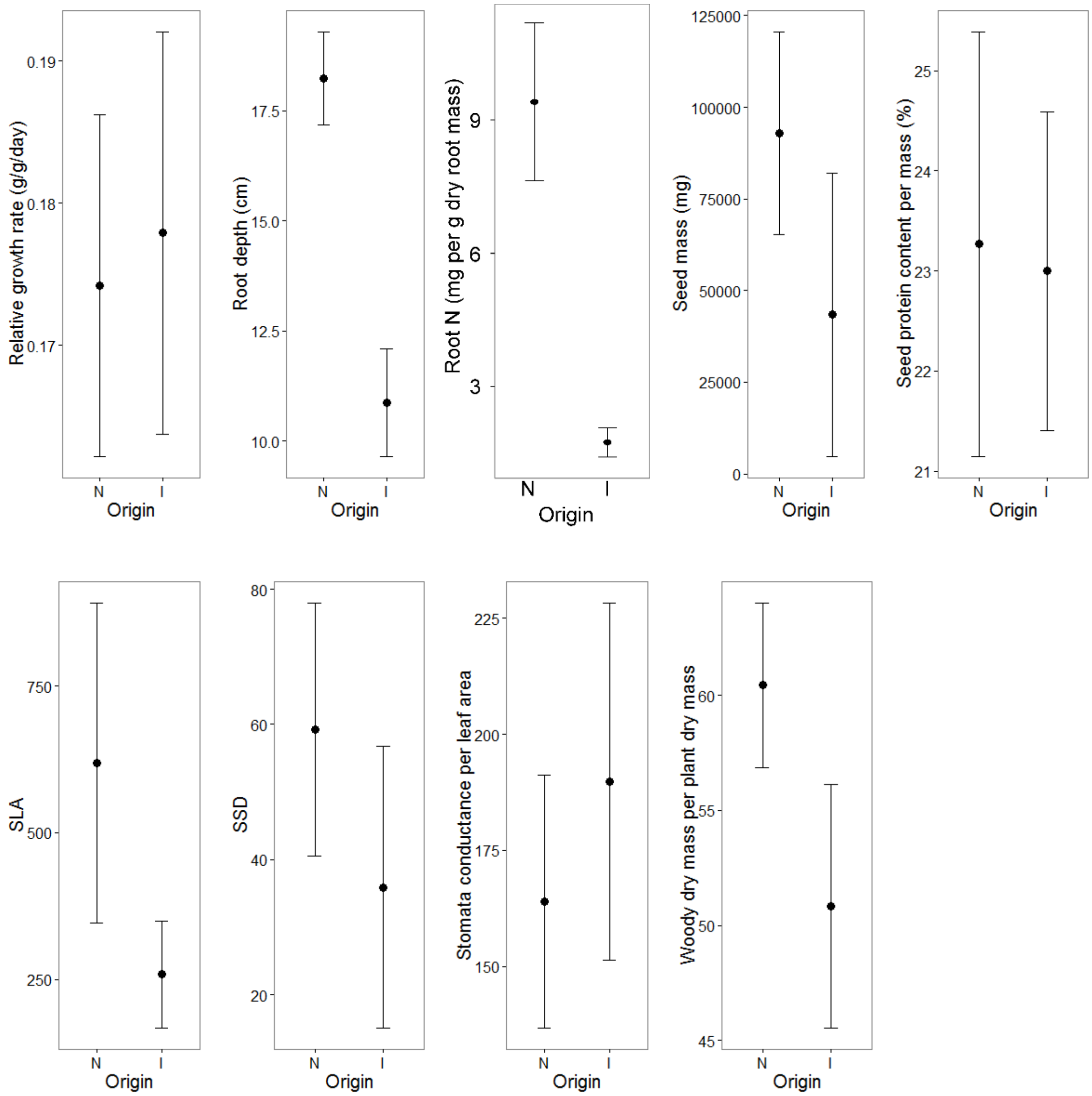


Figure 6-7 continued.

Chapter 7: Conclusions

One of the most longstanding and profound questions in ecology is what determines the diversity and species composition of ecological communities (Hutchinson 1959, Connell and Orias 1964, Ricklefs 1987, Huston 1994, Brown et al. 2001). By taking a variety of approaches to address this question in specific communities, we can attempt to provide a more thorough understanding of mechanisms governing community diversity and composition. Identifying the mechanisms governing diversity and species coexistence in riparian zones may be particularly fruitful in this regard, given frequent observations that riparian plant communities are highly diverse (Gregory et al. 1991, Naiman et al. 1993, Naiman and Décamps 1997, Goebel et al. 2003), but potentially also serve as havens for introduced species (DeFerrari and Naiman 1994, Planty-Tabacchi et al. 1996, Stohlgren et al. 1998, Alpert et al. 2000, Tickner et al. 2001, Brown and Peet 2003). Much of our knowledge about riparian plant communities comes from relatively large river floodplains. Community diversity, assembly and composition in the riparian zones of small streams have been understudied relative to those in larger rivers, even though small streams cover a much greater portion of the landscape than do large rivers. The different conditions experienced in the riparian zones of small streams may lead to different patterns in riparian vegetation that those found for riparian zones of rivers.

In this dissertation, I described the diversity and species composition of the riparian zones of small streams in the Upper Hudson watershed (New York). I used multiple lines of evidence, including field surveys at multiple spatial scales, greenhouse experiments, and the traits of native and introduced plants within these communities, to examine potential mechanisms governing diversity and composition in this system. The results presented here include evidence of the role riparian zones play in maintaining regional plant biodiversity, a number of potential mechanisms likely to contribute to species composition in these habitats, and factors that may affect the success of introduced species in these communities.

In contrast to previous studies of riparian communities, primarily focused on the floodplains of larger rivers, I found no difference in diversity or species composition between riparian and upland areas – potentially a feature of small stream systems (Chapter 3). I did find, however, that the riparian zones of small streams together harbored more species overall than did the upland sites across the same region, validating the hypothesis that riparian zones can be harbors of biodiversity. Additionally, I found that variation in riparian community composition throughout the Upper Hudson watershed was correlated with variation in annual mean temperature, soil texture, and abundance of wetlands in the immediate area (Chapter 4). Community composition was spatially autocorrelated, suggesting that dispersal among riparian plant communities may also be an important factor in determining their species composition. Additionally, while regional climate factors were able to explain some portion of variation in community composition, smaller-scale conditions likely also play a large role.

One smaller-scale condition that may contribute to community condition is the influence of flooding on individual plants. In greenhouse experiments, I found that riparian ruderal plants largely tolerate rather than thrive under various flooding conditions (submergence under water, burial under sediments, and nutrient addition) (Chapter 5). Some upland ruderal plants were also capable of tolerating these conditions. While one of the three upland species performed poorly under submergence and burial conditions, the remaining two upland species did not perform especially poorly under any flooded conditions. This suggests that flooding conditions alone are not a sufficient explanation for the exclusion of the upland species from the riparian zone.

In a survey of riparian plant communities of small streams throughout the Upper Hudson watershed, I found that introduced species differed strongly from the native portion of the riparian plant community in a suite of 19 plant traits (Chapter 6). These results suggest that introduced species may succeed in these environments due to these trait differences, which may allow them to avoid competition with natives. On average, introduced plant species allocated more nitrogen to leaves than did natives, and less nitrogen to their roots. Introduced species also produced more, smaller seeds than did the average native species. Overall, the suite of traits possessed by introduced plant species was suggestive of an opportunistic strategy (e.g., fast-growing colonizers), which may explain their success in these habitats. It is also possible that introduced species in these communities have outcompeted native species that share similar traits, leaving only dissimilar natives in the community. Examination of the trait composition of the regional species pool may help to distinguish these two alternative hypotheses. The hypothesis that introduced species are outcompeting natives would be supported if the difference in traits between native and introduced species is found only in the local riparian zones studied and not when compared to the regional native species pool.

The concept of disturbance has been an important component of studies of biological invasions and riparian ecology. But, the considerable breadth in the use of the term disturbance in ecology may hinder a general understanding of the ecological effects of disturbances, especially in the context of invasion biology or the ecology of riparian communities. Therefore, in addition to my field and experimental work, I conducted a systematic literature review and developed a framework to facilitate classification of disturbance studies in these systems (Chapter 2). The framework I developed to classify disturbances contains three dimensions: (1) disturbances as causal agents or disturbances as effects; (2) disturbances as biotic or abiotic; and

(3) temporal scale of disturbance. I found that most studies of invasion in riparian plant communities addressed flooding disturbances. This included both natural flooding and alteration to the natural flow regime by human activity (e.g., damming and channelization). The majority of studies addressing the role of disturbance in plant invasions across habitats defined disturbance quite broadly. Many studies referred to general anthropogenic effects, making comparisons between urban and rural habitats or across gradients of land development. Future synthesis about the role of disturbance in these systems, and in ecology more broadly, would benefit from moving beyond a disturbed-undisturbed dichotomy to more specific characterization of the disturbances under investigation, such as the classifications identified here?. In addition, more studies addressing particular effects of flooding in riparian zones (such as those described in Chapter 5) would provide a more mechanistic understanding of how flood events structure riparian communities and which particular events might facilitate invasion in these communities.

The research presented in this dissertation has identified several potential mechanisms structuring riparian plant communities, and highlighted the potential for the use of plant traits to understand patterns in community composition and trends in biological invasions. However, some persistent questions remain that would benefit from additional experimental, observational, and synthesis studies. Although trait databases such as TRY-DB (Kattge et al. 2011) are incredibly valuable for trait-based analyses, direct measurements of traits within a community will provide more accurate information about a community than the averages obtained from a global database. This is usually not tractable for a study incorporating many traits or seeking trait syndromes, but, the use of trait databases can represent an exploratory step to inform future studies. Confirming the trait differences between native and introduced species seen in Chapter 6 through direct trait measurements in focal riparian communities would strengthen the inferences made from the trait database approach.

Dispersal was not directly addressed in this dissertation, but the spatial autocorrelation of community structure shown in Chapter 4 and the seed traits of introduced species described in Chapter 6 both suggest that differential ability of species to disperse throughout riparian habitats across the landscape may influence these communities. Future work should address the role of connectivity and propagule dispersal in determining the composition of riparian plant communities for both native and introduced species. Longitudinal studies to examine not only the role of dispersal and colonization in riparian plant communities, but also the degree to which their composition changes within and across seasons are especially needed to extrapolate beyond the observations made in this dissertation and to further assess the mechanisms governing plant community assembly and species co-existence in the riparian zone.

References

Ackerly, D. D., and W. K. Cornwell. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. Ecology Letters 10:135–45.

Aguiar, F. C., M. T. Ferreira, and I. Moreira. 2001. Exotic and native vegetation establishment following channelization of a western Iberian river. Regulated Rivers: Research and Management 17:509–526.

Alpert, P., E. Bone, and C. Holzapfel. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3:52–66.

Andersen, K. M., M. J. Endara, B. L. Turner, and J. W. Dalling. 2012. Trait-based community assembly of understory palms along a soil nutrient gradient in a lower montane tropical forest. Oecologia 168:519–531.

Auble, G. T., J. M. Friedman, and M. L. Scott. 1994. Relating riparian vegetation to present and future streamflows. Ecological Applications 4:544–554.

Beauchamp, V. B., and J. C. Stromberg. 2008. Changes to herbaceous plant communities on a regulated desert river. River Research and Applications 770:754–770.

Bendix, J. 1994. Scale, direction, and pattern in riparian vegetation-environment relationships. Annals of the Association of American Geographers 84:652–665.

Bendix, J., and C. R. Hupp. 2000. Hydrological and geomorphological impacts on riparian plant communities. Hydrological Processes 14:2977–2990.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society 57:289–300.

Biswas, S. R., and A. U. Mallik. 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. Ecology 91:28–35.

Boenisch, G., and J. Kattge. 2015. TRY Members. TRY Database Version 3.0. Accessed January 30, 2015. https://www.try-db.org/TryWeb/Participants.php.

Bohn, C. C., and K. Gebhardt. 1989. Comparison of hydrometer settling times in soil particle size. Journal of Range Management 42:81–83.

Bohn, K., R. Pavlick, B. Reu, and A. Kleidon. 2014. The Strengths of r- and K-selection shape diversity-disturbance relationships. PLoS ONE 9:e95659.

Bonham, C. D., D. E. Mergen, and S. Montoya. 2004. Plant cover estimation: a contiguous Daubenmire frame. Rangelands 26:17–22.

ter Braak, C. J. F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69:69–77.

ter Braak, C. J. F., A. Cormont, and S. P. Dray. 2012. Improved testing of species traits-environment relationships in the fourth-corner problem. Ecology 93:1525–1526.

Brown, J. H., S. K. M. Ernest, J. M. Parody, and J. P. Haskell. 2001. Regulation of diversity: maintenance of species richness in changing environments. Oecologia 126:321–332.

Brown, R. L., and R. K. Peet. 2003. Diversity and invasibility of southern Appalachian plant communities. Ecology 84:32–39.

Brym, Z. T., J. K. Lake, D. Allen, and A. Ostling. 2011. Plant functional traits suggest novel ecological strategy for an invasive shrub in an understorey woody plant community. Journal of Applied Ecology 48:1098–1106.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology 77:776–790.

Cadotte, M. W., and L. Lovett-Doust. 2001. Ecological and taxonomic differences between native and introduced plants of southwestern Ontario. Ecoscience 8:230–238.

Carter, M. F., and J. B. Grace. 1990. Relationships between flooding tolerance, life history, and short-term competitive performance in three species of *Polygonum*. American Journal of Botany 77:381–387.

Casanova, M. T., and M. A. Brock. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? Plant Ecology 147:237–250.

Catford, J. A., B. J. Downes, C. J. Gippel, and P. A. Vesk. 2011. Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands. Journal of Applied Ecology 48:432–442.

Catford, J. A., and R. Jansson. 2014. Drowned, buried and carried away: Effects of plant traits on the distribution of native and alien species in riparian ecosystems. New Phytologist:19–36.

Chabot, B. F., and H. A. Mooney. 1985. Physiological Ecology in North American Plant Communities. Chapman and Hall, New York.

Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. The American Naturalist 150:519–553.

Chesson, P. L., and R. R. Warner. 1990. Environmental variability promotes coexistence in lottery competitive systems. The American Naturalist 135:284–290.

Clarke, K. R., and M. Ainsworth. 1993. A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92:205–219.

Cleland, E. E., C. M. Clark, S. L. Collins, J. E. Fargione, L. Gough, K. L. Gross, S. C. Pennings, and K. N. Suding. 2011. Patterns of trait convergence and divergence among native and exotic species in herbaceous plant communities are not modified by nitrogen enrichment. Journal of Ecology 99:1327–1338.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

Connell, J. H., and E. Orias. 1964. The ecological regulation of species diversity. The American Naturalist 98:399–414.

Cornwell, W. K., and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecological Monographs 79:109–126.

Daehler, C. C. 2001. Darwin's naturalization hypothesis revisited. The American Naturalist 158:324–330.

Daleo, P., J. Alberti, and O. Iribarne. 2009. Biological invasions and the neutral theory. Diversity and Distributions 15:547–553.

Darwin, C. 1859. On the Origin of Species by Means of Natural Selection: or the Presevation of Favoured Races in the Struggle for Life. Murray, London.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

Décamps, H. 2011. River networks as biodiversity hotlines. Comptes Rendus Biologies 334:420–434.

DeFerrari, C. M., and R. J. Naiman. 1994. A multi-scale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. Journal of Vegetation Science 5:247–258.

Diez, J. M., J. J. Sullivan, P. E. Hulme, G. Edwards, and R. P. Duncan. 2008. Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. Ecology Letters 11:674–681.

Dittmar, L. A., and R. K. Neely. 1999. Wetland seed bank response to sedimentation varying in loading rate and texture. Wetlands 19:341–351.

Dray, S., P. Choler, S. Dolédec, P. R. Peres-Neto, W. Thuiller, S. Pavoine, and C. J. F. ter Braak. 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95:14–21.

Dray, S., and A. B. Dufour. 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22:1 – 20.

Dray, S., and P. Legendre. 2008. Testing the species traits-environment relationships: the fourth-corner problem revisited. Ecology 89:3400–3412.

Duncan, R. P., and P. A. Williams. 2002. Darwin's naturalization hypothesis challenged. Nature 417:608–609.

Dunne, T., and L. B. Leopold. 1978. Water in Environmental Planning. Macmillan, New York.

Edwards, A. L., R. Wyatt, and R. R. Sharitz. 1994. Seed buoyancy and viability of the wetland milkweed *Asclepias perennis* and an upland milkweed, *Asclepias exaltata*. Bulletin of the Torrey Botanical Club 121:160–169.

Ehrenfeld, J. G., B. Ravit, and K. Elgersma. 2005. Feedback in the plant-soil system. Annual Review of Environment and Resources 30:75–115.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London.

Evans, A. R. D., J. Belnap, and S. Ecology. 2008. Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. Ecology 80:150–160.

Ewing, K. 1996. Tolerance of four wetland plant species to flooding and sediment deposition. Environmental and Experimental Botany 36:131–146.

Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences of the United States of America 100:8916–1920.

Fenster, C. B. 1997. Ecotypic differentiation for flood-tolerance and its morphological correlates in *Chamaecrista fasciculata*. Aquatic Botany 56:215–231.

Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. Trends in Ecology and Evolution 28:86–92.

Franklin, J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. Progress in Physical Geography 19:474–499.

Gleason, H., and A. Cronquist. 1991. Manual of the Vascular Plants of the Northeastern United States and Adjacent Canada. Second edition. New York Botanical Garden, New York.

Goebel, P. C., B. J. Palik, and K. S. Pregitzer. 2003. Plant diversity contributions of riparian areas in watersheds of the Northern Lake States, USA. Ecological Applications 13:1595–1609.

Goff, F. G., G. A. Dawson, and J. J. Rochow. 1982. Site examination for threatened and endangered plant species. Environmental Management 6:307–316.

Goslee, S. C., and D. L. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal Of Statistical Software 22:1–19.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540–551.

Grime, J. P. 1974. Vegetation classification by reference to strategies. Nature 250:26–31.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111:1169–1194.

Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. Journal of Vegetation Science 17:255–260.

Gross, N., T. M. Robson, S. Lavorel, C. Albert, Y. Le Bagousse-Pinguet, and R. Guillemin. 2008. Plant response traits mediate the effects of subalpine grasslands on soil moisture. The New Phytologist 180:652–62.

Guisan, A., T. C. Edwards Jr., and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157:89–100.

Haddad, N. M., M. Holyoak, T. M. Mata, K. F. Davies, B. A. Melbourne, and K. Preston. 2008. Species' traits predict the effects of disturbance and productivity on diversity. Ecology Letters 11:348–356.

Hall, A. R., A. D. Miller, H. C. Leggett, S. H. Roxburgh, A. Buckling, and K. Shea. 2012. Diversity-disturbance relationships : frequency and intensity interact. Biology Letters 8:768–771.

Hamilton, M. A., M. W. Cadotte, and B. R. Murray. 2009. Phylogenetic relatedness and plant invader success across two spatial scales. Diversity and Distributions 15:481–488.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292–1297.

Hastie, T. J., and D. Pregibon. 1992. Generalized linear models. *in* J. M. Chambers and T. J. Hastie, editors. Statistical Models in S. Wadsworth and Brooks/Cole Advanced Books and Software.

Hayden, B. P. 1998. Regional climate and the distribution of tallgrass prairie. Pages 19–34 *in* A. K. Knapp and J. M. Brigg, editors. Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie. Oxford University Press, New York.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:324–337.

Hodges, K. E. 2008. Defining the problem: terminology and progress in ecology. Frontiers in Ecology and the Environment 6:35–42.

Hood, W. G., and R. J. Naiman. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. Plant Ecology 148:105–114.

Horton, R. E. 1945. Erosional development of streams and their drainage basins: hydrophysical approach to quantitative morphology. Geological Society of America Bulletin 56:275–370.

Hoskins, B., and D. Ross. 2011. Soil sample preparation and extraction. Pages 11–19 Recommended Soil Testing Procedures for the Northeastern United States. Third edition. The Northeast Coordinating Committee for Soil Testing.

Houser, J. N., P. J. Mulholland, and K. O. Maloney. 2005. Catchment disturbance and stream metabolism: patterns in ecosystem respiration and gross primary production along a gradient of upland soil and vegetation disturbance. Journal of the North American Benthological Society 24:538.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ.

Huebner, C. D. 2007. Detection and monitoring of invasive exotic plants: a comparison of four sampling methods. Northeastern Naturalist 14:183–206.

Hupp, C. R., and W. R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. Ecology 66:670–681.

Hupp, C. R., and W. R. Osterkamp. 1996. Riparian vegetation and fluvial geomorphic processes. Geomorphology 14:277–295.

Huston, M. 1979. A general hypothesis of species diversity. The American Naturalist 113:81–101.

Huston, M. A. 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes.

Cambridge University Press, Cambridge, UK.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? The American Naturalist 93:145–159.

Jansson, R., U. Zinko, D. M. Merritt, and C. Nilsson. 2005. Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river. Journal of Ecology 93:1094–1103.

Jiang, L., J. Tan, and Z. Pu. 2010. An experimental test of Darwin's naturalization hypothesis. The American Naturalist 175:415–23.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences 106:110–127.

Kalliola, R., and M. Puhakka. 1988. River dynamics and vegetation mosaicism: a case study of the River Kamajohka, northernmost Finland. Journal of Biogeography 15:703–719.

Kardol, P., T. M. Bezemer, and W. H. van der Putten. 2006. Temporal variation in plant-soil feedback controls succession. Ecology Letters 9:1080–1088.

Kardol, P., M. J. Cornips, M. M. L. van Kempen, M. T. Bakx-Schotman, and W. H. van der Putten. 2007. Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. Ecological Monographs 77:147–162.

Katabuchi, M., H. Kurokawa, S. J. Davies, S. Tan, and T. Nakashizuka. 2011. Soil resource availability shapes community trait structure in a species-rich dipterocarp forest. Journal of Ecology 100:643–651.

Kattge, J., S. Díaz, S. Lavorel, I. C. Prentice, P. Leadley, G. Bönisch, E. Garnier, M. Westoby, P. B. Reich, I. J. Wright, J. H. C. Cornelissen, C. Violle, S. P. Harrison, P. M. Van Bodegom, M. Reichstein, B. J. Enquist, N. A. Soudzilovskaia, D. D. Ackerly, M. Anand, O. Atkin, M. Bahn, T. R. Baker, D. Baldocchi, R. Bekker, C. C. Blanco, B. Blonder, W. J. Bond, R. Bradstock, D. E. Bunker, F. Casanoves, J. Cavender-Bares, J. Q. Chambers, F. S. Chapin, J. Chave, D. Coomes, W. K. Cornwell, J. M. Craine, B. H. Dobrin, L. Duarte, W. Durka, J. Elser, G. Esser, M. Estiarte, W. F. Fagan, J. Fang, F. Fernández-Méndez, A. Fidelis, B. Finegan, O. Flores, H. Ford, D. Frank, G. T. Freschet, N. M. Fyllas, R. V. Gallagher, W. A. Green, A. G. Gutierrez, T. Hickler, S. I. Higgins, J. G. Hodgson, A. Jalili, S. Jansen, C. A. Joly, A. J. Kerkhoff, D. Kirkup, K. Kitajima, M. Kleyer, S. Klotz, J. M. H. Knops, K. Kramer, I. Kühn, H. Kurokawa, D. Laughlin, T. D. Lee, M. Leishman, F. Lens, T. Lenz, S. L. Lewis, J. Lloyd, J. Llusià, F. Louault, S. Ma, M. D. Mahecha, P. Manning, T. Massad, B. E. Medlyn, J. Messier, A. T. Moles, S. C. Müller, K. Nadrowski, S. Naeem, Ü. Niinemets, S. Nöllert, A. Nüske, R. Ogaya, J. Oleksyn, V. G. Onipchenko, Y. Onoda, J. Ordoñez, G. Overbeck, W. A. Ozinga, S. Patiño, S. Paula, J. G. Pausas, J. Peñuelas, O. L. Phillips, V. Pillar, H. Poorter, L. Poorter, P. Poschlod, A. Prinzing, R. Proulx, A. Rammig, S. Reinsch, B. Reu, L. Sack, B. Salgado-Negret, J. Sardans, S. Shiodera, B. Shipley, A. Siefert, E. Sosinski, J. F. Soussana, E. Swaine, N. Swenson, K. Thompson, P. Thornton, M. Waldram, E. Weiher, M. White, S. White, S. J. Wright, B. Yguel, S. Zaehle, A. E. Zanne, and C. Wirth. 2011. TRY - a global database of plant traits. Global Change Biology 17:2905–2935.

Kearney, M., S. J. Simpson, D. Raubenheimer, and B. Helmuth. 2010. Modelling the ecological niche from functional traits. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:3469–3483.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.

Kerkhoff, A. J., W. F. Fagan, J. J. Elser, and B. J. Enquist. 2006. Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. The American Naturalist 168:E103–E122.

Kershaw, H. M., and A. U. Mallik. 2013. Predicting plant diversity response to disturbance: applicability of the intermediate disturbance hypothesis and mass ratio hypothesis. Critical Reviews in Plant Sciences 32:383–395.

Kilmer, V. J., and L. T. Alexander. 1949. Methods of making mechanical analyses of soils. Soil Science 68:15–24.

Kimbro, D. L., and E. D. Grosholz. 2006. Disturbance influences oyster community richness and evenness, but not diversity. Ecology 87:2378–2388.

van Kleunen, M., W. Dawson, D. Schlaepfer, J. M. J. M. Jeschke, and M. Fischer. 2010. Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. Ecology letters 13:947–958.

Kleyer, M. 1999. Distribution of plant functional types along gradients of disturbance intensity and resource supply in an agricultural landscape. Journal of Vegetation Science 10:697–708.

Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417:67–70.

Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold. 2008. Plant-soil feedbacks: a meta-analytical review. Ecology Letters 11:980–992.

Lake, J. C., and M. R. Leishman. 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biological Conservation 117:215–226.

Laliberté, E., H. Lambers, D. A. Norton, J. M. Tylianakis, and M. A. Huston. 2013. A long-term experimental test of the dynamic equilibrium model of species diversity. Oecologia 171:439–448.

Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545–556.

Legendre, P., R. Galzin, and M. Harmelin-Vivien. 1997. Relating behavior to habitat: solutions to the fourth-corner problem. Ecology 78:547–562.

Lichstein, J. W. 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. Plant Ecology 188:117–131.

Lowry, E., E. J. Rollinson, A. J. Laybourn, T. Scott, M. Aiello-Lammens, S. M. Gray, J. Mickley, and J. Gurevitch. 2013. Biological invasions: a field synopsis, systematic review, and database of the literature. Ecology and Evolution 3:182–196.

MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101:377–385.

Mackey, R. L., and D. J. Currie. 2000. A re-examination of the expected effects of disturbance on diversity. Oikos 88:483–493.

Mackey, R. L., and D. J. Currie. 2001. The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82:3479–3492.

Mason, N. W. H., D. Mouillot, W. G. Lee, and J. B. Wilson. 2005. Functional richness, functional and functional evenness divergence: the primary of functional components diversity. Oikos 111:112–118.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21:178–185.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. The American Naturalist 130:730–757.

Messier, J., B. J. McGill, and M. J. Lechowicz. 2010. How do traits vary across ecological scales? A case for trait-based ecology. Ecology Letters 13:838–48.

Miller, A. D., S. H. Roxburgh, and K. Shea. 2011. How frequency and intensity shape diversity-disturbance relationships. Proceedings of the National Academy of Sciences 108:5643–5648.

Montgomery, D. R. 1999. Process domains and the river continuum. Journal of the American Water Resources Association 35:397–410.

Montgomery, D. R., and S. M. Bolton. 2003. Hydrogeomorphic variability and river restoration. Pages 39–80 *in* R. C. Wissmar and P. A. Bisson, editors. Strategies for Restoring River Systems: Sources of Variability and Uncertainty in Natural and Managed Systems. American Fisheries Society.

Morse, J. L., J. P. Megonigal, and M. R. Walbridge. 2004. Sediment nutrient accumulation and nutrient availability in two tidal freshwater marshes along the Mattaponi River, Virginia, USA. Biogeochemistry 69:175–206.

Mou, P., T. J. Fahey, and J. W. Hughes. 1993. Effects of soil disturbance on vegetation recovery and nutrient accumulation following whole-tree harvest of a northern hardwood ecosystem. Journal of Applied Ecology1 30:661–675.

Müller-Schärer, H., and T. Steinger. 2004. Predicting evolutionary change in invasive, exotic plants and its consequences for plant-herbivore interactions. Pages 137–162 *in* L. E. Ehler, R. Sforza, and T. Mateille, editors. Genetics, Evolution and Biological Control. CAB International, Cambridge, MA.

Naiman, R. J., and H. Décamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621–658.

Naiman, R. J., H. Décamps, and M. E. McClain. 2005. Riparia - Ecology, Conservation and Management of Streamside Communities. Elsevier Academic Press, Burlington, VT.

Naiman, R. J., H. Décamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3:209–212.

Ness, J. H., E. J. Rollinson, and K. D. Whitney. 2011. Phylogenetic distance can predict susceptibility to attack by natural enemies. Oikos 120:1327–1334.

Niinemets, Ü. 1999. Components of leaf dry mass per area - thickness and density - alter leaf photosynthetic capacity in reverse directions in woody plants. New Phytologist 144:35–47.

Niinemets, Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. Ecology 82:453–469.

Nilsson, C., G. Grelsson, M. Johansson, and U. Sperens. 1989. Patterns of plant species richness along riverbanks. Ecology 70:77–84.

Noe, G. B., and C. R. Hupp. 2009. Retention of riverine sediment and nutrient loads by coastal plain floodplains. Ecosystems 12:728–746.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. Vegan: community ecology package. R package version 2.0-10.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs 51:145–178.

Palik, B., S. W. Golladay, P. C. Goebel, and B. W. Taylor. 1998. Geomorphic variation in riparian tree mortality and stream coarse woody debris recruitment from record flooding in a coastal plain stream. Ecoscience 5:551–560.

Pausas, J., G. M. Rusch, and J. Lepš. 2003. Plant functional types in relation to disturbance and land use. Journal of Vegetation Science 14:305–416.

Pavoine, S., J. Vallet, A. B. Dufour, S. Gachet, and H. Daniel. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. Oikos 118:391–402.

Pearson, D. E., Y. K. Ortega, and S. J. Sears. 2012. Darwin's naturalization hypothesis up-close: intermountain grassland invaders differ morphologically and phenologically from native community dominants. Biological Invasions 14:901–913.

Peet, R. K. 1992. Community structure and ecosystem function. Pages 103–151 *in* D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. Plant Succession: Theory and Prediction. Chapman and Hall, Cambridge, UK.

Peet, R. K., T. R. Wentworth, and P. S. White. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63:262–274.

Peterson, D. W., and P. B. Reich. 2008. Fire frequency and tree canopy structure plant species in a forest-grassland ecotone. Plant Ecology 194:5–16.

Pickett, S. T. A., J. Kolasa, J. J. Armesto, and S. L. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54:129–136.

Pickett, S. T. A., and P. S. White. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, FL.

Planty-Tabacchi, A.-M., E. Tabacchi, R. J. Naiman, and C. M. DeFerrari. 1996. Invasibility of species-rich communities in riparian zones. Conservation Biology 10:598–607.

Pollock, M. M., R. J. Naiman, and T. A. Hanley. 1998. Plant species richness in riparian wetlands - a test of biodiversity theory. Ecology 79:94–105.

Price, J. N., and M. Pärtel. 2013. Can limiting similarity increase invasion resistance? A meta-analysis of experimental studies. Oikos 122:649–656.

Pyšek, P., and K. Prach. 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to Central Europe. Journal of Biogeography 20:413–420.

Pyšek, P., and K. Prach. 1994. How important are rivers for supporting plant invasions? Pages 45–54 *in* L. C. de Waal, L. E. Child, P. M. Wade, and J. H. Brock, editors. Ecology and Management of Invasive Riverside Plants. John Wiley and Sons Ltd., Chichester, UK.

Pyšek, P., and D. M. Richardson. 2008. Traits associated with invasiveness in alien plants: where do we stand? Pages 97–125 *in* W. Nentwig, editor. Biological Invasions. Springer, Berlin Heidelberg.

R Core Team. 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rao, P., S. K. Barik, H. N. Pandey, and R. S. Tripathi. 1990. Community composition and tree population structure in a sub-tropical broad-leaved forest along a disturbance gradient. Vegetatio 88:151–162.

Regan, H. M., M. Colyvan, and M. A. Burgman. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. Ecological Applications 12:618–628.

Rejmánek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology 77:1655–1661.

Reynolds, C. S., J. Padisak, and U. Sommer. 1993. Intermediate disturbance in the ecology of phytoplankton and the maintenance of species diversity: a synthesis:183–188.

Ricciardi, A., and S. K. Atkinson. 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecology Letters 7:781–784.

Richardson, D. M., P. M. Holmes, K. J. Esler, S. M. Galatowitsch, J. C. Stromberg, S. P. Kirkman, P. Pyšek, and R. J. Hobbs. 2007. Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Diversity and Distributions 13:126–139.

Richardson, J. S., and R. J. Danehy. 2007. A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. Forest Science 53:131–147.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. Science 235:167–171.

Rykiel, E. J. J. 1985. Towards a definition of ecological disturbance. Australian Journal of Ecology 10:361–365.

Sabo, J. L., and C. U. Soykan. 2006. Riparian zones increase regional richness by supporting different, not more, species: reply. Ecology 87:2128–2131.

Sabo, J. L., R. Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz, C. Soykan, J. Watts, and J. Welter. 2005. Riparian zones increase regional species richness by harboring different, not more, species. Ecology 86:56–62.

Salehi, M. H., O. H. Beni, H. B. Harchegani, I. E. Borujeni, and H. R. Motaghian. 2011. Refining soil organic matter determination by loss-on-ignition. Pedosphere 21:473–482.

Salo, J., R. Kalliola, I. Häkkinen, Y. Mäkinen, P. Niemelä, M. Puhakka, and P. D. Coley. 1986. River dynamics and the diversity of Amazon lowland forest. Nature 322:254–258.

Schaefer, H., O. J. Hardy, L. Silva, T. G. Barraclough, and V. Savolainen. 2011. Testing Darwin's naturalization hypothesis in the Azores. Ecology Letters 14:389–396.

Schnitzer, S. A., J. N. Klironomos, J. HilleRisLambers, L. L. Kinkel, P. B. Reich, K. Xiao, M. C. Rillig, B. A. Sikes, R. M. Callaway, S. A. Mangan, E. H. van Nes, and M. Scheffer. 2011. Soil microbes drive the classic plant diversity-productivity pattern. Ecology 92:1385–1392.

Schulte, E. E., and B. Hoskins. 2009. Recommended soil organic matter tests. Pages 63–74 Cooperative Bulletin No. 493. University of Delaware College of Agriculture and Natural Resources Cooperative Extension.

Scott, M. L., G. T. Auble, and J. M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. Ecological Applications 7:677–690.

Seifan, M., T. Seifan, K. Schiffers, F. Jeltsch, and K. Tielbörger. 2013. Beyond the competition-colonization trade-off: linking multiple trait response to disturbance characteristics. The American Naturalist 181:151–160.

Shea, K., S. H. Roxburgh, and E. S. J. Rauschert. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecology Letters 7:491–508.

Shipley, B., D. Vile, and E. Garnier. 2006. From plant traits to plant communities: a statistical mechanistic approach to biodiversity. Science 314:812–814.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353–391.

Sprugel, D. G. 1985. Natural disturbance and ecosystem energetics. Pages pp. 335–352 *in* S. T. A. Pickett and P. S. White, editors. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego, CA.

Stephenson, N. L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. Journal of Biogeography 25:855–870.

Stohlgren, T. J., K. A. Bull, Y. Otsuki, C. A. Villa, and M. Lee. 1998. Riparian zones as havens for exotic plant species in the central grasslands. Plant Ecology 138:113–125.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions of the

American Geophysical Union 38:913–920.

Strauss, S. Y., C. O. Webb, and N. Salamin. 2006. Exotic taxa less related to native species are more invasive. Proceedings of the National Academy of Sciences of the United States of America 103:5841–5845.

Strayer, D. L., S. E. G. Findlay, D. Miller, H. M. Malcom, D. T. Fischer, and T. Coote. 2012. Biodiversity in Hudson River shore zones: influence of shoreline type and physical structure. Aquatic Sciences 74:597–610.

Stromberg, J. C. 2007. Seasonal reversals of upland-riparian diversity gradients in the Sonoran Desert. Diversity and Distributions 13:70–83.

Stromberg, J. C., S. J. Lite, P. B. Shafroth, R. Marler, J. M. White, C. Paradzick, M. S. White, and D. Shorrock. 2007. Altered stream-flow regimes and invasive plant species: the *Tamarix* case. Global Ecology and Biogeography 16:381–393.

Suding, K. N., S. Lavorel, F. S. Chapin, J. H. C. Cornelissen, S. Díaz, E. Garnier, D. Goldberg, D. U. Hooper, S. T. Jackson, and M.-L. Navas. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology 14:1125–1140.

Sutton-Grier, A. E., J. P. Wright, B. M. McGill, and C. Richardson. 2011. Environmental conditions influence the plant functional diversity effect on potential denitrification. PLoS ONE 6:e16584.

Svensson, J. R., M. Lindegarth, P. R. Jonsson, and H. Pavia. 2012. Disturbance-diversity models: what do they really predict and how are they tested? Proceedings of the Royal Society B: Biological Sciences 279:2163–2170.

Tabacchi, E., D. L. Correll, R. Hauer, G. Pinay, A. M. Planty-Tabacchi, and R. C. Wissmar. 1998. Development, maintenance and role of riparian vegetation in the river landscape. Freshwater Biology 40:497–516.

Tansley, A. G. 1939. The British Islands and their Vegetation. Cambridge University Press, Cambridge, UK.

Thébaud, C., and M. Debussche. 1991. Rapid invasion of *Fraxinus ornus* L. along the Herault River system in Southern France: the importance of seed dispersal by water. Journal of Biogeography 18:7–12.

Therneau, T. M. 2015. A package for survival analysis in S. http://cran.r-project.org/package=survival.

Tickner, D. P., P. G. Angold, A. M. Gurnell, and J. O. Mountford. 2001. Riparian plant invasions: hydrogeomorphological control and ecological impacts. Progress in Physical Geography 25:22–52.

Toner, M., and P. Keddy. 1997. River hydrology and riparian wetlands: a predictive model for ecological assembly. Ecological Applications 7:236–246.

Vandersande, M. 2001. Tolerance of five riparian plants from the lower Colorado River to salinity drought and inundation. Journal of Arid Environments 49:147–159.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. Journal of Statistical Software 36:1–48.

Violle, C., A. Bonis, M. Plantegenest, C. Cudennec, C. Damgaard, B. Marion, D. Le Cœur, and J.-B. Bouzillé. 2010. Plant functional traits capture species richness variations along a flooding gradient. Oikos:389–398.

Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos 116:882–892.

Vitousek, P. M. 1985. Community turnover and ecosystem nutrient dynamics. Pages 325–333 *in* S. T. A. Pickett and P. S. White, editors. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego, CA.

Vought, L. B. M., J. Dahl, C. L. Pedersen, and J. O. Lacoursiere. 1994. Nutrient retention in riparian ecotones. Ambio 23:342–348.

Warwick, N. W. M., and M. A. Brock. 2003. Plant reproduction in temporary wetlands: the effects of seasonal timing, depth, and duration of flooding. Aquatic Botany 77:153–167.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. Botanical Review 45:229–299.

White, P. S., and A. Jentsch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. Progress in Botany 62:399–449.

Whitney, K. D., and C. A. Gabler. 2008. Rapid evolution in introduced species, “invasive traits” and recipient communities: challenges for predicting invasive potential. Diversity and Distributions 14:569–580.

Winward, A. H. 2000. Monitoring the Vegetation Resources in Riparian Areas. USDA. Ogden, UT.

Woodward, F. I., and B. G. Williams. 1987. Climate and plant distribution at global and local scales. Vegetatio 69:189–197.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Yang, J., T. E. Dilts, L. A. Condon, P. L. Turner, and P. J. Weisberg. 2011. Longitudinal- and transverse-scale environmental influences on riparian vegetation across multiple levels of ecological organization. Landscape Ecology 26:381–395.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends in Ecology and Evolution 12:266–269.

Appendices

Appendix A: Bibliography of papers used in the first systematic review presented in Chapter 2.

Abbott, I. 1992. Biogeography of grasses (Poaceae) on islands of southwestern Australia. Australian Journal of Ecology 17:289–296.

Affre, L., C. M. Suehs, S. Charpentier, M. Vilà, G. Brundu, P. Lambdon, A. Traveset, and P. E. Hulme. 2010. Consistency in the habitat degree of invasion for three invasive plant species across Mediterranean islands. Biological Invasions 12:2537–2548.

Aguiar, F. C., M. T. Ferreira, and I. Moreira. 2001. Exotic and native vegetation establishment following channelization of a western Iberian river. Regulated Rivers: Research and Management 17:509–526.

Alston, K. P., and D. M. Richardson. 2006. The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. Biological Conservation 132:183–198.

Anderson, R. 1999. Disturbance as a factor in the distribution of sugar maple and the invasion of Norway maple into a modified woodland. Rhodora 101:264–273.

Aplet, G. H., S. J. Anderson, and C. P. Stone. 1991. Association between feral pig disturbance and the composition of some alien plant assemblages in Hawaii Volcanos National Park. Vegetatio 95:55–62.

Appleby, M. W. A. 1998. The incidence of exotic species following clearfelling of *Eucalyptus regnans* forest in the Central Highlands, Victoria. Australian Journal of Ecology 23:457–465.

Barbosa, N. P. U., G. W. Fernandes, M. A. A. Carneiro, and L. A. C. Júnior. 2010. Distribution of non-native invasive species and soil properties in proximity to paved roads and unpaved roads in a quartzitic mountainous grassland of southeastern Brazil (rupestrian fields). Biological Invasions 12:3745–3755.

Baret, S., and D. Strasberg. 2005. The effects of opening trails on exotic plant invasion in protected areas on La Réunion Island (Mascarene Archipelago, Indian Ocean). Revue D'Écologie-La Terre et la Vie 60:325–332.

Baret, S., L. Cournac, C. Thébaud, P. Edwards, and D. Strasberg. 2008. Effects of canopy gap size on recruitment and invasion of the non–indigenous *Rubus alceifolius* in lowland tropical rain forest on Réunion. Journal of Tropical Ecology 24:337–345.

Bartuszevige, A. M., D. L. Gorchov, and L. Raab. 2006. The relative importance of landscape and community features in the invasion of an exotic shrub in a fragmented landscape. Ecography 29:213–222.

Bartuszevige, A. M., R. L. Hrenko, and D. L. Gorchov. 2007. Effects of leaf litter on establishment, growth and survival of invasive plant seedlings in a deciduous forest. American Midland Naturalist 158:472–477.

Baruch, Z., and B. Bilbao. 1999. Effects of fire and defoliation on the life history of native and invader C_4 grasses in a Neotropical savanna. Oecologia 119:510–520.

Bellingham, P. J., E. V. J. Tanner, and J. R. Healey. 2005. Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests. Journal of Vegetation Science 16:675–684.

Belote, R. T., R. H. Jones, S. M. Hood, and B. W. Wender. 2008. Diversity-invasibility across an experimental disturbance gradient in Appalachian forests. Ecology 89:183–192.

Bergelson, J., J. A. Newman, and E. M. Floresroux. 1993. Rate of weed spread in spatially heterogeneous environments. Ecology 74:999–1011.

Boulant, N., A. Garnier, T. Curt, and J. Lepart. 2009. Disentangling the effects of land use, shrub cover and climate on the invasion speed of native and introduced pines in grasslands. Diversity and Distributions 15:1047–1059.

Boulant, N., G. Kunstler, S. Rambal, and J. Lepart. 2008. Seed supply, drought, and grazing determine spatio-temporal patterns of recruitment for native and introduced invasive pines in grasslands. Diversity and Distributions 14:862–874.

Brandon, A. L., D. J. Gibson, and B. A. Middleton. 2004. Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. Biological Invasions 6:483–493.

Brandt, C. A., and W. H. Rickard. 1994. Alien taxa in the North American shrub-steppe four decades after cessation of livestock grazing and cultivation agriculture. Biological Conservation 68:95–105.

Brewer, J. S. 2002. Disturbances increase seedling emergence of an invasive native shrub in pitcher-plant bogs. Natural Areas Journal 22:4–10.

Broncano, M. J., M. Vilà, and M. Boada. 2005. Evidence of *Pseudotsuga menziesii* naturalization in montane Mediterranean forests. Forest Ecology and Management 211:257–263.

Brooks, M. L., and K. H. Berry. 2006. Dominance and environmental correlates of alien annual plants in the Mojave Desert, USA. Journal of Arid Environments 67:100–124.

Brooks, M. L., J. R. Matchett, and K. H. Berry. 2006. Effects of livestock watering sites on alien and native plants in the Mojave Desert, USA. Journal of Arid Environments 67:125–147.

Brooks, M. L., and J. R. Matchett. 2003. Plant community patterns in unburned and burned blackbrush (*Coleogyne ramosissima* Torr.) shrublands in the Mojave Desert. Western North American Naturalist 63:283–298.

Brown, C. D., and C. Boutin. 2009. Linking past land use, recent disturbance, and dispersal mechanism to forest composition. Biological Conservation 142:1647–1656.

Brown, J. R., and S. Archer. 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. Ecology 80:2385–2396.

Buckland, S. M., K. Thompson, J. G. Hodgson, and J. P. Grime. 2001. Grassland invasions: effects of manipulations of climate and management. Journal of Applied Ecology 38:301–309.

Bulleri, F., and L. Airoldi. 2005. Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. Journal of Applied Ecology 42:1063–1072.

Bullock, J. M. 2009. A long–term study of the roles of competition and facilitation in the establishment of an invasive pine following heathland fires. Journal of Ecology 97:646–656.

Burls, K., and C. McClaugherty. 2008. Landscape position influences the distribution of garlic mustard, an invasive species. Northeastern Naturalist 15:541–556.

Burnham, K. M., and T. D. Lee. 2010. Canopy gaps facilitate establishment, growth, and reproduction of invasive *Frangula alnus* in a *Tsuga canadensis* dominated forest. Biological Invasions 12:1509–1520.

Bustamante, R. O., and J. A. Simonetti. 2005. Is *Pinus radiata* invading the native vegetation in central Chile? Demographic responses in a fragmented forest. Biological Invasions 7:243–249.

Call, L. J., and E. T. Nilsen. 2003. Analysis of spatial patterns and spatial association between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robinia pseudoacacia*). American Midland Naturalist 150:1–14.

Cameron, D. S., D. J. Leopold, and D. J. Raynal. 1997. Effect of landscape position on plant diversity and richness on electric transmission rights-of-way in New York State. Canadian Journal of Botany-Revue Canadienne de Botanique 75:242–251.

Capers, R. S., R. Selsky, G. J. Bugbee, and J. C. White. 2009. Species richness of both native and invasive aquatic plants influenced by environmental conditions and human activity. Canadian Journal of Botany-Revue Canadienne de Botanique 87:306–314.

Carboni, M., W. Thuiller, F. Izzi, and A. Acosta. 2010. Disentangling the relative effects of environmental versus human factors on the abundance of native and alien plant species in Mediterranean sandy shores. Diversity and Distributions 16:537–546.

Catford, J. A., and B. J. Downes. 2010. Using multi-scale species distribution data to infer drivers of biological invasion in riparian wetlands. Diversity and Distributions 16:20–32.

Cavallero, L., and E. Raffaele. 2010. Fire enhances the 'competition-free' space of an invader shrub: *Rosa rubiginosa* in northwestern Patagonia. Biological Invasions 12:3395–3404.

Chabrerie, O., K. Verheyen, R. Saguez, and G. Decocq. 2008. Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest. Diversity and Distributions 14:204–212.

Chapman, H. M., and P. Bannister. 1990. The spread of heather, *Calluna vulgaris* (L.) Hull, into indigenous plant communities of Tongariro National Park. New Zealand Journal of Ecology 14:7–16.

Cherwin, K. L., T. R. Seastedt, and K. N. Suding. 2009. Effects of nutrient manipulations and grass removal on cover, species composition, and invasibility of a novel grassland in Colorado. Restoration Ecology 17:818–826.

Christen, D. C., and G. R. Matlack. 2009. The habitat and conduit functions of roads in the spread of three invasive plant species. Biological Invasions 11:453–465.

Chytry, M., V. Jarosik, P. Pyšek, O. Hajek, I. Knollova, L. Tichy, and J. Danihelka. 2008. Separating habitat invasibility by alien plants from the actual level of invasion. Ecology 89:1541–1553.

Coffman, G. C., R. F. Ambrose, and P. W. Rundel. 2010. Wildfire promotes dominance of invasive giant reed (*Arundo donax*) in riparian ecosystems. Biological Invasions 12:2723–2734.

Compagnoni, A., and C. B. Halpern. 2009. Properties of native plant communities do not determine exotic success during early forest succession. Ecography 32:449–458.

Crawford, J. S., C. H. A. Wahren, S. Kyle, and W. H. Moir. 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. Journal of Vegetation Science 12:261–268.

Creese, C., A. Lee, and L. Sack. 2011. Drivers of morphological diversity and distribution in the Hawaiian fern flora: trait associations with size, growth form, and environment. American Journal of Botany 98:956–966.

Crooks, J. A., A. L. Chang, and G. M. Ruiz. 2011. Aquatic pollution increases the relative success of invasive species. Biological Invasions 13:165–176.

Damascos, M. A., and G. G. Gallopin. 1992. Ecology of an introduced shrub (*Rosa rubiginosa* L. = *Rosa eglanteria* L.) – invasion risks and effects on the plant communities of the Andean Patagonic region of Argentina. Revista Chilena de Historia Natural 65:395–407.

D'Antonio, C. M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. Ecology 74:83–95.

Dark, S. J. 2004. The biogeography of invasive alien plants in California: an application of GIS and spatial regression analysis. Diversity and Distributions 10:1–9.

Dean, W. R. J., S. J. Milton, P. G. Ryan, and C. L. Moloney. 1994. The role of disturbance in the establishment of indigenous and alien plants at Inaccessible and Nightingale islands in the South Atlantic Ocean. Vegetatio 113:13–23.

Décamps, H., A. M. Planty-Tabacchi, and E. Tabacchi. 1995. Changes in the hydrological regime and invasions by plant–species along riparian systems of the Adour River, France. Regulated Rivers: Research and Management 11:23–33.

DeFerrari, C. M., and R. J. Naiman. 1994. A multiscale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. Journal of Vegetation Science 5:247–258.

Dickens, S. J. M., F. Gerhardt, and S. K. Collinge. 2005. Recreational portage trails as corridors facilitating non–native plant invasions of the Boundary Waters Canoe Area Wilderness (USA). Conservation Biology 19:1653–1657.

Domenech, R., and M. Vilà. 2006. The role of successional stage, vegetation type and soil disturbance in the invasion of the alien grass *Cortaderia selloana*. Journal of Vegetation Science 17:591–598.

Domenech, R., and M. Vilà. 2007. *Cortaderia selloana* invasion across a Mediterranean coastal strip. Acta Oecologica-International Journal of Ecology 32:255–261.

Edward, E., P. K. T. Munishi, and P. E. Hulme. 2009. Relative roles of disturbance and propagule pressure on the invasion of humid tropical forest by *Cordia alliodora* (Boraginaceae) in Tanzania. Biotropica 41:171–178.

Ehrenfeld, J. G. 2008. Exotic invasive species in urban wetlands: environmental correlates and implications for wetland management. Journal of Applied Ecology 45:1160–1169.

Eldridge, D. J., and R. Simpson. 2002. Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands. Basic and Applied Ecology 3:19–29.

Erneberg, M., B. Strandberg, M. Strandberg, B. D. Jensen, and J. Weine. 2008. Effects of soil disturbance and disease on the growth and reproduction of *Lolium perenne* (Poaceae) introduced to semi-natural grasslands. Polish Journal of Ecology 56:593–604.

Eschtruth, A. K., and J. J. Battles. 2009. Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. Ecological Monographs 79:265–280.

Essl, F. 2007. From ornamental to detrimental? The incipient invasion of Central Europe by *Paulownia tomentosa*. Preslia 79:377–389.

Fensham, R. J. 1998. The grassy vegetation of the Darling Downs, south–eastern Queensland, Australia. Floristics and grazing effects. Biological Conservation 84:301–310.

Fensham, R. J., R. J. Fairfax, and R. J. Cannell. 1994. The invasion of *Lantana camara* L. in Forty Mile Scrub National Park, North Queensland. Australian Journal of Ecology 19:297–305.

Figueroa, J. A., L. A. Cavieres, S. Gomez-Gonzalez, M. A. Molina-Montenegro, and F. M. Jaksic. 2009. Do heat and smoke increase emergence of exotic and native plants in the matorral of central Chile? Acta Oecologica-International Journal of Ecology 35(2):335–340.

Fisher, J. L., W. A. Loneragan, K. Dixon, J. Delaney, and E. J. Veneklaas. 2009. Altered vegetation structure and composition linked to fire frequency and plant invasion in a biodiverse woodland. Biological Conservation 142:2270–2281.

Fleischmann, K. 1997. Invasion of alien woody plants on the islands of Mahe and Silhouette, Seychelles. Journal of Vegetation Science 8:5–12.

Fleishman, E., D. D. Murphy, and D. W. Sada. 2006. Effects of environmental heterogeneity and disturbance on the native and non-native flora of desert springs. Biological Invasions 8:1091–1101.

Fleming, G. M., J. E. Diffendorfer, and P. H. Zedler. 2009. The relative importance of disturbance and exotic plant abundance in California coastal sage scrub. Ecological Applications 19:2210–2227.

Florentine, S. K., M. E. Westbrooke, K. Gosney, G. Ambrose, and M. O'Keefe. 2006. The arid land invasive weed *Nicotiana glauca* R. Graham (Solanaceae): population and soil seed bank dynamics, seed germination patterns and seedling response to flood and drought. Journal of Arid Environments 66:218–230.

Flory, S. L., and K. Clay. 2006. Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA. Plant Ecology 184:131–141.

Flory, S. L., and K. Clay. 2009. Effects of roads and forest successional age on experimental plant invasions. Biological Conservation 142:2531–2537.

Fornwalt, P. J., M. R. Kaufmann, and T. J. Stohlgren. 2010. Impacts of mixed severity wildfire on exotic plants in a Colorado ponderosa pine-Douglas-fir forest. Biological Invasions 12:2683–2695.

Foxcroft, L. C., M. Parsons, C. A. McLoughlin, and D. M. Richardson. 2008. Patterns of alien plant distribution in a river landscape following an extreme flood. South African Journal of Botany 74:463–475.

Foxcroft, L. C., M. Rouget, D. M. Richardson, and S. Mac Fadyen. 2004. Reconstructing 50 years of *Opuntia stricta* invasion in the Kruger National Park, South Africa: environmental determinants and propagule pressure. Diversity and Distributions 10:427–437.

Foxcroft, L. C., V. Jarosik, P. Pyšek, D. M. Richardson, and M. Rouget. 2011. Protected-area boundaries as filters of plant invasions. Conservation Biology 25:400–405.

Frenot, Y., J. C. Gloaguen, L. Masse, and M. Lebouvier. 2001. Human activities, ecosystem disturbance and plant invasions in subantarctic Crozet, Kerguelen and Amsterdam Islands. Biological Conservation 101:33–50.

Friday, J. B., P. G. Scowcroft, and A. Ares. 2008. Responses of native and invasive plant species to selective logging in an *Acacia koa-Metrosideros polymorpha* forest in Hawai'i. Applied Vegetation Science 11:471–482.

Frieswyk, C. B., and J. B. Zedler. 2007. Vegetation change in great lakes coastal wetlands: deviation from the historical cycle. Journal of Great Lakes Research 33:366–380.

Garcia-Serrano, H., J. Escarre, J., and F. X. Sans. 2004. Factors that limit the emergence and establishment of the related aliens *Senecio inaequidens* and *Senecio pterophorus* and the native *Senecio malacitanus* in Mediterranean climate. Canadian Journal of Botany-Revue Canadienne de Botanique 82:1346–1355.

Gasso, N., D. Sol, J. Pino, E. D. Dana, F. Lloret, M. Sanz-Elorza, E. Sobrino, and M. Vilà. 2009. Exploring species attributes and site characteristics to assess plant invasions in Spain. Diversity and Distributions 15:50–58.

Gelbard, J. L., and S. Harrison. 2005. Invasibility of roadless grasslands: an experimental study of yellow starthistle. Ecological Applications 15:1570–1580.

Goergen, E., and C. C. Daehler. 2001. Reproductive ecology of a native Hawaiian grass (*Heteropogon contortus*; Poaceae) versus its invasive alien competitor (*Pennisetum setaceum*; Poaceae). International Journal of Plant Sciences 162:317–326.

Gomez-Gonzalez, S., and L. A. Cavieres. 2009. Litter burning does not equally affect seedling emergence of native and alien species of the Mediterranean-type Chilean matorral. International Journal of Wildland Fire 18:213–221.

Gomez-Gonzalez, S., C. Torres-Diaz, G. Valencia, P. Torres–Morales, L. A. Cavieres, and J. G. Pausas. 2011. Anthropogenic fires increase alien and native annual species in the Chilean coastal matorral. Diversity and Distributions 17:58–67.

Gordon, D. R., C. H. Greenberg, S. H. Crownover, and O. L. Slapcinsky. 2005. Effects of unpaved road soils on persistence of three non–native grass species. Natural Areas Journal 25:257–262.

Gosper, C. R., C. J. Yates, S. M. Prober, and M. R. Williams. 2011. Fire does not facilitate invasion by alien annual grasses in an infertile Australian agricultural landscape. Biological Invasions 13:533–544.

Gower, S. T. 2008. Are horses responsible for introducing non-native plants along forest trails in the eastern United States? Forest Ecology and Management 256:997–1003.

Green, E. K., and S. M. Galatowitsch. 2002. Effects of *Phalaris arundinacea* and nitrate-N addition on the establishment of wetland plant communities. Journal of Applied Ecology 39:134–144.

Greenberg, C. H., S. H. Crownover, and D. R. Gordon. 1997. Roadside soils: a corridor for invasion of xeric scrub by nonindigenous plants. Natural Areas Journal 17:99–109.

Grigulis, K., A. W. Sheppard, J. E. Ash, and R. H. Groves. 2001. The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges. Journal of Applied Ecology 38:281–290.

Gurevitch, J., T. G. Howard, I. W. Ashton, E. A. Leger, K. M. Howe, E. Woo, and M. Lerdau. 2008. Effects of experimental manipulation of light and nutrients on establishment of seedlings of native and invasive woody species in Long Island, NY forests. Biological Invasions 10:821–831.

Hager, H. A. 2004. Differential effects of *Typha* litter and plants on invasive *Lythrum salicaria* seedling survival and growth. Biological Invasions 6:433–444.

Hansen, M. J., and A. P. Clevenger. 2005. The influence of disturbance and habitat on the presence of non–native plant species along transport corridors. Biological Conservation 125:249–259.

Hata, K., J. I. Suzuki, N. Kachi, and Y. Yamamura. 2006. A 19-year study of the dynamics of an invasive alien tree, *Bischofia javanica,* on a subtropical oceanic island. Pacific Science 60:455–470.

Hebel, C. L., J. E. Smith, and K. Cromack Jr. 2009. Invasive plant species and soil microbial response to wildfire burn severity in the Cascade Range of Oregon. Applied Soil Ecology 42:150–159.

Hendrickson, C., T. Bell, K. Butler, and L. Hermanutz. 2005. Disturbance-enabled invasion of *Tussilago farfara* (L.) in Gros Morne National Park, Newfoundland: management implications. Natural Areas Journal 25:263–274.

Herrick, B. M., and A. T. Wolf. 2005. Invasive plant species in diked vs. undiked Great Lakes wetlands. Journal of Great Lakes Research 31:277–287.

Hierro, J. L., D. Villarreal, O. Eren, J. M. Graham, and R. M. Callaway. 2006. Disturbance facilitates invasion: the effects are stronger abroad than at home. American Naturalist 168:144–156.

Higgins, S. I., and D. M. Richardson. 1998. Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. Plant Ecology 135:79–93.

Hill, S. J., P. J. Tung, and M. R. Leishman. 2005. Relationships between anthropogenic disturbance, soil properties and plant invasion in endangered Cumberland Plain Woodland, Australia. Austral Ecology 30:775–788.

HilleRisLambers, J., S. G. Yelenik, B. P. Colman, and J. M. Levine. 2010. California annual grass invaders: the drivers or passengers of change? Journal of Ecology 98:1147–1156.

Hobbs, R. J., and L. Atkins. 1988. Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the western Australian wheat belt. Australian Journal of Ecology 13:171–179.

Huebner, C. D. 2010. Establishment of an invasive grass in closed-canopy deciduous forests across local and regional environmental gradients. Biological Invasions 12:2069–2080.

Huels, J., A. Otte, and R. L. Eckstein. 2007. Population life-cycle and stand structure in dense and open stands of the introduced tall herb *Heracleum mantegazzianum*. Biological Invasions 9:799–811.

Hussain, A., C. Sun, X. Zhou, and I. A. Munn. 2008. Ecological and economic determinants of invasive tree species on Alabama forestland. Forest Science 54:339–348.

Hwang, B. C., and W. K. Lauenroth. 2010. Effect of nitrogen, water and neighbors on the growth of *Hesperis matronalis* in a natural community. American Midland Naturalist 163:212–219.

Incera M., I. Bertocci, and L. Benedetti-Cecchi. 2010. Effects of mean intensity and temporal variability of disturbance on the invasion of *Caulerpa racemosa* var. *cylindracea* (Caulerpales) in rock pools. Biological Invasions 12:501–514.

Jacquemyn, H., R. Brys, and M. G. Neubert. 2005. Fire increases invasive spread of *Molinia caerulea* mainly through changes in demographic parameters. Ecological Applications 15:2097–2108.

Jesson, L., D. Kelly, and A. Sparrow. 2000. The importance of dispersal, disturbance, and competition for exotic plant invasions in Arthur's Pass National Park, New Zealand. New Zealand Journal of Botany 38:451–468.

Johnson, V. S., J. A. Litvaitis, T. D. Lee, and S. D. Frey. 2006. The role of spatial and temporal scale in colonization and spread of invasive shrubs in early successional habitats. Forest Ecology and Management 228:124–134.

Jorgensen, R. H., and J. Kollmann. 2009. Invasion of coastal dunes by the alien shrub *Rosa rugosa* is associated with roads, tracks and houses. Flora 204:289–297.

Kalwij, J. M., S. J. Milton, and M. A, McGeoch. 2007. Road verges: corridors for plant invasions – a spatial hierarchical approach. South African Journal of Botany 73:293–294.

Kalwij, J. M., M. P. Robertson, and B. J. van Rensburg. 2008. Human activity facilitates altitudinal expansion of exotic plants along a road in montane grassland, South Africa. Applied Vegetation Science 11:491–498.

Keeley, J. E., M. Baer-Keeley, and C. J. Fotheringham. 2005. Alien plant dynamics following fire in Mediterranean-climate California shrublands. Ecological Applications 15:2109–2125.

Kellogg, C. H., and S. D. Bridgham. 2004. Disturbance, herbivory, and propagule dispersal control dominance of an invasive grass. Biological Invasions 6:319–329.

Kercher, S. M., Q. J. Carpenter, and J. B. Zedler. 2004. Interrelationships of hydrologic disturbance, reed canary grass (*Phalaris arundinacea* L.), and native plants in Wisconsin wet meadows. Natural Areas Journal 24:316–325.

Kercher, S. M., and J. B. Zedler. 2004. Multiple disturbances accelerate invasion of reed canary grass (*Phalaris arundinacea* L.) in a mesocosm study. Oecologia 138:455–464.

Kercher, S. M., A. Herr-Turoff, and J. B. Zedler. 2007. Understanding invasion as a process: the case of *Phalaris arundinacea* in wet prairies. Biological Invasions 9:657–665.

Kim, K. D. 2005. Invasive plants on disturbed Korean sand dunes. Estuarine Coastal and Shelf Science 62:353–364.

King, S. A., and R. T. Buckney. 2001. Exotic plants in the soil–stored seed bank of urban bushland. Australian Journal of Botany 49:717–720.

King, S. A., and R. T. G. Buckney. 2000. Urbanization and exotic plants in northern Sydney streams. Austral Ecology 25:455–461.

Klein, J., S. Ruitton, M. Verlaque, and C. F. Boudouresque. 2005. Species introductions, diversity and disturbances in marine macrophyte assemblages of the northwestern Mediterranean Sea. Marine Ecology Progress Series 290:79–88.

Knight, T. M., J. L. Dunn, L. A. Smith, J. Davis, and S. Kalisz. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. Natural Areas Journal 29:110–116.

Kollmann, J., L. Frederiksen, P. Vestergaard, and H. H. Bruun. 2007. Limiting factors for seedling emergence and establishment of the invasive non-native *Rosa rugosa* in a coastal dune system. Biological Invasions 9:31–42.

Kota, N. L., R. E. Landenberger, and J. B. McGraw. 2007. Germination and early growth of *Ailanthus* and tulip poplar in three levels of forest disturbance. Biological Invasions 9:197–211.

Kotanen, P. M. 1997. Effects of experimental soil disturbance on revegetation by natives and exotics in coastal Californian meadows. Journal of Applied Ecology 34:631–644.

Kuhn, N. L., and J. B. Zedler. 1997. Differential effects of salinity and soil saturation on native and exotic plants of a coastal salt marsh. Estuaries 20:391–403.

Kyle, G. P., A. Kulmatiski, and K. H. Beard. 2008. Influence of pocket gopher mounds on nonnative plant establishment in a shrubsteppe ecosystem. Western North American Naturalist 68:374–381.

Lambrinos, J. G. 2002. The variable invasive success of *Cortaderia* species in a complex landscape. Ecology 83:518–529.

Larson, D. L. 2003. Native weeds and exotic plants: relationships to disturbance in mixed-grass prairie. Plant Ecology 169:317–333.

Larson, D. L., P. J. Anderson, and W. Newton. 2001. Alien plant invasion in mixed-grass prairie: Effects of vegetation type and anthropogenic disturbance. Ecological Applications 11:128–141.

Lee, C. S., H. J. Cho, and H. Yi. 2004. Stand dynamics of introduced black locust (*Robinia pseudoacacia* L.) plantation under different disturbance regimes in Korea. Forest Ecology and Management 189:281–293.

Lelong, B., C. Lavoie, and M. Theriault. 2009. What are the factors that facilitate the implementation of the common reed (*Phragmites australis*) along roads in Southern Quebec? Ecoscience 16:224–237.

Li, Y., and M. Norland. 2001. The role of soil fertility in invasion of Brazilian pepper (*Schinus terebinthifolius*) in Everglades National Park, Florida. Soil Science 166:400–405.

Lilley, P. L., and M. Vellend. 2009. Negative native-exotic diversity relationship in oak savannas explained by human influence and climate. Oikos 118:1373–1382.

Lonati, M., A. Gorlier, D. Ascoli, R. Marzano, and G. Lombardi. 2009. Response of the alien species *Panicum acuminatum* to disturbance in an Italian lowland heathland. Botanica Helvetica 119:105–111.

Loydi, A., and S. M. Zalba. 2009. Feral horses dung piles as potential invasion windows for alien plant species in natural grasslands. Plant Ecology 201:471–480.

Lynch, R. L., H. Chen, L. A. Brandt, and F. J. Mazzotti. 2009. Old world climbing fern (*Lygodium microphyllum*) invasion in hurricane caused treefalls. Natural Areas Journal 29:210–215.

MacDougall, A. S., and R. Turkington. 2004. Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. Journal of Ecology 92:422–434.

Marshall, J. M., and D. S. Buckley. 2008. Influence of litter removal and mineral soil disturbance on the spread of an invasive grass in a Central Hardwood forest. Biological Invasions 10:531–538.

Martone, R. G., and K. Wasson. 2008. Impacts and interactions of multiple human perturbations in a California salt marsh. Oecologia 158:151–163.

Mazía, C. N., E. J. Chaneton, C. M. Ghersa, and R. J. C. Leon. 2001. Limits to tree species invasion in Pampean grassland and forest plant communities. Oecologia 128:594–602.

Mazía, C. N., E. J. Chaneton, M. Machera, A. Uchitel, M.V. Feler, and C. M. Ghersa. 2010. Antagonistic effects of large- and small-scale disturbances on exotic tree invasion in a native tussock grassland relict. Biological Invasions 12:3109–3122.

McCay, T. S., D. H. McCay, A. V. Caragiulo, and T. L. Mandel. 2009. Demography and distribution of the invasive *Rhamnus cathartica* in habitats of a fragmented landscape. Journal of the Torrey Botanical Society 136:110–121.

McCay, T. S., D. H. McCay, and J. L. Czajka. 2009. Deposition of exotic bird-dispersed seeds into three habitats of a fragmented landscape in the northeastern United States. Plant Ecology 203:59–67.

McDonald, R. I., G. Motzkin, and D. R. Foster. 2008. Assessing the influence of historical factors, contemporary processes, and environmental conditions on the distribution of invasive species. Journal of the Torrey Botanical Society 135:260–271.

McDonald, R. I., and D. L. Urban. 2006. Edge effects on species composition and exotic species abundance in the North Carolina Piedmont. Biological Invasions 8:1049–1060.

McGlone, C. M., C. H. Sieg, and T. E. Kolb. 2011. Invasion resistance and persistence: established plants win, even with disturbance and high propagule pressure. Biological Invasions 13:291–304.

McIntyre, S., P. Y. Ladiges, and G. Adams. 1988. Plant species richness and invasion by exotics in relation to disturbance of wetland communities on the riverine plain, NSW. Australian Journal of Ecology 13:361–373.

McIntyre, S., and S. Lavorel. 1994. Predicting richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. Conservation Biology 8:521–531.

McKinney, M. L. 2002. Influence of settlement time, human population, park shape and age, visitation and roads on the number of alien plant species in protected areas in the USA. Diversity and Distributions 8:311–318.

Meekins, J. F., and B. C. McCarthy. 2001. Effect of environmental variation on the invasive success of a nonindigenous forest herb. Ecological Applications 11:1336–1348.

Minor, E. S., S. M. Tessel, K. A. M. Engelhardt, and T. R. Lookingbill. 2009. The role of landscape connectivity in assembling exotic plant communities: a network analysis. Ecology 90:1802–1809.

Morgan, J. W. 1998. Patterns of invasion of an urban remnant of a species-rich grassland in southeastern Australia by non-native plant species. Journal of Vegetation Science 9:181–190.

Morgan, J. W. 2006. Bryophyte mats inhibit germination of non-native species in burnt temperate native grassland remnants. Biological Invasions 8:159–168.

Mosher, E. S., J. A. Silander Jr., and A. M. Latimer. 2009. The role of land-use history in major invasions by woody plant species in the northeastern North American landscape. Biological Invasions 11:2317–2328.

Murphy, H. T., D. J. Metcalfe, M. G. Bradford, A. F. Ford, K. E. Galway, T. A. Sydes, and D. J. Westcott. 2008. Recruitment dynamics of invasive species in rainforest habitats following Cyclone Larry. Austral Ecology 33:495–502.

Nemec, K. T., C. R. Allen, A. Alai, G. Clements, A. C. Kessler, T. Kinsell, A. Major, and B. J. Stephen. 2011. Woody invasions of urban trails and the changing face of urban forests in the Great Plains, USA. American Midland Naturalist 165:241–256.

Nunes da Cunha, C., and W. J. Junk. 2004. Year-to-year changes in water level drive the invasion of *Vochysia divergens* in Pantanal grasslands. Applied Vegetation Science 7:103–110.

Otfinowski, R., and N. C. Kenkel. 2010. Covariance between disturbance and soil resources dictates the invasibility of northern fescue prairies. Biological Invasions 12:1349–1361.

Parendes, L. A., and J. A. Jones. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. Conservation Biology 14:64–75.

Parker, I. M., S. K. Mertens, and D. W. Schemske. 1993. Distribution of seven native and two exotic plants in a tallgrass prairie in southeastern Wisconsin – the importance of human disturbance. American Midland Naturalist 130:43–55.

Pauchard, A., and P. B. Alaback. 2006. Edge type defines alien plant species invasions along *Pinus contorta* burned, highway and clearcut forest edges. Forest Ecology and Management 223:327–335.

Pauchard, A., P. B. Alaback, and E. G. Edlund. 2003. Plant invasions in protected areas at multiple scales: *Linaria vulgaris* (Scrophulariaceae) in the west Yellowstone area. Western North American Naturalist 63:416–428.

Pauchard, A., R. A. Garcia, E. Pena, C. Gonzalez, L. A. Cavieres, and R. O. Bustamante. 2008. Positive feedbacks between plant invasions and fire regimes: *Teline monspessulana* (L.) K. Koch (Fabaceae) in central Chile. Biological Invasions 10:547–553.

Pausas, J. G., F. Lloret, and M. Vilà. 2006. Simulating the effects of different disturbance regimes on *Cortaderia selloana* invasion. Biological Conservation 128:128–135.

Paynter, Q., S. V. Fowler, J. Memmott, and A. W. Sheppard. 1998. Factors affecting the establishment of *Cytisus scoparius* in southern France: implications for managing both native and exotic populations. Journal of Applied Ecology 35:582–595.

Pergl, J., I. Perglova, P. Pyšek, and H. Dietz. 2006. Population age structure and reproductive behavior of the monocarpic perennial *Heracleum mantegazzianum* (Apiaceae) in its native and invaded distribution ranges. American Journal of Botany 93:1018–1028.

Pino, J., X. Font, J. Carbo, M. Jove, and L. Pallares. 2005. Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). Biological Conservation 122:339–350.

Pino, J., J. M. Segui, and N. Alvarez. 2006. Invasibility of four plant communities in the Llobregat delta (Catalonia, NE of Spain) in relation to their historical stability. Hydrobiologia 570:257–263.

Poll, M., B. J. Naylor, J. M. Alexander, P. J. Edwards, and H. Dietz. 2009. Seedling establishment of Asteraceae forbs along altitudinal gradients: a comparison of transplant experiments in the native and introduced ranges. Diversity and Distributions 15:254–265.

Pyle, L. L. 1995. Effects of disturbance on herbaceous exotic plant species on the floodplain of the Potomac River. American Midland Naturalist 134:244–253.

Radford, I. J., K. J. M. Dickinson, and J. M. Lord. 2010. Does disturbance, competition or resource limitation underlie *Hieracium lepidulum* invasion in New Zealand? Mechanisms of establishment and persistence, and functional differentiation among invasive and native species. Austral Ecology 35:282–293.

Rao, L. E., and E. B. Allen. 2010. Combined effects of precipitation and nitrogen deposition on native and invasive winter annual production in California deserts. Oecologia 162:1035–1046.

Reed, H. E., T. R. Seastedt, and J. M. Blair. 2005. Ecological consequences of C_4 grass invasion of a C_4 grassland: a dilemma for management. Ecological Applications 15:1560–1569.

Restrepo, C., and P. Vitousek. 2001. Landslides, alien species, and the diversity of a Hawaiian montane mesic ecosystem. Biotropica 33:409–420.

Rodgers, J. C., and K. C. Parker. 2003. Distribution of alien plant species in relation to human disturbance on the Georgia Sea Islands. Diversity and Distributions 9:385–398.

Rosas, H. L., P. Moreno-Casasola, and I. A. Mendelssohn. 2006. Effects of experimental disturbances on a tropical freshwater marsh invaded by the African grass *Echinochloa pyramidalis*. Wetlands 26:593–604.

Rose, A. B., L. R. Basher, S. K. Wiser, K. H. Platt, and I. H. Lynn. 1998. Factors predisposing short-tussock grasslands to *Hieracium* invasion in Marlborough, New Zealand. New Zealand Journal of Ecology 22:121–140.

Rose, M., and L. Hermanutz. 2004. Are boreal ecosystems susceptible to alien plant invasion? Evidence from protected areas. Oecologia 139:467–477.

Rouget, M., D. M. Richardson, S. J. Milton, and D. Polakow. 2001. Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. Plant Ecology 152:79–92.

Safford, H. D., and S. P. Harrison. 2001. Grazing and substrate interact to affect native vs. exotic diversity in roadside grasslands. Ecological Applications 11:1112–1122.

Scarisbrick, D. H., H. J. Harvey, and J. D. Ivins. 1970. Effect of cutting on subsequent growth of introduced ribgrass (*Plantago lanceolata*) seedlings. Journal of the British Grassland Society 25:207–209.

Scherber, C., M. J. Crawley, and S. Porembski. 2003. The effects of herbivory and competition on the invasive alien plant *Senecio inaequidens* (Asteraceae). Diversity and Distributions 9:415–426.

Schramm, J. W., and J. G. Ehrenfeld. 2010. Leaf litter and understory canopy shade limit the establishment, growth and reproduction of *Microstegium vimineum*. Biological Invasions 12:3195–3204.

Scott, N. A., S. Saggar, and P. D. McIntosh. 2001. Biogeochemical impact of *Hieracium* invasion in New Zealand's grazed tussock grasslands: sustainability implications. Ecological Applications 11:1311–1322.

Sharma, G. P., and A. S. Raghubanshi. 2009. Plant invasions along roads: a case study from central highlands, India. Environmental Monitoring and Assessment 157:191–198.

Sharma, G. P., and A. S. Raghubanshi. 2010. How *Lantana* invades dry deciduous forest: a case study from Vindhyan highlands, India. Tropical Ecology 51:305–316.

Sheppard, A. W., P. Hodge, Q. Paynter, and M. Rees. 2002. Factors affecting invasion and persistence of broom *Cytisus scoparius* in Australia. Journal of Applied Ecology 39:721–734.

Sher, A. A., D. L. Marshall, and J. P. Taylor. 2002. Establishment patterns of native *Populus* and *Salix* in the presence of invasive nonnative *Tamarix*. Ecological Applications 12:760–772.

Siemann, E., and W. E. Rogers. 2003. Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. Journal of Ecology 91:923–931.

Silliman, B. R., and M. D. Bertness. 2004. Shoreline development drives invasion of *Phragmites australis* and the loss of plant diversity on New England salt marshes. Conservation Biology 18:1424–1434.

Smith, M. D., and A. K. Knapp. 1999. Exotic plant species in a C_4-dominated grassland: invasibility, disturbance, and community structure. Oecologia 120:605–612.

Smith, M. D., and A. K. Knapp. 2001. Size of the local species pool determines invasibility of a C_4-dominated grassland. Oikos 92:55–61.

Sobrino, E., M. Sanz-Elorza, E. D. Dana, and A. Gonzalez-Moreno. 2002. Invasibility of a coastal strip in NE Spain by alien plants. Journal of Vegetation Science 13:585–594.

Stapanian, M. A., S. D. Sundberg, G. A. Baumgardner, and A. Liston. 1998. Alien plant species composition and associations with anthropogenic disturbance in North American forests. Plant Ecology 139:49–62.

Stevens, J. T., and B. Beckage. 2009. Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). New Phytologist 184:365–375.

Stevens, J. T., and B. Beckage. 2010. Fire effects on demography of the invasive shrub Brazilian pepper (*Schinus terebinthifolius*) in Florida pine savannas. Natural Areas Journal 30:53–63.

Stohlgren, T. J., G. W. Chong, L. D. Schell, K. A. Rimar, Y. Otsuki, M. Lee, M. A. Kalkhan, and C. A. Villa. 2002. Assessing vulnerability to invasion by nonnative plant species at multiple spatial scales. Environmental Management 29:566–577.

Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. Ecological Applications 9:45–64.

Stover, M. E., and P. L. Marks. 1998. Successional vegetation on abandoned cultivated and pastured land in Tompkins County, New York. Journal of the Torrey Botanical Society 125:150–164.

Sullivan, J. J., P. A. Williams, S. M. Timmins, and M. C. Smale. 2009. Distribution and spread of environmental weeds along New Zealand roadsides. New Zealand Journal of Ecology 33:190–204.

Surrette, S. B., and S. J. Brewer. 2008. Inferring relationships between native plant diversity and *Lonicera japonica* in upland forests in north Mississippi, USA. Applied Vegetation Science 11:205–214.

Sutton, J. R., T. J. Stohlgren, and K. G. Beck. 2007. Predicting yellow toadflax infestations in the flat tops wilderness of Colorado. Biological Invasions 9:783–793.

Tassin, J., and J. N. Riviere. 2003. Species richness altitudinal gradient of invasive plants on Réunion Island (Mascareigne archipelago, Indian Ocean). Revue D’Écologie-La Terre et la Vie 58:257–270.

Taylor, B., and G. G. Ganf. 2005. Comparative ecology of two co–occurring floodplain plants: the native *Sporobolus mitchellii* and the exotic *Phyla canescens*. Marine and Freshwater Research 56:431–440.

Thuiller, W., D. M. Richardson, M. Rouget, S. Procheş, and J. R. U. Wilson. 2006. Interactions between environment, species traits, and human uses describe patterns of plant invasions. Ecology 87:1755–1769.

Todorovic, S., D. Bozic, A. Simonovic, B. Filipovic, M. Dragicevic, Z. Giba, and D. Grubisic. 2010. Interaction of fire-related cues in seed germination of the potentially invasive species *Paulownia tomentosa* Steud. Plant Species Biology 25:193–202.

Totland, O., P. Nyeko, A. L. Bjerknes, S. J. Hegland, and A. Nielsen. 2005. Does forest gap size affects population size, plant size, reproductive success and pollinator visitation in *Lantana camara*, a tropical invasive shrub? Forest Ecology and Management 215:329–338.

Trtikova, M. 2009. Effects of competition and mowing on growth and reproduction of the invasive plant *Erigeron annuus* at two contrasting altitudes. Botanica Helvetica 119:1–6.

Ullmann, I., P. Bannister, and J. B. Wilson. 1998. Lateral differentiation and the role of exotic species in roadside vegetation in southern New Zealand. Flora 193:149–164.

Uowolo, A. L., D. Binkley, and E. C. Adair. 2005. Plant diversity in riparian forests in northwest Colorado: Effects of time and river regulation. Forest Ecology and Management 218:107–114.

van der Wal, R., A. M. Truscott, I. S. K. Pearce, L. Cole, Lisa, M. P. Harris, and S. Wanless. 2008. Multiple anthropogenic changes cause biodiversity loss through plant invasion. Global Change Biology 14:1428–1436.

Veldman, J. W., B. Mostacedo, M. Pena-Claros, and F. E. Putz. 2009. Selective logging and fire as drivers of alien grass invasion in a Bolivian tropical dry forest. Forest Ecology and Management 258:1643–1649.

Vidal, E., F. Medail, T. Tatoni, P. Roche, and P. Vidal. 1998. Impact of gull colonies on the flora of the Riou archipelago (Mediterranean islands of south-east France). Biological Conservation 84:235–243.

de Villalobos, A. E., Vazquez, D. P., and J. L. Martin. 2010. Soil disturbance, vegetation cover and the establishment of the exotic shrub *Pyracantha coccinea* in southern France. Biological Invasions 12:1023–1029.

von Holle, B., and G. Motzkin. 2007. Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England. Biological Conservation 136:33–43.

Walter, H. S., and G. A. Levin. 2008. Feral sheep on Socorro Island: facilitators of alien plant colonization and ecosystem decay. Diversity and Distributions 14:422–431.

Webster, C. R., J. H. Rock, R. E. Froese, and M. A. Jenkins. 2008. Drought-herbivory interaction disrupts competitive displacement of native plants by *Microstegium vimineum*, 10-year results. Oecologia 157:497–508.

Williams, J. L., H. Auge, and J. L. Maron. 2010. Testing hypotheses for exotic plant success: parallel experiments in the native and introduced ranges. Ecology 91:1355–1366.

Williams, M. C., and G. M. Wardle. 2005. The invasion of two native Eucalypt forests by *Pinus radiata* in the Blue Mountains, New South Wales, Australia. Biological Conservation 125:55–64.

Williams, P. A., and R. P. Buxton. 1995. Aspects of the ecology of two species of *Passiflora* (*Passiflora mollissima* (Kunth) L Bailey and *P. pinnatistipula* Cav.) as weeds in South Island, New Zealand. New Zealand Journal of Botany 33:315–323.

Williamson, J., and S. Harrison. 2002. Biotic and abiotic limits to the spread of exotic revegetation species. Ecological Applications 12:40–51.

Woitke, M., and H. Dietz. 2002. Shifts in dominance of native and invasive plants in experimental patches of vegetation. Perspectives in Plant Ecology Evolution and Systematics 5:165–184.

Wolfson, B. A. S., T. E. Kolb, C. H. Sieg, and K. M. Clancy. 2005. Effects of post–fire conditions on germination and seedling success of diffuse knapweed in northern Arizona. Forest Ecology and Management 216:342–358.

Wu, S. H., J. K. Tsai, J. K., H. T. Sun, H. T.C. F. Chen, and C. R. Chiou. 2009. Patterns of plant invasions in the preserves and recreation areas of Shei-Pa National Park in Taiwan. Botanical Studies 50:217–227.

Yager, L. Y., D. L. Miller, and J. Jones. 2010. Susceptibility of longleaf pine forest associations in south Mississippi to invasion by cogongrass [*Imperata cylindrica* (L.) Beauv.]. Natural Areas Journal 30:226–232.

Zampella, R. A., and K. J. Laidig. 1997. Effect of watershed disturbance on Pinelands stream vegetation. Journal of the Torrey Botanical Society 124:52–66.

Appendix B: Bibliography of papers used in the second systematic review presented in Chapter 2.

Aguiar, F. C., M. T. Ferreira, and A. Albuquerque. 2006. Patterns of exotic and native plant species richness and cover along a semi–arid Iberian river and across its floodplain. Plant Ecology 184:189–202.

Aguiar, F. C., M. T. Ferreira, A. Albuquerque, and I. Bernez. 2005. Invasibility patterns of knotgrass (*Paspalum distichum*) in Portuguese riparian habitats. Weed Technology 19:509–516.

Aguiar, F. C., M. T. Ferreira, A. Albuquerque, and I. Moreira. 2007. Alien and endemic flora at reference and non-reference sites in Mediterranean–type streams in Portugal. Aquatic Conservation: Marine and Freshwater Ecosystems 17:335–347.

Aguiar, F. C., M. T. Ferreira, and I. Moreira. 2001. Exotic and native vegetation establishment following channelization of a western Iberian river. Regulated Rivers: Research and Management 17:509–526.

Akamatsu, F., K. Ide, K. Shimano, and H. Toda. 2011. Nitrogen stocks in a riparian area invaded by N-fixing black locust (*Robinia pseudoacacia* L.). Landscape and Ecological Engineering 7:109–115.

Al-Chokhachy, R., A. M. Ray, B. B. Roper, and E. Archer. 2013. Exotic plant colonization and occupancy within riparian areas of the Interior Columbia River and Upper Missouri River Basins, USA. Wetlands 33:409–420.

Andrew, S. M., S. R. Moe, O. Totland, and P. K. T. Munishi. 2012. Species composition and functional structure of herbaceous vegetation in a tropical wetland system. Biodiversity and Conservation 21:2865–2885.

Angiolini, C., A. Nucci, M. Landi, and G. Bacchetta. G. 2013. Distribution of endemic and alien plants along Mediterranean rivers: a useful tool to identify areas in need of protection? Comptes Rendus Biologies 336:416–423.

Asaeda, T., M. H. Rashid, S. Kotagiri, and T. Uchida. 2011. The role of soil characteristics in the succession of two herbaceous lianas in a modified river floodplain. River Research and Applications 27:591–601.

Bagstad, K. J., S. J. Lite, and J. C. Stromberg. 2006. Vegetation, soils, and hydrogeomorphology of riparian patch types of a dryland river. Western North American Naturalist 66:23–44.

Barrat-Segretain, M. H., and B. Cellot. 2007. Response of invasive macrophyte species to drawdown: the case of *Elodea* sp. Aquatic Botany 87:255–261.

Beauchamp, V. B., and J. C. Stromberg. 2007. Flow regulation of the Verde River, Arizona encourages *Tamarix* recruitment but has minimal effect on *Populus* and *Salix* stand density. Wetlands 27:381–389.

Belmar, O., D. Bruno, F. Martinez-Capel, J. Barquin, and J. Velasco. 2013. Effects of flow regime alteration on fluvial habitats and riparian quality in a semiarid Mediterranean basin. Ecological Indicators 30:52–64.

Birken, A. S., and D. J. Cooper. 2006. Processes of *Tamarix* invasion and floodplain development along the lower Green River, Utah. Ecological Applications 16:1103–1120.

Bottollier-Curtet, M., A. M. Planty-Tabacchi, and E. Tabacchi. 2013. Competition between young exotic invasive and native dominant plant species: implications for invasions within riparian areas. Journal of Vegetation Science 24:1033–1042.

Boyd, L., R. Mac Nally, and J. Read. 2005. Does fallen timber on floodplains influence distributions of nutrients, plants and seeds? Plant Ecology 177:165–176.

Braatne, J. H., R. Jamieson, K. M. Gill, and S. B. Rood. 2007. Instream flows and the decline of riparian cottonwoods along the Yakima River, Washington, USA. River Research and Applications 23:247–267.

Brown, R. L., and J. Chenoweth. 2008. The effect of Glines Canyon Dam on hydrochorous seed dispersal in the Elwha River. Northwest Science 82:197–209.

Brzyski, J. R., and B. A. Schulte. 2009. Beaver (*Castor canadensis*) impacts on herbaceous and woody vegetation in Southeastern Georgia. American Midland Naturalist 162:74–86.

Busch, D. E., and S. D. Smith. 1993. Effects of fire on water and salinity relations of riparian woody taxa. Oecologia 94:186–194.

Busch, D. E., and S. D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the Southwestern US. Ecological Monographs 65:347–370.

Castro-Diez, P., G. Valle, N. Gonzalez-Munoz, and A. Alonso. 2014. Can the life-history strategy explain the success of the exotic trees *Ailanthus altissima* and *Robinia pseudoacacia* in Iberian floodplain forests? PLoS ONE 9:e100254.

Catford, J. A., and B. J. Downes. 2010. Using multi-scale species distribution data to infer drivers of biological invasion in riparian wetlands. Diversity and Distributions 16:20–32.

Catford, J. A., B. J. Downes, C. J. Gippel, and P. A. Vesk. 2011. Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands. Journal of Applied Ecology 48:432–442.

Catford, J. A., and R. Jansson. 2014. Drowned, buried and carried away: effects of plant traits on the distribution of native and alien species in riparian ecosystems. New Phytologist 204:19–36.

Catford, J. A., W. K. Morris, P. A. Vesk, C. J. Gippel, and B. J. Downes. 2014. Species and environmental characteristics point to flow regulation and drought as drivers of riparian plant invasion. Diversity and Distributions 20:1084–1096.

Chipps, S. R., D. E. Hubbard, K. B. Werlin, N. J. Haugerud, K. A. Powell, J. Thompson, and T. Johnson. 2006. Association between wetland disturbance and biological attributes in floodplain wetlands. Wetlands 26:497–508.

Chytry, M., J. Wild, P. Pysek, L. Tichy, J. Danihelka, and I. Knollova. 2009. Maps of the level of invasion of the Czech Republic by alien plants. Preslia 81:187–207.

Cogger, B. J., N. R. De Jager, M. Thomsen, and C. R. Adams. 2014. Winter browse selection by white-tailed deer and implications for bottomland forest restoration in the Upper Mississippi River Valley, USA. Natural Areas Journal 34:144–153.

Colleran, B. P., and K. E. Goodall. 2014. In situ growth and rapid response management of flood–dispersed Japanese knotweed (*Fallopia japonica*). Invasive Plant Science and Management 7:84–92.

Cooper, D. J., D. C. Andersen, and R. A. Chimner. 2003. Multiple pathways for woody plant establishment on floodplains at local to regional scales. Journal of Ecology 91:182–196.

Corenblit, D., J. Steiger, E. Tabacchi, E. Gonzalez, and A. M. Planty-Tabacchi. 2014. Ecosystem engineers modulate exotic invasions in riparian plant communities by modifying hydrogeomorphic connectivity. River Research and Applications 30:45–59.

Décamps, H., A. M. Planty-Tabacchi, and E. Tabacchi. 1995. Changes in the hydrological regime and invasions by plant species along riparian systems of the Adour River, France. Regulated Rivers: Research and Management 11:23–33.

DeFerrari, C. M., and R. J. Naiman. 1994. A multiscale assessment of the occurrence of exotic plants on the Olympic peninsula, Washington. Journal of Vegetation Science 5:247–258.

Dommanget, F., T. Spiegelberger, P. Cavaille, and A. Evette. 2013. Light availability prevails over soil fertility and structure in the performance of Asian knotweeds on riverbanks: new management perspectives. Environmental Management 52:1453–1462.

Drinkard, M. K., M. W. Kershner, A. Romito, J. Nieset, and F. A. de Szalay. 2011. Responses of plants and invertebrate assemblages to water–level fluctuation in headwater wetlands. Journal of the North American Benthological Society 30:981–996.

Dyakov, N., and P. Zhelev. 2013. Alien species invasion and diversity of riparian forest according to environmental gradients and disturbance regime. Applied Ecology and Environmental Research 11:249–272.

Earl, R. A., and C. R. Wood. 2002. Upstream changes and downstream effects of the San Marcos River of central Texas. Texas Journal of Science 54:69–88.

Erskine, W. D., N. Terrazzolo, and R. F. Warner. 1999. River rehabilitation from the hydrogeomorphic impacts of a large hydro–electric power project: Snowy River, Australia. Regulated Rivers–Research and Management 15:3–24.

Ferreira, M. T., P. M. Rodriguez-Gonzalez, F. C. Aguiar, and A. Albuquerque. 2005. Assessing biotic integrity in Iberian rivers: development of a multimetric plant index. Ecological Indicators 5:137–149.

Foxcroft, L. C., M. Parsons, C. A. McLoughlin, and D. M. Richardson. 2008. Patterns of alien plant distribution in a river landscape following an extreme flood. South African Journal of Botany 74:463–475.

Frangi, J. L., and A. E. Lugo. 1998. A flood plain palm forest in the Luquillo Mountains of Puerto Rico five years after Hurricane Hugo. Biotropica 30:339–348.

Gonzalez-Munoz, N., P. Castro–Diez, and O. Godoy. 2014. Lack of superiority of invasive over co-occurring native riparian tree seedling species. Biological Invasions 16:269–281.

Greene, B., and B. Blossey. 2014. Patterns of privet: urbanizing watersheds, invasive *Ligustrum sinense*, and performance of native plant species in piedmont floodplain forests. Ecosystems 17:990–1001.

Greet, J., R. D. Cousens, and J. A. Webb. 2013. Flow regulation is associated with riverine soil seed bank composition within an agricultural landscape: potential implications for restoration. Journal of Vegetation Science 24:157–167.

Greet, J., R. D. Cousens, and J. A. Webb. 2013. More exotic and fewer native plant species: riverine vegetation patterns associated with altered seasonal flow patterns. River Research and Applications 29:686–706.

Greet, J., R. D. Cousens, and J. A. Webb. 2013. Seasonal timing of inundation affects riparian plant growth and flowering: implications for riparian vegetation composition. Plant Ecology 214:87–101.

Greet, J., J.A. Webb, and B. J. Downes. 2011. Flow variability maintains the structure and composition of in–channel riparian vegetation. Freshwater Biology 56:2514–2528.

Harris, C. J., M. R. Leishman, K. Fryirs, and G. Kyle. 2012. How does restoration of native canopy affect understory vegetation composition? Evidence from riparian communities of the Hunter Valley Australia. Restoration Ecology 20:584–592.

Hood, W. G., and R. J. Naiman. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. Plant Ecology 148:105–114.

Horner, G. J., S. C. Cunningham, J. R. Thomson, P. J. Baker, and R. Mac Nally. 2012. Forest structure, flooding and grazing predict understorey composition of floodplain forests in southeastern Australia. Forest Ecology and Management 286:148–158.

Howard, J. J. 2012. Hurricane Katrina impact on a leveed bottomland hardwood forest in Louisiana. American Midland Naturalist 168:56–69.

Howell, J., and D. Benson. 2000. Predicting potential impacts of environmental flows on weedy riparian vegetation of the Hawkesbury-Nepean River, south-eastern Australia. Austral Ecology 25:463–475.

Hudon, C. 2004. Shift in wetland plant composition and biomass following low-level episodes in the St. Lawrence River: looking into the future. Canadian Journal of Fisheries and Aquatic Sciences 61:603–617.

Hughes, J. W., and W. B. Cass. 1997. Pattern and process of a floodplain forest, Vermont, USA: predicted responses of vegetation to perturbation. Journal of Applied Ecology 34:594–612.

Jackson, B. K., and S. M. P. Sullivan. 2009. Influence of wildfire severity on riparian plant community heterogeneity in an Idaho, USA wilderness. Forest Ecology and Management 259:24–32.

Jakalaniemi, A., J. Tuomi, P. Siikamaki, and A. Kilpia. 2005. Colonization-extinction and patch dynamics of the perennial riparian plant, *Silene tatarica*. Journal of Ecology 93:670–680.

Jansson, R., C. Nilsson, and B. Renofalt. 2000. Fragmentation of riparian floras in rivers with multiple dams. Ecology 81:899–903.

Johansson, M. E., and C. Nilsson. 2002. Responses of riparian plants to flooding in free–flowing and regulated boreal rivers: an experimental study. Journal of Applied Ecology 39:971–986.

Johnson, W. C., M. D. Dixon, M. L. Scott, L. Rabbe, G. Larson, M. Volke, and B. Werner. 2012. Forty years of vegetation change on the Missouri River Floodplain. Bioscience 62:123–135.

Kalliola, R., J. Salo, M. Puhakka, and M. Rajasilta. 1991. New site formation and colonizing vegetation in primary succession on the western Amazon floodplains. Journal of Ecology 79:877–901.

Katz, G. L., J. C. Stromberg, and M. W. Denslow. 2009. Streamside herbaceous vegetation response to hydrologic restoration on the San Pedro River, Arizona. Ecohydrology 2:213–225.

Kopec, D., N. Ratajczyk, A. Wolanska-Kaminska, M. Walisch, and A. Kruk. 2014. Floodplain forest vegetation response to hydroengineering and climatic pressure – a five decade comparative analysis in the Bzura River valley (Central Poland). Forest Ecology and Management 314:120–130.

Landis, C. L., and D. J. Leopold. 2014. Natural plant establishment along an urban stream, Onondaga Creek, New York. Northeastern Naturalist 21:303–322.

Lesica, P., and S. Miles. 1999. Russian olive invasion into cottonwood forests along a regulated river in north-central Montana. Canadian Journal of Botany-Revue Canadienne de Botanique 77:1077–1083.

Lesica, P., and S. Miles. 2001. Natural history and invasion of Russian olive along eastern Montana rivers. Western North American Naturalist 61:1–10.

Lesica, P., and S. Miles. 2004. Beavers indirectly enhance the growth of Russian olive and tamarisk along eastern Montana Rivers. Western North American Naturalist 63:93–100.

Levine, C. M., and J. C. Stromberg. 2001. Effects of flooding on native and exotic plant seedlings: implications for restoring south-western riparian forests by manipulating water and sediment flows. Journal of Arid Environments 49:111–131.

Lunt, I. D., A. Jansen, and D. L. Binns. 2012. Effects of flood timing and livestock grazing on exotic annual plants in riverine floodplains. Journal of Applied Ecology 49:1131–1139.

Lyon, J., and N. M. Gross. 2005. Patterns of plant diversity and plant–environmental relationships across three riparian corridors. Forest Ecology and Management 204:267–278.

Madurapperuma, B. D, P. G. Oduor, M. J. Anar, and L. A. Kotchman. 2013. Understanding factors that correlate or contribute to exotic Russian olive (*Elaeagnus angustifolia*) invasion at a wildland-urban interface ecosystem. Invasive Plant Science and Management 6:130–139.

Magee, T. K., P. L. Ringold, and M. A. Bollman. 2008. Alien species importance in native vegetation along wadeable streams, John Day River basin, Oregon, USA. Plant Ecology 195:287–307.

Maheu-Giroux, M., and S. de Blois. 2007. Landscape ecology of *Phragmites australis* invasion in networks of linear wetlands. Landscape Ecology 22:285–301.

Maskell, L. C., J. M. Bullock, S. M. Smart, K. Thompson, and P. E. Hulme. 2006. The distribution and habitat associations of non-native plant species in urban riparian habitats. Journal of Vegetation Science 17:499–508.

Masters, J. A., and S. M. Emery. 2015. Leaf litter depth has only a small influence on *Ranunculus ficaria* (Ranunculaceae) biomass and reproduction. American Midland Naturalist 173:30–37.

Mayence, C. E., D. J. Marshall, and R. C. Godfree. 2010. Hydrologic and mechanical control for an invasive wetland plant, *Juncus ingens*, and implications for rehabilitating and managing Murray River floodplain wetlands, Australia. Wetlands Ecology and Management 18:717–730.

Meek, C. S., D. M. Richardson, and L. Mucina. 2010. A river runs through it: land use and the composition of vegetation along a riparian corridor in the Cape Floristic Region, South Africa. Biological Conservation 143:156–164.

Menuz, D. R., and K. M. Kettenring. 2013. The importance of roads, nutrients, and climate for invasive plant establishment in riparian areas in the northwestern United States. Biological Invasions 15:1601–1612.

Merritt, D. M., and N. L. Poff. 2010. Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western North American rivers. Ecological Applications 20:135–152.

Michel, J. T., J. M. Helfield, and D. U. Hooper. 2011. Seed rain and revegetation of exposed substrates following dam removal on the Elwha River. Northwest Science 85:15–29.

Mortenson, S. G., and P. J. Weisberg. 2010. Does river regulation increase the dominance of invasive woody species in riparian landscapes? Global Ecology and Biogeography 19:562–574.

Mortenson, S. G., P. J. Weisberg, and B. E. Ralston. 2008. Do beavers promote the invasion of non-native *Tamarix* in the Grand Canyon riparian zone? Wetlands 28:666–675.

Mortenson, S. G., P. J. Weisberg, and L. E. Stevens. 2012. The influence of floods and precipitation on *Tamarix* establishment in Grand Canyon, Arizona: consequences for flow regime restoration. Biological Invasions 14:1061–1076.

Mumba, M., and J. R. Thompson. 2005. Hydrological and ecological impacts of dams on the Kafue Flats floodplain system, southern Zambia. Physics and Chemistry of the Earth 30:442–447.

Muranaka, T. 2009. The restoration of gravelly floodplain vegetation and endemic plants to riparian habitat in a Japanese river. Landscape and Ecological Engineering 5:11–21.

Muranaka, T. 2012. Influences of vegetation status on seedling survival of a river-endemic plant *Aster kantoensis* in the floodplain. Landscape and Ecological Engineering 8:197–205.

Nagler, P. L., O. Hinojosa–Huerta, E. P. Glenn, J. Garcia-Hernandez, R. Romo, C. Curtis, A. R. Huete, and S. G. Nelson. 2005. Regeneration of native trees in the presence of invasive saltcedar in the Colorado River delta, Mexico. Conservation Biology 19:1842–1852.

Nakayama, N., J. Nishihiro, Y. Kayaba, T. Muranaka, and I. Washitani. 2007. Seed deposition of *Eragrostis curvula*, an invasive alien plant on a river floodplain. Ecological Research 22:696–701.

Natale, E., S. M. Zalba, A. Oggero, and H. Reinoso. 2010. Establishment of *Tamarix ramosissima* under different conditions of salinity and water availability: implications for its management as an invasive species. Journal of Arid Environments 74:1399–1407.

Oneal, A. S., and J. T. Rotenberry. 2008. Riparian plant composition in an urbanizing landscape in southern California, USA. Landscape Ecology 23:553–567.

Osawa, T., H. Mitsuhashi, and H. Niwa. 2013. Many alien invasive plants disperse against the direction of stream flow in riparian areas. Ecological Complexity 15:26–32.

Osunkoya, O. O., S. Ali, T. Nguyen, C. Perrett, A. Shabbir, S. Navie, A. Belgeri, K. Dhileepan, and S. Adkins. 2014. Soil seed bank dynamics in response to an extreme flood event in a riparian habitat. Ecological Research 29:1115–1129.

Oszlanyi, J. 1995. Changes in ecological value of the Danube floodplain forest in last five decades. Ekologia–Bratislava 14:135–141.

Patino, J., K. Hylander, and J. M. Gonzalez-Mancebo. 2010. Effect of forest clear–cutting on subtropical bryophyte communities in waterfalls, on dripping walls, and along streams. Ecological Applications 20:1648–1663.

Patrick, M. J., and W. N. Ellery. 2007. Plant community and landscape patterns of a floodplain wetland in Maputaland, Northern KwaZulu–Natal, South Africa. African Journal of Ecology 45:175–183.

Pennington, D. N., J. R. Hansel, and D. L. Gorchov. 2010. Urbanization and riparian forest woody communities: diversity, composition, and structure within a metropolitan landscape. Biological Conservation 143:182–194.

Pettit, N. E., R. H. Froend, and P. M. Davies. 2001. Identifying the natural flow regime and the relationship with riparian vegetation for two contrasting western Australian rivers. Regulated Rivers: Research and Management 17:201–215.

Planty-Tabacchi, A. M., E. Tabacchi, R. J. Naiman, C. DeFerrari, and H. Décamps. 1996. Invasibility of species rich communities in riparian zones. Conservation Biology 10:598–607.

Pollen-Bankhead, N., R. E. Thomas, A. M. Gurnell, T. Liffen, A. Simon, and M. T. O'Hare. 2011. Quantifying the potential for flow to remove the emergent aquatic macrophyte *Sparganium erectum* from the margins of low-energy rivers. Ecological Engineering 37:1779–1788.

Predick, K. I., and M. G. Turner. 2008. Landscape configuration and flood frequency influence invasive shrubs in floodplain forests of the Wisconsin River (USA). Journal of Ecology 96:91–102.

Pyle, L. L. 1995. Effects of disturbance on herbaceous exotic plant species on the floodplain of the Potomac River. American Midland Naturalist 134:244–253.

Radford, I. J., A. C. Grice, B. N. Abbott, D. M. Nicholas, and L. Whiteman. 2008. Impacts of changed fire regimes on tropical riparian vegetation invaded by an exotic vine. Austral Ecology 33:151–167.

Rahlao, S. J., S. J. Milton, K. J. Esler, and P. Barnard. 2010. The distribution of invasive *Pennisetum setaceum* along roadsides in western South Africa: the role of corridor interchanges. Weed Research 50:537–543.

Renofalt, B. M., D. M. Merritt, and C. Nilsson. 2007. Connecting variation in vegetation and stream flow: the role of geomorphic context in vegetation response to large floods along boreal rivers. Journal of Applied Ecology 44:147–157.

Reynolds, L. V., D. J. Cooper, and N. T. Hobbs. 2014. Drivers of riparian tree invasion on a desert stream. River Research and Applications 30:60–70.

Ringold, P. L., T. K. Magee, and D. V. Peck. 2008. Twelve invasive plant taxa in US western riparian ecosystems. Journal of the North American Benthological Society 27:949–966.

Robertson, H. A., and K. R. James. 2007. Plant establishment from the seed bank of a degraded floodplain wetland: a comparison of two alternative management scenarios. Plant Ecology 188:145–164.

Robertson, K. M. 2006. Distributions of tree species along point bars of ten rivers in the south–eastern US Coastal Plain. Journal of Biogeography 33:121–132.

Roe, A. M., C. B. Meyer, N. P. Nibbelink, and M. Ben-David. 2010. Differential tree and shrub production in response to fertilization and disturbance by coastal river otters in Alaska. Ecology 91:3177–3188.

Rood, S. B., J. H. Braatne, and L. A. Goater. 2010. Favorable fragmentation: river reservoirs can impede downstream expansion of riparian weeds. Ecological Applications 20:1664–1677.

Rossell, C. R., S. Arico, H. D. Clarke, J. L. Horton, J. R. Ward, and S. C. Patch. 2014. Forage selection of native and nonnative woody plants by beaver in a rare–shrub community in the Appalachian Mountains of North Carolina. Southeastern Naturalist 13:649–662.

Salinas, M. J., G. Blanca, and A. T. Romero. 2000. Evaluating riparian vegetation in semi–arid Mediterranean watercourses in the south-eastern Iberian Peninsula. Environmental Conservation 27:24–35.

Salinas, M. J., and J. J. Casas. 2007. Riparian vegetation of two semi-arid Mediterranean rivers: basin-scale responses of woody and herbaceous plants to environmental gradients. Wetlands 27:831–845.

Samarakoon, M. B., N. Tanaka, and J. Yagisawa. 2013. Effects of local scouring and saturation of soil due to flooding on maximum resistive bending moment for overturning *Robinia pseudoacacia*. Landscape and Ecological Engineering 9:11–25.

Santos, M. J. 2010. Encroachment of upland Mediterranean plant species in riparian ecosystems of southern Portugal. Biodiversity and Conservation 19:2667–2684.

Schaich, H., M. Rudner, and W. Konold. 2010. Short-term impact of river restoration and grazing on floodplain vegetation in Luxembourg. Agriculture Ecosystems and Environment 139:142–149.

Schmiedel, D., and O. Tackenberg. 2013. Hydrochory and water induced germination enhance invasion of *Fraxinus pennsylvanica*. Forest Ecology and Management 304:437–443.

Schnitzler, A., D. Aumaître, and C. Schnitzler. 2011. From rurality to ferality: a case study from the Upper Moselle Valley, France. Revue D'Écologie–La Terre et la Vie 66(2):117–133.

Shafroth, P. B., M. L. Scott, J. M. Friedman, and R. D. Laven. 1994. Establishment, sex structure and breeding system of an exotic riparian willow, *Salix* x *rubens*. American Midland Naturalist 132:159–172.

Shafroth, P. B., J. C. Stromberg, and D. T. Patten. 2002. Riparian vegetation response to altered disturbance and stress regimes. Ecological Applications 12:107–123.

Sharip, Z., A. T. A. Zaki, and S. Zakaria. 2014. Flooding effects on the population dynamics of *Cabomba furcata* and *Nelumbo nucifera* in a shallow floodplain wetland. Wetlands 34:713–723.

Sher, A. A., D. L. Marshall, and J. P. Taylor. 2002. Establishment patterns of native *Populus* and *Salix* in the presence of invasive nonnative *Tamarix*. Ecological Applications 12:760–772.

Simmons, M. E., X. B. Wu, and S. G. Whisenant. 2011. Plant and soil responses to created microtopography and soil treatments in bottom land hardwood forest restoration. Restoration Ecology 19:136–146.

Sousa, W. T. Z., S. M. Thomaz, and K. J. Murphy. 2010. Response of native *Egeria najas* Planch. and invasive *Hydrilla verticillata* (L.f.) Royle to altered hydroecological regime in a subtropical river. Aquatic Botany 92:40–48.

Spackman, S. C., and J. W. Hughes. 1995. Assessment of minimum stream corridor width for biological conservation – species richness and distribution along mid-order streams in Vermont, USA. Biological Conservation 71:325–332.

Stokes, K., K. Ward, and M. Colloff. 2010. Alterations in flood frequency increase exotic and native species richness of understorey vegetation in a temperate floodplain eucalypt forest. Plant Ecology 211:219–233.

Stokes, K. E. 2008. Exotic invasive black willow (*Salix nigra*) in Australia: influence of hydrological regimes on population dynamics. Plant Ecology 197:91–105.

Stromberg, J. C. 1997. Growth and survivorship of Fremont cottonwood, Goodding willow, and salt cedar seedlings after large floods in central Arizona. Great Basin Naturalist 57:198–208.

Stromberg, J. C., K. J. Bagstad, J. M. Leenhouts, S. J. Lite, and E. Makings. 2005. Effects of stream flow intermittency on riparian vegetation of a semiarid region river (San Pedro River, Arizona). River Research and Applications 21:925–938.

Stromberg, J. C., S. J. Lite, R. Marler, C. Paradzick, P. B. Shafroth, D. Shorrock, J. M. White, and M. S. White. 2007. Altered stream-flow regimes and invasive plant species: the *Tamarix* case. Global Ecology and Biogeography 16:381–393.

Stromberg, J. C., B. D. Richter, D. T. Patten, and L. G. Wolden. 1993. Response of a Sonoran riparian forest to a 10-year return flood. Great Basin Naturalist 53:118–130.

Stromberg, J. C., P. B. Shafroth, and A. F. Hazelton. 2012. Legacies of flood reduction on a dryland river. River Research and Applications 28:143–159.

Sung, C. Y., M. H. Li, G. O. Rogers, A. Volder, and Z. F. Wang. 2011. Investigating alien plant invasion in urban riparian forests in a hot and semi-arid region. Landscape and Urban Planning 100:278–286.

Tabacchi, E. 1995. Structural variability and invasions of pioneer plant communities in riparian habitats of the middle Adour River (SW France). Canadian Journal of Botany–Revue Canadienne De Botanique 73:33–44.

Tabacchi, E., and A. M. Planty-Tabacchi. 2005. Exotic and native plant community distributions within complex riparian landscapes: a positive correlation. Ecoscience 12:412–423.

Tabacchi, E., A. M. Planty-Tabacchi, L. Roques, and E. Nadal. 2005. Seed inputs in riparian zones: implications for plant invasion. River Research and Applications 21:299–313.

Tabacchi, E., A. M. Planty-Tabacchi, M. J. Salinas, and H. Décamps. 1996. Landscape structure and diversity in riparian plant communities: a longitudinal comparative study. Regulated Rivers: Research and Management 12:367–390.

Taylor, B., and G. G. Ganf. 2005. Comparative ecology of two co-occurring floodplain plants: the native *Sporobolus mitchellii* and the exotic *Phyla canescens*. Marine and Freshwater Research 56:431–440.

Taylor, J. P., D. B. Wester, and L. M. Smith. 1999. Soil disturbance, flood management, and riparian woody plant establishment in the Rio Grande floodplain. Wetlands 19:372–382.

Terwei, A., S. Zerbe, A. Zeileis, P. Annighofer, H. Kawaletz, I. Molder, and C. Ammer. 2013. Which are the factors controlling tree seedling establishment in North Italian floodplain forests invaded by non-native tree species? Forest Ecology and Management 304:192–203.

Thébaud, C., and M. Debussche. 1991. Rapid invasion of *Fraxinus ornus* L. along the Herault River system in southern France – the importance of seed dispersal by water. Journal of Biogeography 18:7–12.

Thomaz, S. M., M. J. Silviera, and T. S. Michelan. 2012. The colonization success of an exotic Poaceae is related to native macrophyte richness, wind disturbance and riparian vegetation. Aquatic Sciences 74:809–815.

Tiegs, S. D., J. F. O'Leary, M. M. Pohl, and C. L. Munill. 2005. Flood disturbance and riparian species diversity on the Colorado River Delta. Biodiversity and Conservation 14:1175–1194.

Toth, L. A. 2010. Restoration response of relict broadleaf marshes to increased water depths. Wetlands 30:263–274.

Toth, L. A. 2010. Unrealized expectations for restoration of a floodplain plant community. Restoration Ecology 18:810–819.

Truscott, A. M., S. C. F. Palmer, C. Soulsby, and P. E. Hulme. 2008. Assessing the vulnerability of riparian vegetation to invasion by *Mimulus guttatus*: relative importance of biotic and abiotic variables in determining species occurrence and abundance. Diversity and Distributions 14:412–421.

Truscott, A. M., C. Soulsby, S. C. F. Palmer, L. Newell, and P. E. Hulme. 2006. The dispersal characteristics of the invasive plant *Mimulus guttatus* and the ecological significance of increased occurrence of high-flow events. Journal of Ecology 94:1080–1091.

Uowolo, A. L., D. Binkley, and E. C. Adair. 2005. Plant diversity in riparian forests in northwest Colorado: effects of time and river regulation. Forest Ecology and Management 218:107–114.

Van Pelt, R., T. C. O'Keefe, J. J. Latterell, and R. J. Naiman. 2006. Riparian forest stand development along the Queets River in Olympic National Park, Washington. Ecological Monographs 76:277–298.

Vandersande, M. W., E. P. Glenn, and J. L. Walworth. 2001. Tolerance of five riparian plants from the lower Colorado River to salinity drought and inundation. Journal of Arid Environments 49:147–159.

Vivian, L. M., D. J. Marshall, and R. C. Godfree. 2014. Response of an invasive native wetland plant to environmental flows: Implications for managing regulated floodplain ecosystems. Journal of Environmental Management 132:268–277.

Vivian, L. M., K. A. Ward, A. B. Zwart, and R. C. Godgree. 2014. Environmental water allocations are insufficient to control an invasive wetland plant: evidence from a highly regulated floodplain wetland. Journal of Applied Ecology 51:1292–1303.

Vosse, S., J. J. Esler, D. M. Richardson, and P. M. Holmes. 2008. Can riparian seed banks initiate restoration after alien plant invasion? Evidence from the Western Cape, South Africa. South African Journal of Botany 74:432–444.

Wang, R., J. F. Wang, Z. J. Qiu, B. Meng, F. H. Wan, and Y. Z. Wang. 2011. Multiple mechanisms underlie rapid expansion of an invasive alien plant. New Phytologist 191:828–839.

Watterson, N. A., and J. A. Jones. 2006. Flood and debris flow interactions with roads promote the invasion of exotic plants along steep mountain streams, western Oregon. Geomorphology 78:107–123.

Williams, L., P. Reich, S. J. Capon, and E. Raulings. 2008. Soil seed banks of degraded riparian zones in southeastern Australia and their potential contribution to the restoration of understorey vegetation. River Research and Applications 24:1002–1017.

Appendix C: Supplement to Chapter 3

Table C-1 All species observed in the study and their origin (i.e., native or introduced to the United States, represented by N or I; species of uncertain origin or identity are marked n/a). For each species, presence or absence in greenline and upslope transects is indicated. Empty cells in the table indicate absence. Plants that were unable to be identified to species are not included in the table.

	Origin	**Greenline**	**Upslope**
Acalypha rhomboidea	N	present	
Acer negundo	N		present
Acer platanoides	I	present	present
Acer rubrum	N	present	present
Acer saccharinum	N	present	present
Acer saccharum	N	present	present
Acer spicatum	N	present	
Adiantum pedatum	N	present	present
Ageratina altissima	N	present	present
Agrimonia gryposepala	N	present	
Agrostis perennans	N	present	present
Agrostis scabra	N	present	present
Alisma subcordatum	N	present	
Alliaria petiolata	I	present	present
Ambrosia artemisiifolia	n/a	present	
Ambrosia trifida	N	present	present
Amelanchier arborea	N	present	present
Amphicarpaea bracteata	N	present	present
Anemone canadensis	N	present	present
Apios americana	N	present	present
Arctium lappa	I	present	
Arisaema triphyllum	N		present
Asarum canadense	N	present	present
Athyrium filix-femina var. *angustum*	N	present	present
Berberis thunbergii	I	present	
Betula alleghaniensis	N		present
Betula lenta	N	present	present
Betula populifolia	N		present
Bidens connata	N	present	
Bidens frondosa	N	present	
Boehmeria cylindrica	N	present	present
Brassica nigra	I	present	present
Bromus ciliatus	N	present	
Calystegia sepium	n/a	present	present
Carex bullata	N	present	

	Origin	**Greenline**	**Upslope**
Carpinus caroliniana	N	present	present
Carya cordiformis	N	present	present
Carya ovata	N	present	present
Catalpa speciosa	N		present
Caulophyllum thalictroides	N		present
Cephalanthus occidentalis	N	present	
Chamaesyce maculata	N	present	
Chelone glabra	N	present	
Cicuta maculata	N	present	
Cinna arundinacea	N		present
Circaea lutetiana ssp. *canadensis*	N	present	present
Clematis virginiana	N	present	present
Cornus obliqua	N	present	present
Cornus rugosa	N	present	
Cornus sericea	N	present	present
Cryptotaenia canadensis	N	present	
Cynodon dactylon	I	present	
Cyperus compressus	N	present	
Cyperus strigosus	N	present	present
Dactylis glomerata	I	present	
Daucus carota	I	present	present
Decodon verticillatus	N	present	
Dichanthelium clandestinum	N	present	present
Didiplis diandra	N	present	
Digitaria cognata	N	present	
Digitaria sanguinalis	I	present	
Dryopteris camyloptera	N	present	present
Dryopteris carthusiana	N		present
Dryopteris marginalis	N	present	
Echinochloa muricata	N	present	
Echinocystis lobata	N		present
Eleocharis intermedia	N	present	
Elymus canadensis	N	present	
Elymus virginicus	N	present	
Epilobium hirsutum	I		present
Euonymus alatus	I	present	present
Eupatorium purpureum	N	present	
Eurybia divaricata	N	present	present
Eutrochium purpureum	N	present	
Fagus grandifolia	N		present
Fallopia japonica	N	present	present
Fragaria vesca	N	present	present

	Origin	**Greenline**	**Upslope**
Fraxinus americana	N	present	present
Fraxinus nigra	N	present	present
Galium aparine	N	present	present
Galium asprellum	N	present	
Galium boreale	N	present	
Galium palustre	N	present	present
Galium triflorum	N	present	present
Geranium maculatum	N		present
Geum laciniatum	N	present	present
Glechoma hederacea	I	present	present
Glyceria borealis	N	present	present
Halenia deflexa	N	present	
Hamamelis virginiana	N		present
Helianthus giganteus	N		present
Helianthus strumosus	N	present	present
Heliopsis helianthoides	N	present	
Hemerocallis fulva	I	present	
Hieracium paniculatum	N		present
Hydrocotyle americana	N	present	present
Hylotelephium telephium	I		present
Hyperium mutilum	N	present	
Impatiens capensis	N	present	present
Impatiens pallida	N	present	present
Juglans cinerea		present	
Lactuca canadensis	N	present	
Laportea canadensis	N	present	present
Leersia oryzoides	N	present	present
Lobelia cardinalis	N	present	
Ludwigia palustris	N	present	
Lycopus uniflorus	N	present	present
Lysimachia ciliata	N	present	present
Lysimachia nummularia	I	present	present
Lysimachia vulgaris	I	present	
Lythrum salicaria	I	present	present
Maianthemum canadense	N	present	
Maianthemum racemosum ssp. *racemosum*	N	present	present
Malus pumila	I		present
Marrubium vulgare	I		present
Matteuccia struthiopteris	N	present	present
Menispermum canadense	N	present	present
Mimulus ringens	N	present	
Mitchella repens	N		present

	Origin	**Greenline**	**Upslope**
Muhlenbergia mexicana	N		present
Muhlenbergia schreberi	N	present	present
Muhlenbergia sobolifera	N	present	
Myosotis laxa	N	present	
Myosoton aquaticum	I	present	
Oenothera biennis	N	present	
Onoclea sensibilis	N	present	present
Ostrya virginiana		present	present
Oxalis grandis	N		present
Oxalis stricta	N	present	present
Panicum capillare	N	present	
Panicum dichotomiflorum	N	present	present
Parthenocissus quinquefolia	N	present	present
Paspalum setaceum	N	present	
Pastinaca sativa	I	present	present
Peltandra virginica	N	present	
Penthorum sedoides	N	present	
Petasites frigidus	N		present
Phytolacca americana	N		present
Pilea pumila	N	present	present
Pinus strobus			present
Plantago major	I	present	
Polygonum arifolium	N	present	
Polygonum cespitosum	I	present	present
Polygonum hydropiper	I		present
Polygonum hydropiperoides	N	present	
Polygonum lapathifolium	N	present	present
Polygonum persicaria	I	present	present
Polygonum sagittatum	N	present	present
Polygonum virginianum	N	present	present
Polystichum acrostichoides	N	present	present
Populus deltoides	N	present	present
Populus tremuloides	N	present	present
Potentilla simplex	N	present	present
Prunella vulgaris	N	present	present
Prunus serotina	N		present
Prunus virginiana	N	present	present
Quercus alba	N	present	present
Quercus macrocarpa	N		present
Quercus rubra	N	present	present
Ranunculus recurvatus	N	present	
Rhamnus alnifolia	N	present	present

	Origin	**Greenline**	**Upslope**
Rhamnus cathartica	I	present	present
Ribes americanum	N	present	
Ribes rubrum	I	present	present
Robinia pseudoacacia	N		present
Rosa multiflora	I	present	present
Rubus allegheniensis	N		present
Rubus hispidus	N		present
Rubus occidentalis	N	present	present
Rubus odoratus	N		present
Rubus pubescens	N	present	present
Rubus sp.	n/a	present	
Rumex obtusifolius	I		present
Rumex triangulivalvis	N	present	
Salix alba	I	present	
Salix lucida	N		present
Salix nigra	N	present	
Sambucus canadensis	N	present	present
Sanicula odorata	N		present
Scirpus polyphyllus	N	present	present
Scutellaria lateriflora	N	present	present
Sinapis arvensis	I		present
Smilax glauca	N		present
Solanum dulcamara	I	present	present
Solanum ptycanthum	N	present	
Solidago altissima	N	present	present
Solidago canadensis	N		present
Solidago flexicaulis	N	present	present
Solidago gigantea	N	present	present
Stellaria pubera	N	present	present
Symphyotrichum dumosum	N	present	present
Symphyotrichum lateriflorum	N	present	present
Teucrium canadense	N		present
Thalictrum pubescens	N	present	
Thalictrum thalictroides	N	present	
Thelypteris noveboracensis	N		present
Thelypteris palustris	N	present	
Tilia americana	N	present	present
Toxicodendron radicans	N	present	present
Trifolium arvense	I	present	
Trifolium campestre	I		present
Trifolium pratense	I	present	
Trifolium repens	I	present	

	Origin	**Greenline**	**Upslope**
Tsuga canadensis	N	present	present
Ulmus rubra	N	present	present
Urtica dioica	N	present	present
Veronica americana	N	present	
Viburnum acerifolium	N	present	present
Viburnum lentago	N		present
Viburnum recognitum	N	present	
Viola fimbriatula	N	present	
Viola pubescens	N	present	
Vitis riparia	N	present	
Xanthium strumarium	N	present	
Zanthoxylum americanum	N	present	

Table C-2 Dispersion parameters for the generalized linear models for each response variable. The error distribution used for herbaceous cover, native herb cover, and introduced herb cover was quasi-binomial; the error distribution for all other models was Quasi-Poisson. In all models, df = 23 for null deviance and df = 12 for the residual deviance. Quasi-Poisson and Quasi-Binomial likelihood models remedy overdispersed data by introducing a dispersion parameter into the Poisson and binomial models (respectively) such that the conditional variance of the response becomes a linear function of the mean.

Response variable	**Dispersion par.**
Number of species	4.576
Number of native species	3.912
Number of introduced species	2.129
Number of individuals	75.012
Number of native individuals	82.227
Number of introduced individuals	26.565
Herbaceous cover	0.187
Native herb cover	0.202
Introduced herb cover	0.027

Table C-3 Dispersion parameters for the generalized linear models used to compare abundance of native and introduced species. The error distribution used for herbaceous cover was Quasi-Binomial; a Quasi-Poisson model was used for species richness and number of individual plants. In all models, df = 47 for null deviance and df = 35 for residual deviance.

Response variable	**Dispersion par.**
Number of species	2.797
Number of individuals	54.72
Herbaceous cover	0.105

Table C-4 Coefficient estimates from the generalized linear model for each response variable. The error distribution used in the generalized linear model for each response variable is given in parentheses. Significant values of P at α = 0.05 are marked with asterisks. The “bank” effect shown is the coefficient of change from riparian to upland samples.

	Coef. Est.	SE	T	P
Number of species (Quasi-Poisson)				
Intercept	-0.171	0.278	-0.614	0.551
Ind	-0.027	0.374	-0.073	0.943
Kay	0.484	0.383	-1.262	0.231
Bal * Site	-0.187	0.385	-0.487	0.635
Ind * Site	0.325	0.342	0.949	0.361
Kay * Site	-0.058	0.399	-0.146	0.887
Bal * SiteB1 * Bank	-0.397	0.461	-0.862	0.406
Bal * SiteB2 * Bank	-0.198	0.410	-0.484	0.637
Ind * SiteI1 * Bank	-0.318	0.339	-0.938	0.367
Ind * Site I2 * Bank	-0.305	0.382	-0.799	0.440
Kay * SiteK1 * Bank	-0.160	0.443	-0.363	0.723
Kay * SiteK2 * Bank	-0.130	0.397	-0.329	0.748
Number of native species (Quasi-Poisson)				
Intercept	-0.398	0.289	-1.381	0.193
Ind	-0.013	0.387	-0.033	0.974
Kay	-0.662	0.415	-1.595	0.137
Bal * Site	-0.164	0.396	-0.414	0.686
Ind * Site	0.312	0.353	0.883	0.395
Kay * Site	-0.183	0.468	-0.391	0.703
Bal * SiteB1 * Bank	-0.262	0.458	-0.573	0.578
Bal * SiteB2 * Bank	-0.131	0.411	-0.318	0.756
Ind * SiteI1 * Bank	-0.279	0.347	-0.805	0.437
Ind * Site I2 * Bank	-0.271	0.389	-0.697	0.499
Kay * SiteK1 * Bank	-0.059	0.520	-0.114	0.911
Kay * SiteK2 * Bank	-0.065	0.441	-0.148	0.885
Number of introduced species (Quasi-Poisson)				
Intercept	-2.051	0.486	-4.218	0.001*
Ind	-0.646	0.769	-0.840	0.418
Kay	0.040	0.601	0.067	0.948
Bal * Site	-0.872	0.814	-1.071	0.305
Ind * Site	0.791	0.741	1.068	0.307
Kay * Site	-0.236	0.565	-0.417	0.684
Bal * SiteB1 * Bank	-2.043	1.538	-1.328	0.209
Bal * SiteB2 * Bank	-0.097	0.979	-0.099	0.922
Ind * SiteI1 * Bank	-0.313	0.637	-0.491	0.632
Ind * Site I2 * Bank	-0.428	0.942	-0.454	0.658
Kay * SiteK1 * Bank	0.010	0.622	0.016	0.988
Kay * SiteK2 * Bank	-0.240	0.550	-0.437	0.670

Number of individuals (Quasi-Poisson)				
Intercept	2.365	0.317	7.453	7.71×10^{-6}*
Ind	-0.308	0.457	-0.675	0.513
Kay	-0.745	0.466	-1.596	0.136
Bal * Site	-0.709	0.505	-1.405	0.185
Ind * Site	0.726	0.413	1.758	0.104
Kay * Site	1.121	0.404	2.774	0.017*
Bal * SiteB1 * Bank	-1.079	0.668	-1.616	0.132
Bal * SiteB2 * Bank	-0.569	0.681	-0.837	0.419
Ind * SiteI1 * Bank	-1.020	0.450	-2.266	0.043*
Ind * Site I2 * Bank	-0.371	0.510	-0.727	0.481
Kay * SiteK1 * Bank	-0.574	0.360	-1.592	0.137
Kay * SiteK2 * Bank	-0.225	0.529	-0.426	0.678
Number of native individuals (Quasi-Poisson)				
Intercept	2.160	0.368	5.869	7.61×10^{-5}*
Ind	-0.213	0.517	-0.411	0.688
Kay	-1.085	0.597	-1.818	0.094
Bal * Site	-0.645	0.574	-1.123	0.283
Ind * Site	0.517	0.476	1.087	0.299
Kay * Site	1.373	0.538	2.551	0.025*
Bal * SiteB1 * Bank	-1.013	0.755	-1.341	0.205
Bal * SiteB2 * Bank	-0.537	0.756	-0.710	0.491
Ind * SiteI1 * Bank	-0.985	0.546	-1.804	0.096.
Ind * Site I2 * Bank	-0.548	0.596	-0.920	0.376
Kay * SiteK1 * Bank	-1.236	0.553	-2.234	0.045*
Kay * SiteK2 * Bank	-0.314	0.747	-0.420	0.682
Number of introduced individuals (Quasi-Poisson)				
Intercept	0.657	0.444	1.481	0.165
Ind	-1.711	1.027	-1.666	0.121
Kay	-0.783	0.659	-1.188	0.258
Bal * Site	-1.361	0.880	-1.546	0.148
Ind * Site	2.389	0.975	2.449	0.031*
Kay * Site	0.932	0.593	1.573	0.142
Bal * SiteB1 * Bank	-3.653	3.008	-1.214	0.248
Bal * SiteB2 * Bank	-0.758	1.406	-0.540	0.599
Ind * SiteI1 * Bank	-1.012	0.551	-1.836	0.091
Ind * Site I2 * Bank	-1.259	1.952	-0.645	0.531
Kay * SiteK1 * Bank	-0.544	0.559	-0.973	0.350
Kay * SiteK2 * Bank	0.693	0.608	1.140	0.277
Herbaceous cover (Quasi-Binomial)				
Intercept	0.087	0.612	0.141	0.890
Ind	-0.498	0.875	-0.570	0.579
Kay	-0.759	0.890	-0.852	0.411
Bal * Site	-1.153	0.931	-1.239	0.239
Ind * Site	-0.363	0.907	-0.400	0.696

Kay * Site	1.558	0.933	1.670	0.121
Bal * SiteB1 * Bank	-2.098	1.129	-1.859	0.088
Bal * SiteB2 * Bank	-1.888	1.574	-1.199	0.254
Ind * SiteI1 * Bank	-0.666	1.019	-0.654	0.526
Ind * Site I2 * Bank	-0.325	0.904	-0.359	0.726
Kay * SiteK1 * Bank	-0.355	0.924	-0.384	0.708
Kay * SiteK2 * Bank	-0.026	0.916	-0.028	0.978
Native herb cover (Quasi-Binomial)				
Intercept	-0.128	0.637	-0.201	0.844
Ind	-0.369	0.913	-0.404	0.694
Kay	-1.059	0.984	-1.076	0.303
Bal * Site	-1.069	0.986	-1.084	0.300
Ind * Site	-0.604	0.984	-0.614	0.551
Kay * Site	1.818	1.004	1.810	0.095
Bal * SiteB1 * Bank	-1.883	1.172	-1.606	0.134
Bal * SiteB2 * Bank	-1.921	1.747	-1.099	0.293
Ind * SiteI1 * Bank	-0.527	1.129	-0.467	0.649
Ind * Site I2 * Bank	-0.253	0.944	-0.268	0.793
Kay * SiteK1 * Bank	-1.155	0.936	-1.233	0.241
Kay * SiteK2 * Bank	0.082	1.050	0.078	0.939
Introduced herb cover (Quasi-Binomial)				
Intercept	-2.871	0.514	-5.577	0.0001*
Ind	-3.879	0.823	-4.713	0.0005*
Kay	-2.151	0.379	-5.669	0.0001*
Bal * Site	-0.835	0.916	-0.911	0.380
Ind * Site	1.225	0.947	1.294	0.220
Kay * Site	0.629	0.485	1.296	0.219
Bal * SiteB1 * Bank	-18.70	3389	-0.006	0.996
Bal * SiteB2 * Bank	-1.232	1.573	-0.783	0.449
Ind * SiteI1 * Bank	-0.921	0.852	-1.081	0.301
Ind * Site I2 * Bank	-1.927	2.274	-0.847	0.413
Kay * SiteK1 * Bank	0.465	0.402	1.157	0.270
Kay * SiteK2 * Bank	-0.245	0.565	-0.433	0.673

Table C-5 Coefficient estimates from the generalized linear models examining abundance of native and introduced species. The error distribution used in the GLM for each response variable is given in parentheses. Significant values of p at α = 0.05 are marked with asterisks. The “bank” effect shown is the coefficient of change from riparian to upland samples.

	Coef. Est.	**SE**	**t**	**p**
Number of species (Quasi-Poisson)				
Intercept	-2.084	0.271	-7.683	5.14×10^{-9}***
Origin Native	1.688	0.181	9.315	5.25×10^{-11}***
Ind	-0.091	0.305	-0.299	0.767
Kay	-0.510	0.310	-1.649	0.108
Bal * Site	-0.249	0.313	-0.795	0.432
Ind * Site	0.367	0.281	1.306	0.200
Kay * Site	-0.198	0.338	-0.585	0.562
Bal * SiteB1 * Bank	-0.405	0.371	-1.094	0.281
Bal * SiteB2 * Bank	-0.128	0.332	-0.385	0.703
Ind * SiteI1 * Bank	-0.284	0.272	-1.043	0.304
Ind * Site I2 * Bank	-0.285	0.315	-0.905	0.372
Kay * SiteK1 * Bank	-0.040	0.374	-0.108	0.915
Kay * SiteK2 * Bank	-0.111	0.321	-0.346	0.731
Number of individual plants (Quasi-Poisson)				
Intercept	0.673	0.328	2.054	0.047*
Origin Native	1.484	0.225	6.606	1.24×10^{-7}*
Ind	-0.365	0.397	-0.920	0.363
Kay	-1.023	0.432	-2.367	0.024*
Bal * Site	-0.743	0.436	-1.702	0.098
Ind * Site	0.748	0.362	2.067	0.046*
Kay * Site	1.287	0.389	3.309	0.002*
Bal * SiteB1 * Bank	-1.198	0.599	-2.000	0.053
Bal * SiteB2 * Bank	-0.557	0.590	-0.944	0.352
Ind * SiteI1 * Bank	-0.991	0.388	-2.555	0.015*
Ind * Site I2 * Bank	-0.572	0.478	-1.197	0.239
Kay * SiteK1 * Bank	-1.085	0.390	-2.783	0.009*
Kay * SiteK2 * Bank	0.024	0.486	0.049	0.961
Herbaceous cover (Quasi-Binomial)				
Intercept	-5.707	0.458	-12.45	2.06×10^{-14}*
Origin Native	1.865	0.314	5.945	9.13×10^{-7}*
Ind	-0.670	0.585	-1.146	0.260
Kay	-1.249	0.603	-2.071	0.046*
Bal * Site	-1.290	0.641	-2.012	0.052
Ind * Site	-0.129	0.631	-0.205	0.839
Kay * Site	1.655	0.583	2.838	0.008*
Bal * SiteB1 * Bank	-1.743	0.805	-2.165	0.037*
Bal * SiteB2 * Bank	-1.690	1.163	-1.453	0.155
Ind * SiteI1 * Bank	-0.822	0.732	-1.124	0.269
Ind * Site I2 * Bank	-0.302	0.628	-0.481	0.633

	Coef. Est.	**SE**	**t**	**p**
Kay * SiteK1 * Bank	-0.517	0.525	-0.985	0.331
Kay * SiteK2 * Bank	0.089	0.642	0.138	0.891

Table C-6 ANOVA table for each descriptor of plant community composition measured among three streams in the Upper Hudson Watershed, different sites along each stream, and riparian and upland transects at each site. Significant p-values at the α = 0.05 level are marked with an asterisk (*). These significant values are also all significant after sequential Bonferroni correction (†). All response variables were corrected for sampled area and transformed to fit assumptions of normality before performing the ANOVA.

Source	**df**	**SS**	**MS**	**F**	**p**
Number of species					
Stream	2	4.128	2.064	120.8	0.001*†
Site within Stream	3	0.051	0.017	0.017	0.997
Bank within Site	6	6.223	1.037	0.916	0.516
Residuals	12	13.585	1.132		
Number of native species					
Stream	2	4.628	2.314	93.57	0.002*†
Site within Stream	3	0.074	0.025	0.050	0.984
Bank within Site	6	2.991	0.499	0.820	0.576
Residuals	12	7.300	0.608		
Number of introduced species					
Stream	2	0.499	0.249	66.64	0.003*†
Site within Stream	3	0.011	0.004	0.080	0.968
Bank within Site	6	0.280	0.048	0.628	0.706
Residuals	12	0.892	0.074		
Total abundance of individuals					
Stream	2	1384.2	692.1	1.803	0.306
Site within Stream	3	1151.4	383.8	0.861	0.511
Bank within Site	6	2675.6	445.9	2.549	0.079
Residuals	12	2099.2	174.9		
Total abundance of native individuals					
Stream	2	6.373	3.187	3.644	0.157
Site within Stream	3	2.623	0.874	0.240	0.866
Bank within Site	6	21.869	3.645	2.685	0.069
Residuals	12	16.289	1.357		
Total abundance of introduced individuals					
Stream	2	11.391	5.696	1.753	0.313
Site within Stream	3	9.7112	3.237	1.959	0.222
Bank within Site	6	9.9153	1.653	1.670	0.212
Residuals	12	11.878	0.990		
Herbaceous cover					
Stream	2	0.104	0.520	14.699	0.028*
Site within Stream	3	0.106	0.035	0.417	0.748
Bank within Site	6	0.5088	0.085	1.843	0.173
Residuals	12	0.552	0.046		

Source	**df**	**SS**	**MS**	**F**	**p**
Native herb cover					
Stream	2	0.186	0.093	0.988	0.468
Site within Stream	3	0.282	0.094	1.916	0.228
Bank within Site	6	0.294	0.049	1.026	0.454
Residuals	12	0.573	0.048		
Introduced herb cover					
Stream	2	0.387	0.193	6.764	0.077
Site within Stream	3	0.0823	0.028	2.200	0.189
Bank within Site	6	0.078	0.013	1.439	0.278
Residuals	12	0.107	0.009		
Shannon diversity					
Stream	2	0.284	0.142	1.985	0.282
Site within Stream	3	0.215	0.072	0.852	0.515
Bank within Site	6	0.504	0.084	0.669	0.677
Residuals	12	1.507	0.126		

Appendix D: Supplement to Chapter 4

Table D-1 Latitudes and longitudes of sampled sites.

River	Latitude	Longitude
Alplaus Kill	42.9297	-73.9827
Ballston Creek	42.9592	-73.8200
Batten Kill	43.0974	-73.1414
Beaver Kill	42.0688	-74.2047
Big Brook	43.3204	-75.3443
Boreas River	43.8917	-74.0150
Bullhead Pond Brook	43.8075	-74.0417
Cadman Creek	43.1018	-74.0430
Cedar River	43.7926	-74.2892
Chester Creek	43.6684	-73.7882
Cobleskill Creek	42.7100	-74.3340
Daly Creek	43.2693	-73.9559
Evas Kill	42.9284	-74.1276
Fawn Lake	42.5681	-74.1762
Fishkill Creek	41.5863	-73.7455
Four Mile Brook	43.3768	-74.7793
Green River	43.1032	-73.2111
Hans Creek	43.1277	-74.1027
Hudson River	44.0161	-74.0542
Indian Brook	41.4113	-73.9144
Indian Kill	42.8711	-73.9086
Jassup River	43.5824	-74.4068
Kayaderosseras Creek	43.0192	-73.8302
Kennyetto Creek	43.0701	-74.1567
Keyser Kill	42.4907	-74.3603
Kinderhook Creek	42.4927	-73.4515
Landsman Kill	41.9233	-73.9110
Lansing Kill	43.4043	-75.3441
Mill Brook	43.7637	-73.7545
Mill Creek	43.4044	-74.2520
Minots Corner	43.0920	-75.0643
Mohawk River	43.0016	-74.5468
New Pond Brook	44.0761	-73.6595
North Branch West Stony Creek	43.2522	-74.3285
Paragon Brook	43.8877	-73.6432
Plotter Kill	42.8455	-74.0129
Potic Creek	42.2753	-73.9281
Quacken Kill	42.7484	-73.5630

River	**Latitude**	**Longitude**
Robbs Creek	43.5098	-74.2862
Roeliff Jansen Kill	42.0062	-73.7157
Saw Kill	42.0371	-74.1234
Sheriff Lake Outlet	43.3901	-74.5940
Snook Kill	43.1985	-73.6554
Sprout Creek	41.5815	-73.8526
Steele Creek	42.9949	-75.0609
Sterling Creek	43.1391	-75.0909
Stewart Creek	43.5300	-74.1448
Stony Creek	42.0467	-73.9108
Timmerman Creek	43.0567	-74.6273
Trout Brook	43.7553	-73.8804
Valatie Kill	42.4420	-73.6652
Wappinger Creek	41.7562	-73.8174
Wharton Hollow Creek	42.5272	-74.5675

Table D-2 Species observed in regional field surveys of riparian zones, excluding the 7 plants that could not be identified to species and were classified as morphospecies. Species origins "N" native, "I" introduced, "I/N" for ambiguous species – e.g., species thought to have some native and some invasive genotypes.

Species	**Origin**	**Lifespan**	**Growth Form**
Abies balsamea	N	perennial	woody
Acer negundo	N	perennial	woody
Acer pensylvanicum	N	perennial	woody
Acer rubrum	N	perennial	woody
Acer saccharinum	N	perennial	woody
Acer saccharum	N	perennial	woody
Acer spicatum	N	perennial	woody
Achillea millefolium	I/N	perennial	herbaceous
Ageratina altissima	N	perennial	herbaceous
Agrimonia gryposepala	N	perennial	herbaceous
Agrostis perennans	N	perennial	herbaceous
Alliaria petiolata	I	biennial	herbaceous
Alnus incana	N	perennial	woody
Ambrosia artemisiifolia	I/N	annual	herbaceous
Ambrosia trifida	N	annual	herbaceous
Amphicarpaea bracteata	N	perennial	herbaceous
Anemone virginiana	N	perennial	herbaceous
Apocynum cannabinum	N	perennial	herbaceous
Arctium lappa	I	biennial	herbaceous
Arisaema triphyllum	N	perennial	herbaceous
Artemisia vulgaris	I	perennial	herbaceous
Asclepias syriaca	N	perennial	herbaceous
Athyrium filix-femina	N	perennial	herbaceous
Barbarea vulgaris	I	biennial	herbaceous
Berberis thunbergii	I	perennial	woody
Betula alleghaniensis	N	perennial	woody
Betula papyrifera	N	perennial	woody
Bidens connata	N	annual	herbaceous
Bidens frondosa	N	annual	herbaceous
Blephilia hirsuta	N	perennial	herbaceous
Boehmeria cylindrica	N	perennial	herbaceous
Brachyelytrum aristosum	N	perennial	herbaceous
Brassica nigra	I	annual	herbaceous
Bromus ciliatus	N	perennial	herbaceous
Bromus inermis	I/N	perennial	herbaceous
Bromus pubescens	N	perennial	herbaceous
Calystegia sepium	I/N	perennial	herbaceous

Species	**Origin**	**Lifespan**	**Growth Form**
Carex crinita	N	perennial	herbaceous
Carex scoparia	N	perennial	herbaceous
Carpinus caroliniana	N	perennial	woody
Carya cordiformis	N	perennial	woody
Carya ovata	N	perennial	woody
Centaurea jacea	I	perennial	herbaceous
Centaurea nigrescens	I	perennial	herbaceous
Centaurea stoebe	I	perennial	herbaceous
Cephalanthus occidentalis	N	perennial	woody
Chelidonium majus	I	biennial	herbaceous
Chelone glabra	N	perennial	herbaceous
Cicuta maculata	N	perennial	herbaceous
Cinna arundinacea	N	perennial	herbaceous
Circaea lutetiana	N	perennial	herbaceous
Clematis virginiana	N	perennial	herbaceous
Clinopodium vulgare	N	perennial	herbaceous
Collinsonia canadensis	N	perennial	herbaceous
Commelina communis	I	annual	herbaceous
Cornus amomum	N	perennial	woody
Cornus canadensis	N	perennial	woody
Cornus obliqua	N	perennial	woody
Cornus rugosa	N	perennial	woody
Cornus sericea	N	perennial	woody
Corylus cornuta	N	perennial	woody
Cryptotaenia canadensis	N	perennial	herbaceous
Cynanchum louiseae	I	perennial	herbaceous
Cyperus strigosus	N	perennial	herbaceous
Dactylis glomerata	I	perennial	herbaceous
Daucus carota	I	biennial	herbaceous
Dianthus armeria	I	biennial	herbaceous
Dichanthelium clandestinum	N	perennial	herbaceous
Digitaria sanguinalis	I	annual	herbaceous
Dioscorea villosa	N	perennial	herbaceous
Doellingeria umbellata	N	perennial	herbaceous
Dryopteris carthusiana	N	perennial	herbaceous
Dryopteris cristata	N	perennial	herbaceous
Echinocystis lobata	N	annual	herbaceous
Elymus canadensis	N	perennial	herbaceous
Elymus hystrix	N	perennial	herbaceous
Elymus repens	I	perennial	herbaceous
Elymus trachycaulus	N	perennial	herbaceous
Elymus virginicus	N	perennial	herbaceous

Species	**Origin**	**Lifespan**	**Growth Form**
Epilobium ciliatum	N	perennial	herbaceous
Epipactis helleborine	I	perennial	herbaceous
Equisetum fluviatile	N	perennial	herbaceous
Equisetum hyemale	N	perennial	herbaceous
Equisetum palustre	N	perennial	herbaceous
Equisetum pratense	N	perennial	herbaceous
Erigeron annuus	N	annual	herbaceous
Euonymus alatus	I	perennial	woody
Eupatorium perfoliatum	N	perennial	herbaceous
Euphorbia maculata	N	annual	herbaceous
Eurybia divaricata	N	annual	herbaceous
Euthamia caroliniana	N	annual	herbaceous
Euthamia graminifolia	N	perennial	herbaceous
Eutrochium maculatum	N	perennial	herbaceous
Eutrochium purpureum	N	perennial	herbaceous
Fagus grandifolia	N	perennial	woody
Fragaria vesca	N	perennial	herbaceous
Fraxinus americana	N	perennial	woody
Fraxinus nigra	N	perennial	woody
Fraxinus pennsylvanica	N	perennial	woody
Galium aparine	N	annual	herbaceous
Galium asprellum	N	perennial	herbaceous
Galium boreale	N	perennial	herbaceous
Galium mollugo	I	perennial	herbaceous
Galium palustre	N	perennial	herbaceous
Galium triflorum	N	perennial	herbaceous
Gentiana linearis	N	perennial	herbaceous
Geum canadense	N	perennial	herbaceous
Glechoma hederacea	I	perennial	herbaceous
Glyceria striata	N	perennial	herbaceous
Hamamelis virginiana	N	perennial	woody
Helianthus divaricatus	N	perennial	woody
Helianthus strumosus	N	perennial	herbaceous
Helianthus tuberosus	N	perennial	herbaceous
Hemerocallis fulva	I	perennial	herbaceous
Heuchera villosa	N	perennial	herbaceous
Hypericum mutilum	N	perennial	herbaceous
Hypericum perforatum	I	perennial	herbaceous
Hypericum punctatum	N	perennial	herbaceous
Impatiens capensis	N	annual	herbaceous
Impatiens pallida	N	annual	herbaceous
Juglans cinerea	N	perennial	woody

Species	**Origin**	**Lifespan**	**Growth Form**
Juglans nigra	N	perennial	woody
Juncus articulatus	N	perennial	herbaceous
Juncus filiformis	N	perennial	herbaceous
Laportea canadensis	N	perennial	herbaceous
Leonurus cardiaca	I	perennial	herbaceous
Leucanthemum vulgare	I	perennial	herbaceous
Linaria vulgaris	I	perennial	herbaceous
Lindera benzoin	N	perennial	woody
Liparis loeselii	N	perennial	herbaceous
Lithospermum officinale	I	perennial	herbaceous
Lobelia cardinalis	N	perennial	herbaceous
Lobelia inflata	N	annual	herbaceous
Lobelia siphilitica	N	perennial	herbaceous
Lonicera japonica	I	perennial	herbaceous
Lonicera morrowii	I	perennial	woody
Lotus corniculatus	I	perennial	herbaceous
Ludwigia palustris	N	perennial	herbaceous
Lycopus americanus	N	perennial	herbaceous
Lycopus rubellus	N	perennial	herbaceous
Lysimachia ciliata	N	perennial	herbaceous
Lysimachia nummularia	I	perennial	herbaceous
Lysimachia quadrifolia	N	perennial	herbaceous
Lysimachia terrestris	N	perennial	herbaceous
Lythrum salicaria	I	perennial	herbaceous
Maianthemum racemosum	N	perennial	herbaceous
Malus pumila	I	perennial	woody
Matteuccia struthiopteris	N	perennial	herbaceous
Melilotus officinalis	I	perennial	herbaceous
Mimulus ringens	N	perennial	herbaceous
Mitchella repens	N	perennial	herbaceous
Monotropa uniflora	N	perennial	herbaceous
Muhlenbergia mexicana	N	perennial	herbaceous
Myosotis laxa	N	perennial	herbaceous
Myosotis scorpioides	I	perennial	herbaceous
Myrica gale	N	perennial	woody
Oclemena acuminata	N	perennial	woody
Oenethera biennis	N	perennial	woody
Onoclea sensibilis	N	perennial	herbaceous
Osmunda cinnamomea	N	perennial	herbaceous
Osmunda regalis	N	perennial	herbaceous
Ostrya virginiana	N	perennial	woody
Oxalis stricta	N	perennial	herbaceous

Species	**Origin**	**Lifespan**	**Growth Form**
Panicum dichotomiflorum	N	annual	herbaceous
Parthenocissus quinquefolia	N	perennial	herbaceous
Peltandra virginica	N	perennial	herbaceous
Phalaris arundinacea	N	perennial	herbaceous
Phegopteris connectilis	N	perennial	herbaceous
Phegopteris hexagonoptera	N	perennial	herbaceous
Phleum pratense	I	perennial	herbaceous
Pilea pumila	N	annual	herbaceous
Pinus strobus	N	perennial	woody
Plantago lanceolata	I	perennial	herbaceous
Plantago major	I	perennial	herbaceous
Platanus occidentalis	N	perennial	woody
Polygonum amphibium	N	perennial	herbaceous
Polygonum arifolium	N	perennial	herbaceous
Polygonum cilinode	N	perennial	herbaceous
Polygonum cuspidatum	I	perennial	herbaceous
Polygonum hydropiper	I	annual	herbaceous
Polygonum hydropiperoides	N	perennial	herbaceous
Polygonum persicaria	I	perennial	herbaceous
Polygonum punctatum	N	perennial	herbaceous
Polygonum sagittatum	N	perennial	herbaceous
Polygonum virginianum	N	perennial	herbaceous
Polystichum acrostichoides	N	perennial	herbaceous
Populus deltoides	N	perennial	woody
Potentilla recta	I	perennial	herbaceous
Potentilla simplex	N	perennial	herbaceous
Prenanthes alba	N	perennial	herbaceous
Prenanthes altissima	N	perennial	herbaceous
Prenanthes trifoliolata	N	perennial	herbaceous
Prunella vulgaris	N	perennial	herbaceous
Prunus americana	N	perennial	woody
Prunus serotina	N	perennial	woody
Prunus virginiana	N	perennial	woody
Pteridium aquilinum	N	perennial	herbaceous
Quercus alba	N	perennial	woody
Quercus prinoides	N	perennial	woody
Quercus velutina	N	perennial	woody
Ranunculus pensylvanicus	N	perennial	herbaceous
Ranunculus recurvatus	N	perennial	herbaceous
Rhamnus alnifolia	N	perennial	woody
Rhamnus cathartica	I	perennial	woody
Rhus typhina	N	perennial	woody

Species	**Origin**	**Lifespan**	**Growth Form**
Robinia pseudoacacia	N	perennial	woody
Rosa multiflora	I	perennial	herbaceous
Rosa palustris	N	perennial	woody
Rubus allegheniensis	N	perennial	woody
Rubus hispidus	N	perennial	woody
Rubus idaeus	N	perennial	woody
Rubus occidentalis	N	perennial	woody
Rubus odoratus	N	perennial	woody
Rubus phoenicolasius	I	perennial	woody
Rubus pubescens	N	perennial	herbaceous
Rudbeckia hirta	N	perennial	herbaceous
Rudbeckia laciniata	N	perennial	herbaceous
Rumex crispus	I	perennial	herbaceous
Rumex obtusifolius	I	perennial	herbaceous
Sagittaria latifolia	N	perennial	herbaceous
Salix alba	I	perennial	woody
Salix nigra	N	perennial	woody
Salix pentandra	I	perennial	woody
Sambucus nigra	I/N	perennial	woody
Saponaria officinalis	I	perennial	herbaceous
Schoenoplectus pungens	N	perennial	herbaceous
Scirpus atrocinctus	N	perennial	herbaceous
Scirpus microcarpus	N	perennial	herbaceous
Scutellaria lateriflora	N	perennial	herbaceous
Securigera varia	I	perennial	herbaceous
Silene vulgaris	I	perennial	herbaceous
Smilax tamnoides	N	perennial	herbaceous
Solanum dulcamara	I	perennial	herbaceous
Solidago altissima	N	perennial	herbaceous
Solidago canadensis	N	perennial	herbaceous
Solidago flexicaulis	N	perennial	herbaceous
Solidago gigantea	N	perennial	herbaceous
Solidago latissimifolia	N	perennial	herbaceous
Sonchus oleraceus	I	annual	herbaceous
Spiraea alba	N	perennial	woody
Stellaria pubera	N	perennial	woody
Symphyotrichum dumosum	N	perennial	woody
Symphyotrichum lanceolatum	N	perennial	herbaceous
Symphyotrichum novae-angliae	N	perennial	herbaceous
Symphyotrichum prenanthoides	N	perennial	herbaceous
Symplocarpus foetidus	N	perennial	herbaceous
Tanacetum vulgare	I	perennial	herbaceous

Species	**Origin**	**Lifespan**	**Growth Form**
Taraxacum officinale	I/N	perennial	herbaceous
Thalictrum dioicum	N	perennial	herbaceous
Thalictrum pubescens	N	perennial	herbaceous
Thalictrum thalictroides	N	perennial	herbaceous
Thelypteris noveboracensis	N	perennial	herbaceous
Thelypteris palustris	N	perennial	herbaceous
Thuja occidentalis	N	perennial	woody
Tilia americana	N	perennial	woody
Toxicodendron radicans	N	perennial	herbaceous
Triadenum virginicum	N	perennial	herbaceous
Trifolium aureum	I	biennial	herbaceous
Trifolium pratense	I	perennial	herbaceous
Trifolium repens	I	perennial	herbaceous
Trillium erectum	N	perennial	herbaceous
Tsuga canadensis	N	perennial	woody
Tussilago farfara	I	perennial	herbaceous
Ulmus americana	N	perennial	woody
Ulmus rubra	N	perennial	woody
Urtica dioica	I/N	perennial	herbaceous
Veratrum viride	N	perennial	herbaceous
Verbascum thapsus	I	biennial	herbaceous
Verbena hastata	N	perennial	herbaceous
Verbena urticifolia	N	perennial	herbaceous
Veronica americana	N	perennial	herbaceous
Veronica anagallis-aquatica	N	perennial	herbaceous
Veronica scutellata	N	perennial	herbaceous
Viburnum acerifolium	N	perennial	woody
Viburnum dentatum	N	perennial	woody
Viburnum lantanoides	N	perennial	woody
Vinca minor	I	perennial	herbaceous
Vitis riparia	N	perennial	herbaceous
Woodsia obtusa	N	perennial	herbaceous
Xanthium strumarium	N	annual	herbaceous

Appendix E: Supplement to Chapter 5

Table E-1 Test of the proportional hazards assumption of the Cox Proportional Hazards regressions based on Schoenfeld residuals.

	χ^2	**p**
Bidens frondosa	3.098	0.377
Solidago flexicaulis	7.763	0.051
Polygonum pensylvanicum	5.900	0.117
Polygonum virginianum	5.930	0.115
Prunella vulgaris	5.900	0.116
Marrubium vulgare	6.934	0.094

Table E-2 Unmodified Cox Proportional Hazards regressions for *Solidago flexicaulis* and *Prunella vulgaris*. For both of these species, no individuals died in the submergence treatment. The CPH regression returns invalid MLE coefficient estimates for groups containing no events. The overall test remains valid, but the z statistic is not valid for the affected treatment contrast. Both of these models meet Cox proportional hazards assumptions (*S. flexicaulis*: $\chi^2 = 5.973$, p = 0.1139; *P. vulgaris*: $\chi^2 = 0.898$, p = 0.993).

	Coef.	**SE**	**Hazard Ratio**	**95% CI (lower)**	**95% CI (upper)**	**z**	**p**
Solidago flexicaulis							
Burial	-1.274	1.124	0.280	0.031	2.532	-1.134	0.257
Nutrient addition	-0.606	0.956	0.546	0.084	3.550	-0.634	0.526
Submergence	-21.93	1600	3.00×10^{-10}	0	Inf	-0.001	0.999
Prunella vulgaris							
Burial	-0.666	0.554	0.516	0.174	1.528	-1.195	0.232
Nutrient addition	-1.26	0.672	0.284	0.076	1.057	-1.877	0.061
Submergence	-21.54	1068	4.44×10^{-10}	0	Inf	-0.002	0.998

Table E-3 Growth responses analyzed with the alternate blocking arrangement (Figure 5-5). Results of a generalized linear model comparing growth (final height and final number leaves) between riparian and upland species, as represented by log response ratios contrasting each experimental treatment to the control. Significant p-values are represented with an asterisk (*). Responses do not differ in significance from those reported in Table 5-2 under the original blocking design (Figure 5-1).

	Est.	95% CI (Lower)	95% CI (Upper)	SE	z	p
Submergence						
Height (cm)						
Intercept	-0.331	-0.716	0.055	0.197	-1.680	0.093
Habitat (Upland)	0.372	-0.198	0.942	0.291	1.279	0.201
Number of leaves						
Intercept	0.115	-0.437	0.667	0.281	0.410	0.682
Habitat (Upland)	-0.362	-1.193	0.468	0.424	-0.854	0.393
Burial						
Height (cm)						
Intercept	-0.062	-0.594	0.471	0.272	-0.226	0.821
Habitat (Upland)	-0.745	-1.446	-0.043	0.358	-2.080	0.038*
Number of leaves						
Intercept	0.289	-0.898	1.478	0.606	0.478	0.633
Habitat (Upland)	-0.737	-2.433	0.959	0.865	-0.852	0.394
Nutrient addition						
Height (cm)						
Intercept	0.248	-0.229	-0.725	0.243	1.018	0.309
Habitat (Upland)	0.293	-0.367	0.953	0.337	0.871	0.384
Number of leaves						
Intercept	0.866	0.055	1.677	0.414	2.094	0.036*
Habitat (Upland)	-0.307	-1.441	0.828	0.579	-0.530	0.596

Table E-4 Results of linear mixed-effects models of plant growth in each species, as measured by height and number of leaves, with treatment effects contrasted against the control treatment and analyzed with the alternate blocking arrangement (Figure 5-5). Model includes all surviving individuals at the conclusion of the experiment. The flooded treatment is not included for *Marrubium vulgare* as no individuals of that species in that treatment survived to the conclusion of the experiment. Significant p-values are represented with an asterisk (*). These results do not differ in significance from the results presented in Table 5-7 following the original blocking design (Figure 5-1).

	β	**SE**	**df**	**t**	**p**
Bidens frondosa (Asteraceae; riparian)					
Height (cm)					
Intercept	17.850	2.878	19	6.203	< 0.0001*
Burial	-4.417	4.984	19	-0.886	0.387
Nutrient addition	0.0333	4.070	19	0.008	0.994
Submergence	-2.150	3.715	19	-0.579	0.570
Number of leaves					
Intercept	19.833	4.982	19	3.981	0.001 *
Burial	4.167	8.629	19	0.483	0.635
Nutrient addition	0.967	7.045	19	0.137	0.892
Submergence	-2.389	6.432	19	-0.371	0.714
Solidago flexicaulis (Asteraecae; upland)					
Height (cm)					
Intercept	9.600	3.732	5	2.572	0.050 *
Burial	-6.400	4.571	5	-1.400	0.220
Nutrient addition	17.666	4.310	5	4.099	0.009 *
Submergence	-0.420	4.089	5	-0.103	0.922
Number of leaves					
Intercept	13.584	2.9291	5	4.637	0.006 *
Burial	-6.000	2.9531	5	-2.032	0.098
Nutrient addition	4.0211	3.0125	5	1.335	0.240
Submergence	-7.1005	2.9425	5	-2.413	0.061
Polygonum pensylvanicum (Polygonaceae; riparian)					
Height (cm)					
Intercept	18.800	6.392	2	2.941	0.099
Burial	3.400	7.829	2	0.434	0.706
Nutrient addition	11.200	9.040	2	1.239	0.341
Submergence	-5.250	7.147	2	-0.735	0.539
Number of leaves					
Intercept	4.00	4.7566	2	0.8409	0.489
Burial	15.50	5.8256	2	2.6607	0.117
Nutrient addition	21.00	6.7268	2	3.1218	0.089
Submergence	2.00	5.3180	2	0.3761	0.743

	β	**SE**	**df**	**t**	**p**
Polygonum virginianum (Polygonaceae; upland)					
Height (cm)					
Intercept	8.500	4.921	16	1.727	0.103
Burial	-2.833	5.682	16	-0.499	0.625
Nutrient addition	6.214	5.261	16	1.181	0.255
Submergence	1.200	5.140	16	0.234	0.818
Number of leaves					
Intercept	5.083	2.058	16	2.470	0.025
Burial	2.938	2.271	16	1.294	0.214
Nutrient addition	5.673	1.952	16	2.906	0.010 *
Submergence	0.364	1.943	16	0.187	0.854
Prunella vulgaris (Lamiaceae; riparian)					
Height (cm)					
Intercept	7.113	1.721	24	4.134	0.0004 *
Burial	0.220	2.011	24	0.109	0.914
Nutrient addition	2.325	1.823	24	1.275	0.214
Submergence	2.258	1.777	24	1.271	0.216
Number of leaves					
Intercept	35.000	8.070	24	4.337	0.0002 *
Burial	-22.000	10.827	24	-2.032	0.053
Nutrient addition	18.625	9.884	24	1.884	0.072
Submergence	-6.0833	9.319	24	-0.653	0.520
Marrubium vulgare (Lamiaceae; upland)					
Height (cm)					
Intercept	9.2906	0.7589	6	12.242	< 0.0001 *
Burial	-6.3921	1.33192	6	-4.799	0.003 *
Nutrient addition	0.8324	1.11387	6	0.747	0.483
Number of leaves					
Intercept	16.410	6.123	6	2.680	0.037 *
Burial	-12.885	9.864	6	-1.306	0.239
Nutrient addition	11.400	8.712	6	1.309	0.239

Appendix F: Supplement to Chapter 6

Table F-1 Correlations among traits used in trait-based analysis of introduced and native species in riparian plant communities. Abbreviations: Leaf C = carbon (mg/g dry leaf); LN = nitrogen (mg/g dry leaf); LP = phosphorus (mg/g dry leaf), LK = potassium (mg/g dry leaf); C:N = leaf carbon:nitrogen ratio; N:P = leaf nitrogen:phosphorus ratio; SLA = specific leaf area (cm^2/g dry leaf); LWR = leaf weight ratio (% of plant); SC = stomata conductance per leaf area; SSD = stem specific density (g/cm^3), WM = woody mass (% of plant); RN = nitrogen (mg/g dry root mass); SN = number of seeds per reproductive unit; SP = seed protein content per mass (%); SM = seed mass (g); RGR = relative growth rate (g/g/day); PR = light-saturated (maximum) photosynthetic rate (nmol CO_2/g dry leaf/s); LR = leaf respiration (nmol CO_2/g dry leaf/s).

	LC	**LN**	**LP**	**LK**	**C:N**	**N:P**	**SLA**	**LWR**	**SC**	**SSD**	**WM**	**RN**	**RD**	**SN**	**SP**	**SM**	**RGR**	**PR**	**LR**
LC	1.00																		
LN	0.72	1.00																	
LP	-0.25	-0.28	1.00																
LK	0.24	0.54	-0.58	1.00															
C:N	-0.11	-0.32	0.22	-0.60	1.00														
N:P	-0.15	0.20	-0.51	-0.01	-0.11	1.00													
SLA	-0.20	-0.11	-0.12	0.35	-0.26	-0.03	1.00												
LWR	-0.15	-0.23	0.26	0.22	0.05	-0.06	-0.20	1.00											
SC	0.04	-0.18	0.26	-0.01	0.16	0.03	-0.13	0.00	1.00										
SSD	-0.32	0.03	0.13	-0.09	0.22	0.24	-0.13	-0.23	0.01	1.00									
WM	-0.08	-0.15	0.03	1.00	0.00	0.14	0.36	-0.65	0.01	-0.01	1.00								
RN	-0.42	0.04	0.33	0.23	0.57	0.23	-0.20	-0.10	0.58	0.24	0.19	1.00							
RD	-0.29	-0.22	0.32	-0.38	0.31	-0.01	-0.13	-0.28	0.44	0.29	0.30	0.44	1.00						
SN	0.24	0.12	-0.11	-0.05	0.16	-0.14	-0.03	-0.06	-0.07	-0.07	-0.11	-0.29	-0.03	1.00					
SP	0.05	0.20	-0.14	-0.78	-0.27	0.20	0.15	-0.03	0.05	-0.13	0.02	0.34	0.28	-0.09	1.00				
SM	0.21	0.13	-0.06	-0.12	0.12	0.04	-0.04	-0.09	-0.14	-0.01	-0.06	0.03	-0.15	-0.02	-0.02	1.00			
RGR	-0.13	0.04	-0.02	0.45	-0.23	0.03	0.10	-0.09	-0.52	-0.10	0.10	-0.45	-0.05	-0.06	-0.24	-0.03	1.00		
PR	0.34	0.38	-0.30	0.35	-0.40	-0.03	-0.11	0.60	0.11	-0.28	-0.53	-0.37	-0.54	-0.16	-0.07	0.01	0.35	1.00	
LR	0.38	0.57	-0.17	0.08	-0.49	0.17	0.06	0.32	0.28	-0.30	-0.78	0.37	-0.46	0.26	-0.11	0.49	0.45	0.65	1.00