The Role of Native Diversity and Successional Processes on Communityinvasibility in Riparian Primary Forest

by

Sean Satterlee

Submitted in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in the

Biology

Program

YOUNGSTOWN STATE UNIVERSITY

December, 2012

The role of native diversity and successional processes on community invasibility riparian primary forest

Sean Satterlee

I hereby release this thesis to the public. I understand that this thesis will be made available from the OhioLINK ETD Center and the Maag Library Circulation Desk for public access. I also authorize the University or other individuals to make copies of this thesis as needed for scholarly research.

Signature:

Sean Satterlee, Student Date

Approvals:

Dr. Thomas Diggins, Thesis Advisor Date

Dr. Ian Renne, Committee Member Date

Prof Carl Chuey, Committee Member Date

Peter J. Kasvinsky, Dean of School of Graduate Studies and Research Date

ABSTRACT

Numerous investigations have elucidated patterns and processes which govern community invasibility but relatively few have examined invasibility in a successional context. Explored here is the potential for biotic resistance to reduce invasibility of riparian successional forests at the landscape scale (~100ha) and address the following: 1) Does exotic species richness and percent cover change across successional time? 2) What is the relationship between native and non-native diversity and does that relationship change through succession? Vegetation surveys were conducted to quantify plant species richness on four raised terraces (understory reinitiation to multi-age old growth), six lower terraces (stem exclusion to understory reinitiation), and seven active channel margins, mid-channel islands, or abandoned channels (stand initiation). Exotic species richness and cover declined throughout succession and no exotic species were found on landforms greater than 136 years of age. However, although native richness remained constant throughout succession, native *assemblages* changed markedly. Thus landform diversity patterns in Zoar Valley likely reflect contemporary and/or past states of high community invasibility, which suggests that invasibility either does not change throughout succession, or that the regional species pool of native species adapted to particular successional stages is similar in size. This finding suggests that minimally invaded, closed canopy forests is due to a lack of exotic species in the regional species pools that are well adapted for establishing in forest understories and opposes the view that these communities are intrinsically less invasible. Future studies of community invasibility, in forests and other systems, may be better served by examining the traits and life-history strategies to which a community is susceptible to being invaded by.

ACKNOWLEDGEMENTS

I would like to thank Dr. Tom Diggins for being the best thesis advisor that I could hope for. Our many trips to Zoar Valley inspired me to become an ecologist and from our interactions over the past seven years I learned what it was to be a great one. His enthusiasm for science and mentoring, patience, and tirelessness allowed this project to be completed and was instrumental in my personal and professional development.

I would also like to thank Dr. Ian Renne for going above and beyond in service as my thesis advisor. His intellectual input was instrumental to making this project the best that it could be. More importantly, the many hours we spent discussing ecology was among the most important drivers of my intellectual development.

I am grateful for Professor Carl Chuey serving as a thesis advisor and for allowing me to draw on his considerable botanical knowledge and for his valuable editorial suggestions

Finally I would like to thank my family who has supported me in every way possible throughout this process. I am particularly grateful for my parents who taught me the value of hard work and for always making me feel like I could accomplish anything.

Table of contents

List of Figures

List of Tables

Introduction

The establishment and spread of invasive species are of great concern as they present ecological (Vitousek et al. 1997) and economic (Pimentel et al. 2005) problems, but can also serve as natural experiments for addressing fundamental questions in ecology (Sax et al. 2007). Numerous studies examine how recipient community traits affect invasibility and primarily focus on those that resist invasion. Elton's (1958) niche-based hypothesis proposes species- and functionally- rich communities are less susceptible to invasion because high diversity assemblages limit establishment opportunities for invaders by reducing access to resources. Subsequent investigations have emphasized the importance of temporal resource availability, disturbance, and competitive interactions in determining community invasibility (Davis et al. 2000, Davis and Pelsor 2001, Tillman 2004, Renne et al. 2006).

The view that species richness increases community invasion resistance has been generally supported by small scale experimental studies (i.e., plots $\leq 10m^2$; Fridley et al. 2007) and species richness is positively correlated with low resource availability (Tillman 1997, Levine 2000, 2001, Naeem et al. 2000, and Kennedy et al. 2002). However, despite experimental and theoretical support for the Eltonian view, observational studies at larger scales (plots $> 10m^2$) have generally found opposing results (Fridley et al. 2007).

Stohlgren et al. (1998, 1999, 2003) argue that plot-scale experiments are not supported by observations at landscape scale because their studies, the strong effects of competition observed in small plot studies become dominated by landscape scale processes (also see Levine 2000, Brown and Peet 2003). At larger spatial scales, community composition is more likely to be driven by immigration processes such as high propagule pressure or low-intensity disturbance (Stohlgren et al. 1999, Levine 2000, Brown and Peet 2003). Other hypotheses suggest that extrinsic, covarying factors across large spatial scales promote both native and non-native species diversity (Levine and D'Antonio 1999, Shea and Chesson 2002) and that resource heterogeneity increases with scale (Davies et al. 2005). Within sites (i.e. at small scales), densities of individuals and their competitive interactions limit diversity of both native and non-native species (Levine 2000). In contrast, among sites (i.e. at large scales) resource heterogeneity contributes to higher species richness for both native and non-native species (Shea and Chesson 2002, Davies et al. 2005). Stohlgren et al. (2003) suggests that environmental factors that promote native species diversity also contribute to exotic species diversity. The positive correlation between native and nonnative species richness may also emerge with the presence of "weak invaders" (nonnative species that are present but do not dominate habitats), while a negative correlation exists in environments with high native species richness and presence of dominant nonnative species (Ortega and Pearson 2005).

While the diversity of native and non-native assemblages is often thought to reflect exogenous influences (thus driving a positive relationship between native and non-native diversity), relatively few studies have examined the relationship in communities where native assemblages are largely driven by endogenous (biotic) processes, particularly strongly directional primary successional communities. Davis et al. (2001) suggests that there has been a historical disassociation between invasion ecology and successional ecology, and that insights into the fundamental drivers of community invasibility may be gained from merging these approaches. Interestingly, strongly directional successional communities are minimally disturbed, but instead are structured by biotic interactions (factors which promote Eltonian resistance), however the community may be inherently invasible by *native* non-residents through time. Understanding the drivers of invasibility in these communities and identifying potential differences in the susceptibility of the community to establishment by non-native residents may help to address the fundamental drivers of the establishment of exotic species.

While few studies have examined exotic species success across gradients in recipient community traits and exogenous community influences, even fewer studies have examined forest invasibility within a successional context (but see Meiners et al. 2002, Meiners 2007, Campagnoni and Halpern 2009, McLane et al. 2012). Late-successional and closed canopy forests appear to be relatively uninvaded (DeFerrari and Naiman 1994, Rejmanek et al. 2005, Martin et al. 2009). This pattern may be partially explained by the majority of human-mediated invasive species introductions consisting of early-successional species (Martin et al. 2008) and/or that exotic species assemblages may follow parallel dynamics to native assemblages during succession (McLane 2012). For example, in closed-canopy forests, low subcanopy light availability may prevent establishment of shade-intolerant herbaceous species (Gilbert and Lechowitz 2005, Meiners 2007).

Diggins (in press) established a greater than 300- year chronosequence of riparian primary succession along an 11km stretch of the Cattaragus Creek in Zoar Valley of western New York State (the study site). Succession on these riparian landforms is strongly directional and community assemblages, once established, appear to be driven by endogenous effects rather than exogenous disturbances from the active channel (Diggins in press). This site provides an excellent opportunity to assess the role of intrinsic community influences on exotic species establishment. Numerous studies have examined potential shifts in invasibility across secondary succession (Meiners et al. 2002, Meiners 2007, Campagnoni and Halpern 2009) but to my knowledge, no study investigates potential shifts in invasibility in 300+ year primary successional forests spanning stages from earliest stand initiation stages through self-replacing old growth.

Tree diversity in the riparian landforms of Zoar Valley is greatest when exogenous processes typically associated with promoting diversity are low (Diggins in press). Examining exotic species richness and percent cover in these primary successional communities presents an interesting opportunity to assess the potential for biotic resistance at the landscape scale. Elucidating patterns of exotic species success and relationships between native and exotic diversity amongst sites of similar age and successional stage may provide insights into succession-based shifts in community invasibility. In this study, I examined non-native species success on primary successional landforms within Zoar Valley NY (Fig. 1) and addressed: 1) does exotic species richness and % cover change across successional time? 2) What is the relationship between native and non-native diversity within our site and does that relationship change through time?

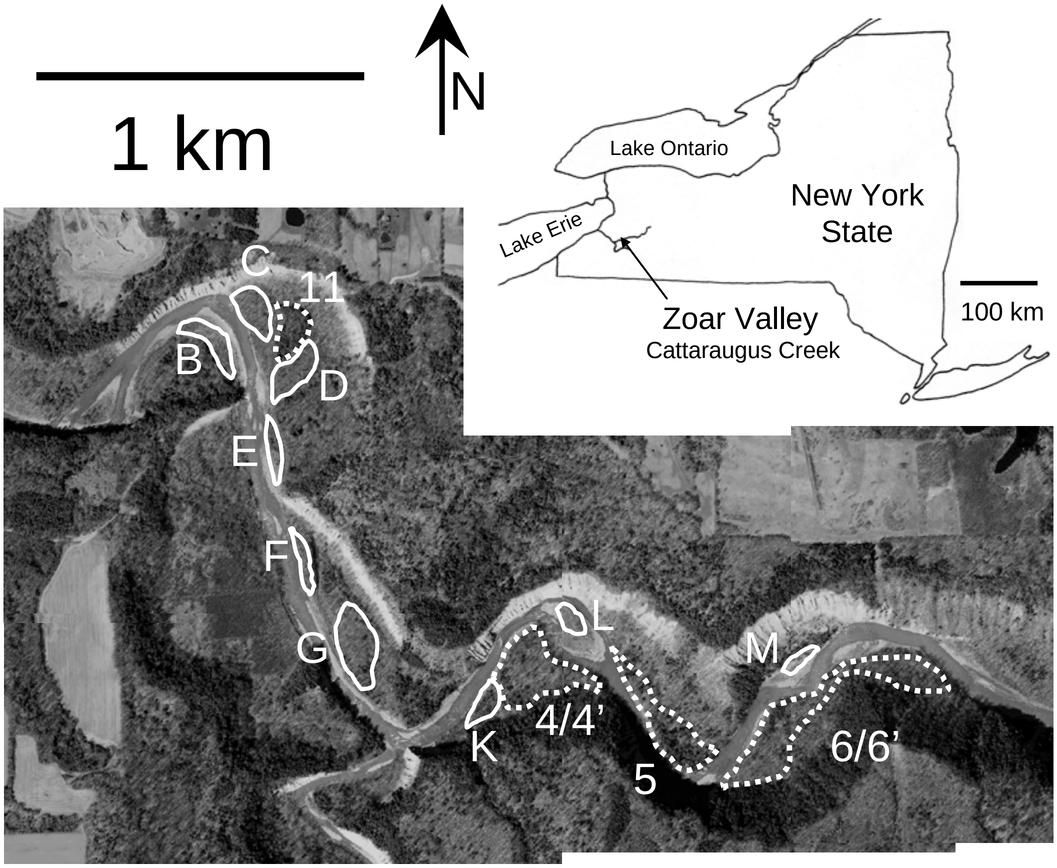

Figure 1. Regional location and detail of Zoar Valley study site (2008 satellite image of Main Branch Cattaraugus Creek, with small portion of South Branch). Flow is east to west. Selected upper terraces are designated by dashed lines and numerals, selected lower terraces/floodplains by solid lines and letters. The letter I is omitted to avoid confusion with the numeral 1. Numeral designations of upper terraces follow Pfeil et al. (2007).

Methods

Study Site

The study was conducted on primary successional landforms within the Zoar Valley Canyon of the 6th order Cattaraugus Creek in Western New York State, USA (N 42º 26’, W 78º 52’). Area of sampled landforms totaled ~25 ha and consisted of: 1) early-successional mid-channel islands, abandoned channels, and active channel margins, 2) mid-successional lower terraces, and 3) late successional raised terraces. Cattaraugus Creek is a county border and landforms north of the river are in Erie County while southerly landforms are in Cattaraugus County. Riparian vegetation within the gorge represents a convincingly directional chronosequence of primary succession spanning more than 300 years (Diggins in press). Early successional landforms during stand initiation (Fig. 2) are dominated by cottonwood/willow thickets, herbaceous species, and/or subcanopy woody vegetation (Diggins in press). Riparian woodlands on terraces of mid- to late-successional development (Fig. 3, 4, 5) are diverse, with 24 tree species present (Pfeil et al. 2007). Sugar maple (*A. saccharum* Marsh.) is the dominant tree within Zoar valley, accounting for ~30% basal area. American beech (*Fagus grandifolia* Ehrh.), tuliptree (*Liriodendron tulipifera* L.*)*, white ash (*Fraxinus americana* L.), and eastern hemlock (*Tsuga canadensis* L.) are also major components in late-successional stands (Pfeil et al. 2007). Eastern cottonwood (*Populus deltoids* Bartr.) dominates early to mid-successional floodplains and lower terraces, comprising up to 74% of their basal area (Diggins in press). Sugar maple, eastern black walnut (*Juglans nigra* L.), American sycamore (*Platanus occidentalis* L.), northern red oak (*Quercus rubra* L.), and black locust (*Robinia pseudoacacia* L.) are also common, with each contributing at least 5% of the basal area on these landforms (Diggins in press). All common names, scientific names, and naming authorities of trees were taken from Burns and Honkala (1990). All other plant names and authority were taken from USDA (2012).

Figure 2. Stand initiation. A. Early stand initiation on landform L, c. 3 – 5 years.

Figure 2-B. Late stand initiation on landform L, c. 30 – 40 years.

Figure 2-C. Overlook of landform L.

Figure 2-D. Overlook of landform E, late stand initiation c. 32 years.

Figure 2-E. Overlook of landform B, late stand initiation c. 36 years.

Figure 3. Stem exclusion. A. Landform F (left-center), c. 56 years.

Abandoned channel in center of view.

Figure 3-B. Landform K, c. 61 years.

Figure 4. Understory reinitiation. A. Landform 4’, c. 110 – 137 years.

Figure 4-B. Understory reinitiation. Landform 6’, c. 110 – 136 years.

Figure 5. Multi-aged old growth. Landform 4, c. 250+ years.

Vegetation Surveys

Exotic species were catalogued on all riparian landforms along a 3km stretch of the Cattaragus Creek during the summer and fall of 2011 and 2012 and voucher specimens were deposited in the herbarium of Youngstown State University. Common shade tolerant exotic species including that have been identified as being capable of establishing under closed canopies (Martin et al. 2008) including: bush honeysuckle (*Lonicera maackii* Rupr.), garlic mustard (*Alliaria petiolata* M. Bieb.), multiflora rose (*Rosa multiflora* Thumb. Ex Murr.), and Japanese knotweed (*Fallopia japonica* Houtt.) individuals were catalogued and coverage estimates were obtained. On three landforms with high coverage of bush honeysuckle, overlook photos were taken during spring 2012, overlain with a grid, and coverage within each grid space and total cover was estimated. One terrace had no available overlook and here, I divided the landform into four Theissen polygons and counted and measured honeysuckle within three10x10 m^2 quadrats per polygon. From these, total landform coverage was estimated.

Total richness of native herbaceous species (excluding ferns) was determined on each landform by vegetation surveys conducted in fall 2012. Abundance and diversity of tree (Diggins in press) and fern (Sinn et al. 2007) species were obtained from previous work.

Regression was used to analyze the relationship between exotic species richness and cover by landform age to resolve whether patterns of exotic species richness and cover changed throughout successional time.

I also examined was the nature of the relationship between native and non-native diversity through successional time by regressing the ratio of non-native to native diversity for each of landforms to see if this relationship changed over time. Regression was again used to examine exotic richness as a function of native richness at the site scale, and within landforms of similar age and successional stage. By examining diversity relationships within and amongst these landforms, changes in community invasibility and the relative strength of biotic resistance can be evaluated.

Landform area (ha)	AGE	Native richness	Non-native Richness	Total Richness
0.17	3	26	28	54
0.33	5	32	31	63
0.8	10	22	6	28
0.68	32	56	14	70
0.96	36	42	20	62
0.52	40	27	10	37
0.64	56	42	5	47
0.84	61	29	4	33
1.08	62	58	3	61
1.16	76	36	3	39
2.04	101	40	5	45
1.12	120	23	3	26
1.64	136	26	1	27
1.66	137	35	0	35
3.96	254	35	4	39
1.82	261	34	0	34
3.08	308	38	0	38

Table 1. Area, overstory stand age, and native and non-native species richness of surveyed landforms. Designations in left-hand column refer to Figure 1.

Results

A total of 161 species were recorded, 45 of which (27.95%) were exotic (Table 1). Total richness on individual landforms ranged from 28 to 70 species. Total richness decreased modestly in a negative log fashion and was marginally significant (Fig 6A; logarithmic R^2= 0.221, P=0.082) as stand age increased. Native richness on successional landforms ranged from 22 species to 58 species and represented 48% to 100% of the flora, while exotic richness ranged from 0 to 31 species (Table 1). While no relationship between native richness and stand age was found (Logarithmic R^2=0 .026, figure 6B) exotic richness was strongly negatively correlated with stand age (Logarithmic R^2= 0.719, P=0.009; Figure. 6B) with the oldest multi-aged old growth stands containing no exotic species. Similarly, the proportion of exotic species on a landform was negatively correlated with stand age (Logarithmic R^2= 0.808, P=0.003; Fig. 7). Surprisingly, no relationship emerged between native and non-native richness among all of the sites (R^2= 0.002) or within sites of similar age or successional stage (Table 2, Fig. 8).

. Only two invasive species were consistently found on landforms greater than 75 years of age: bush honeysuckle and black locust (which is native to the northeastern United States but has expanded its range due to anthropogenic activities; See Burns and Honkala 1990). Exotic species were also more common on disturbance patches such as alluvial/colluvial fans, eroding banks, seepage created wetlands, and former river channels, and their richness and cover decreased through succession (Fig 9 A&B). Canopy gaps caused by blow downs or tree mortality were rarely invaded.

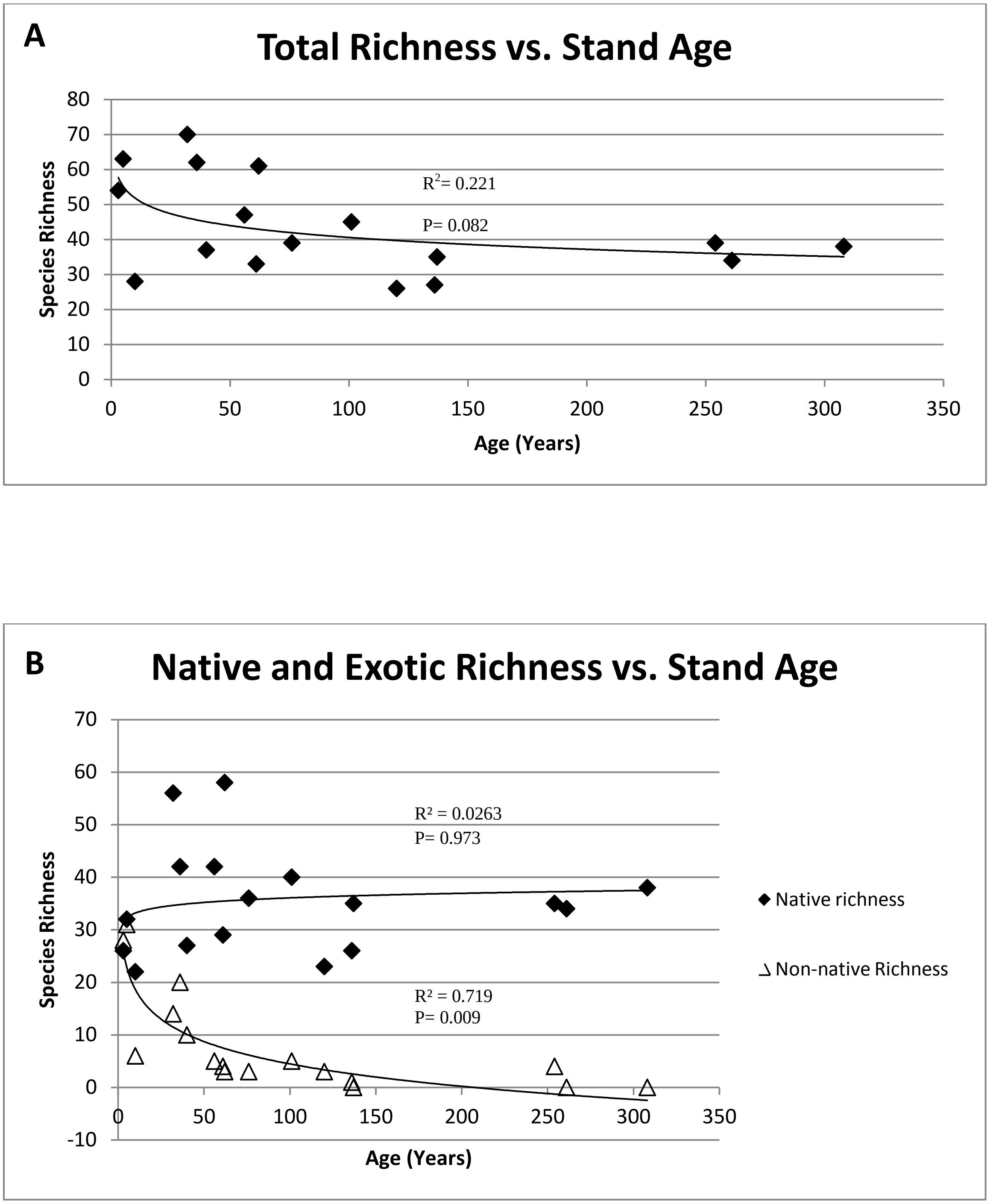

Figure 6. A. Regression of total landform richness as a response to overstory stand age.

B. Regression of native and non-native richness as a response to overstory stand age.

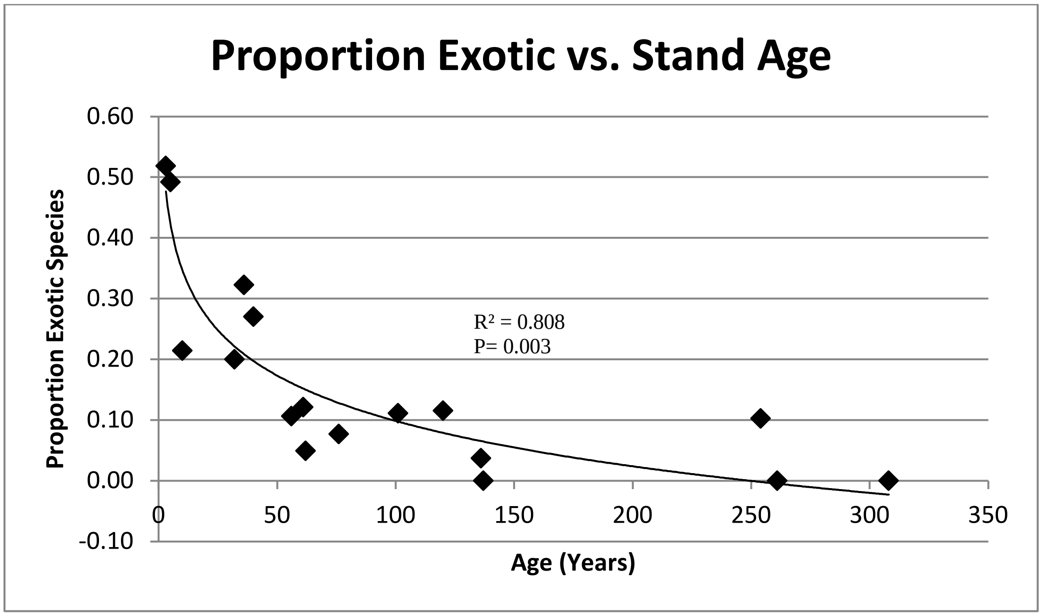

Figure 7. Logarithmic regression of the proportion of exotic species on an individual landform as a response to overstory stand age.

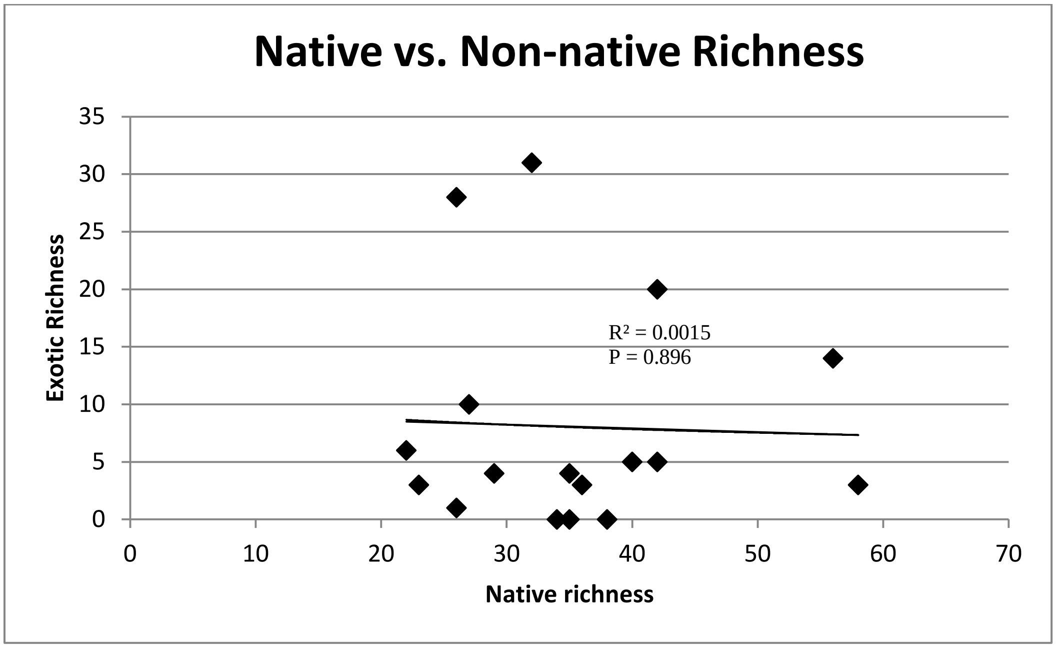

Figure 8. Regression of exotic richness per landform as a response to native richness

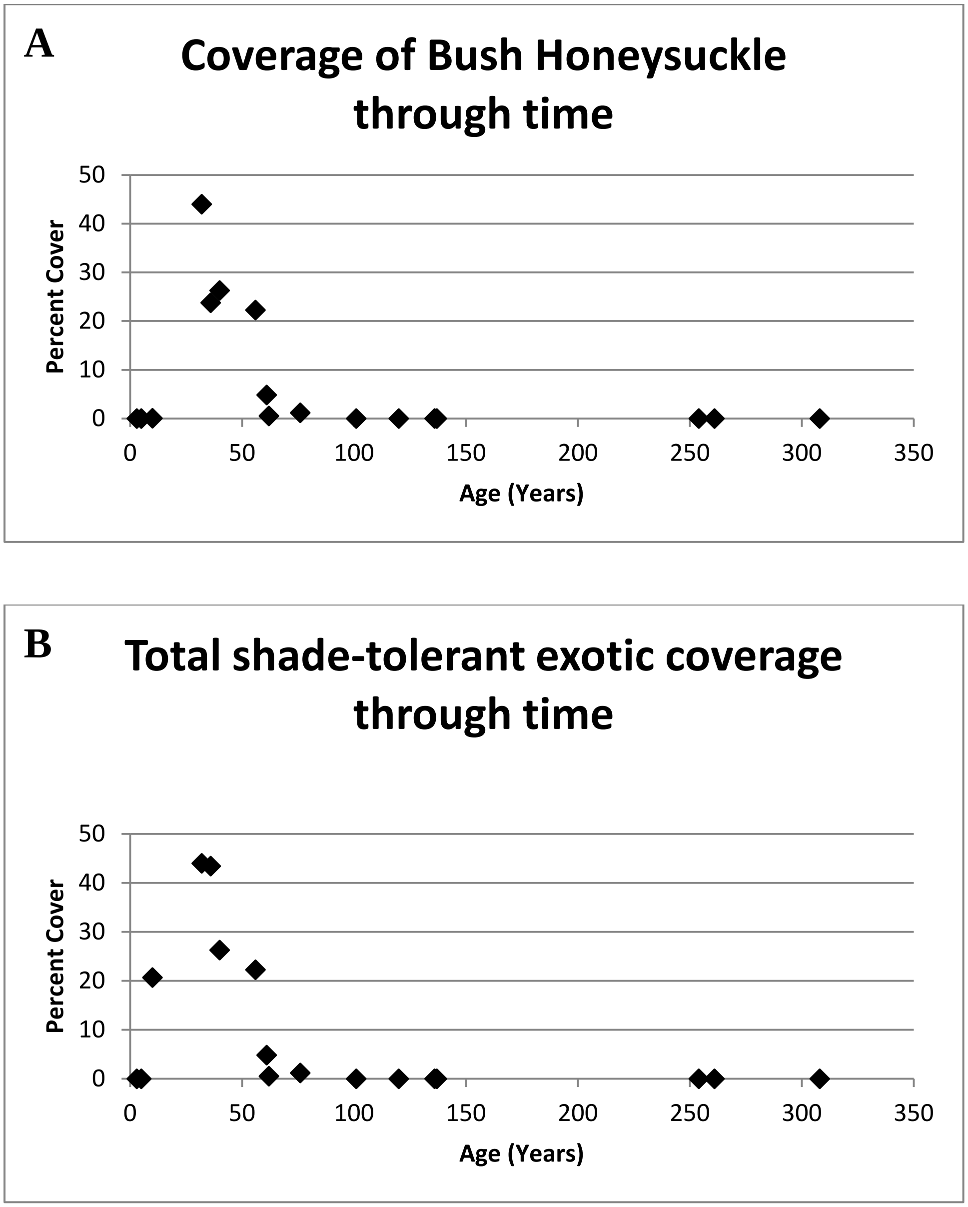

Figure 9. A. Estimated bush honeysuckle coverage as a response to overstory stand age. B. Estimated cover of major shade tolerant exotic species (Bush honeysuckle, multiflora rose, garlic mustard, and Japanese knotweed) as a response to overstory stand age.

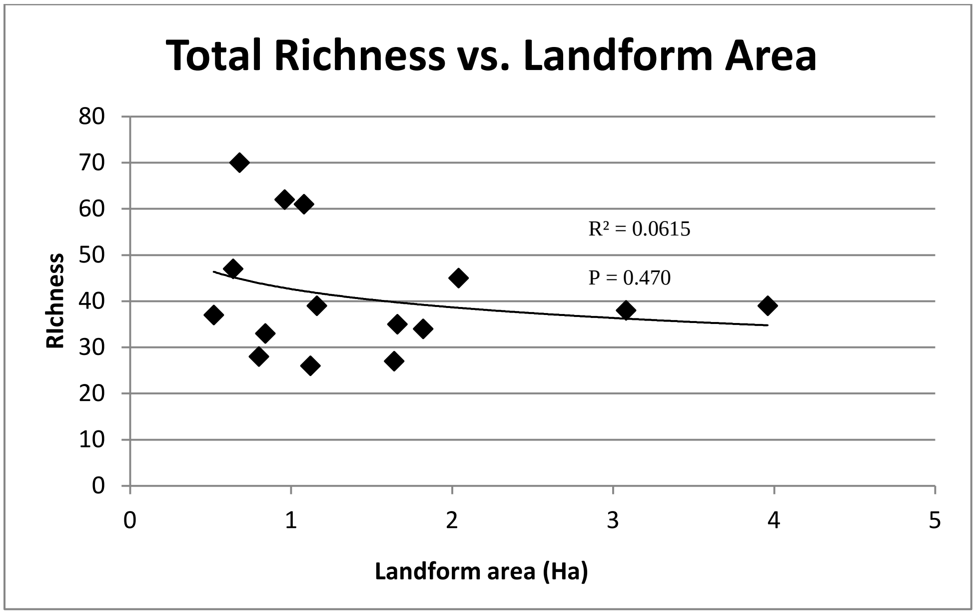

Figure 10. Regression of individual landform richness as a response to landform area.

Discussion

Diversity patterns reflect contemporary or past states of high community invasibility as well as propagule dispersal from the regional species pool. My results suggest that, despite a sharp decline in exotic richness and cover, forest community invasibility does not change through succession as evidenced by constant native species richness along this 300+ year chronosequence (Figure 7 B). Indeed, if older communities were inherently less invasible, few native species would be able to establish and persist, and this was not the case. In addition, intrinsic processes in Zoar Valley appear to have little effect on community invasibility, although the life history traits of assemblages become increasingly dominated by shade tolerant species as succession progresses.

Exotic species on the youngest landforms (≤10 years) were comprised of ruderal and common river-edge species (e.g. purple loostrife [*Lythrum salicaria* L.] and Japanese knotweed). Older stand-initiation sites through early stem exclusion (~10-50 years) were dominated by an exotic shrub layer comprised of bush honeysuckle, multiflora rose, and glossy buckthorn [*Frangula alnus* Mill.]). Landforms from mid-stem exclusion onward (~50 years and older) through multi-aged old growth (300+ years) tend to contain assemblages of shade- tolerant species. Diggins (in press) found a strong positive relationship between stand age and percent of shade tolerant trees, and our surveys of understory and forest floor vegetation showed that species with some degree of shade tolerance (e.g. bush honeysuckle, multiflora rose; see Martin et al. 2008). Black locust individuals were able to persist, but were either slow to recruit or weren’t recruiting in stands between 56-136 years and absent from stands >136 years. Martin et al. (2008) showed nearly all introduced plants are shade- intolerant and suggested that late successional forests may be invasible to exotic species but are not invaded by them because they are simply not likely present. I echo this proposition and state that few late-successional exotic species are not members of the regional species pool. If this is the case, following changes in exotic richness and comparing patterns of native and exotic richness may be insufficient for generalizing states of community invasibility in naturalistic study designs (Martin et al. 2008). In fact, measuring changes in native species richness may be the best metric for elucidating patterns of invasibility in closed canopy forests. That said, this approach assumes the number of species sharing life history strategies suited for particular successional stages is similarly represented in the regional species pool. In Zoar Valley, this appears to be the case.

Historically, ecologists have examined the primary drivers of colonization and establishment by exotic species and by native non-residents in successional systems differently, and some have suggested that this distinction is spurious (Davis et al. 2001). The relationship between recipient community diversity is thought to reflect community invasibility because diversity is thought to be a proxy for the relative strength of competitive interactions or thought to be a reflection of external factors which promote both exotic and native diversity. Iin either instance it should be expected that exotic species and native non-residents should encounter similar establishment opportunities.

While exotic species benefit from escaping enemies (Keane and Crawly 2002), facilitation from invasional meltdowns (Simberloff and Von Holle 1999), and reduced grazing by herbivores (Knight et al. 2009) , it is not clear that the processes driving large-scale patterns of establishment by native and non-native species fundamentally differ. As forest succession proceeds, a community undergoes compositional change mediated by establishment opportunities afforded by the community. Compositional shifts thus reflect a community's susceptibility to particular members of the regional species pool which are adapted for the particular conditions of the recipient community. Total richness, exotic richness, and native richness were all highest in our smallest landforms and we found no relationship between landform area and richness so it is unlikely that changes in richness are explained by species-area relationships (Fig. 10).

Studies of community invasibility in successional forests show that exotic and native assemblages follow similar dynamics through time, with shade-intolerant species dominating young, unforested or open canopy environments and shade- tolerant species dominating later successional stages (Meiners 2002, McLane 2012). Likewise, my results corroborate these findings, as mid to later (56-136 years) successional stands were invaded almost exclusively by shade-tolerant invaders including bush honeysuckle, multiflora rose, and garlic mustard. Indeed, bush honeysuckle was most common within stand ages greater than 70 years (Fig. 9A). Honeysuckle appears to establish on landforms with significant soil development, was very abundant on landforms with stand ages from 32 to 56 years old, and its cover decreased significantly thereafter (Fig. 9A). These shade-tolerant exotics occurred consistently in disturbance patches such as alluvial/colluvial fans, seepage created wetlands, erosional banks, and former river channels. These disturbances patches may provide opportunities for establishment by increasing sub-canopy light availability. Furthermore, native shrubs like spice bush (*Lindera benzoin* L.) are present, but are at low densities in all of our riparian study sites.

Surrounding secondary successional and human-dominated uplands have much higher densities of both native and non-native shrubs. This suggests that despite their ability to tolerate deep shade once established, they may not be adept at recruiting absent disturbances which increase light levels.

I found that biotic resistance does not play a large role in the invasibility of primary successional forest in Zoar Valley. Closed canopy forest was far less invaded by exotic species, and I suggest this is because there are few of them in the regional species pool that are well adapted for low light environments in the regional species pool. While biotic resistance and competitive exclusion can limit establishment opportunities for exotic species in some systems (Levine et al. 2004, Fargione and Tillman 2005), these intrinsic processes do not appear to be strong drivers of exotic species establishment at large spatial scales. Most studies at large spatial scales find positive relationships between native and non-native diversity (Fridley et al. 2007) and this is driven by extrinsic factors that promote establishment opportunities for exotic and native species (Naeem et al. 2000, Shea and Chesson 2002, Byers and Noonburg 2003, Davies et al. 2005). These models predict that negative relationships between native and exotic diversity will occur within sites which are minimally subjected to extrinsic factors. Zoar Valley appears to be a site minimally affected by extrinsic factors (evidenced by its directional primary successional trajectory) yet, relationships between native and non-native diversity are not negative.

Results from this study suggests that community invasibility may be better viewed as the life history strategies to which a community is susceptible to, rather than how native-exotic diversity relationships reflect the state of a community’s invasibility. Other studies have found similar relationships between native and non-native diversity in successional forests, including that native and exotic community composition tends to follow similar shifts in life history strategies through succession (Meiners 2002, Campagnoni and Halpern 2009, Mclane et al. 2012). With ecosystems and community processes becoming more altered by human activity, taking a ‘species traits’ approach to community invasibility may better explain community invasibility patterns and better serve mangers in attempts to mitigate their effects. By assessing the particular species to which traits a community is susceptible to, managers can concentrate their efforts and resources on the particular exotic species that can establish in a system and develop strategies aimed at mitigating the opportunities for establishment by species with those traits.

Works Cited

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

Burns, R.M. and B.H. Honkala. 1990. Silvics of North America, Vol. 1, Conifers. Washington DC: U.S.D.A. Forest Service Agriculture Handbook 654

Byers, M.J. and E.G. Noonburg. 2003. Scale dependent effects of biotic resistance to biological invasions. Ecology 84:1428-1433.

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.

Davies, K. F., P. Chesson, S. Harrison, B. D. Inouye, B. A. Melbourne, and K. J. Rice. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. Ecology 86:1602–1610.

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

Davis, M. A. and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invisibility. Ecol. Lett. 4:421–428.

Davis, M.A., K. Thompson, and J.P. Grime. 2001. Charles S. Elton and the dissociation of invasion ecology from the rest of ecology. Diversity and Distributions 7, 97-102.

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

Diggins T.P. A 300-year successional sequence in an eastern United States riparian hardwood forest (in press) The Journal of the Torrey Botanical Society.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, UK.

Fridley, J.D., J.J. Stachowicz, S. Naeem, D.F. Sax, E.W. Seabloom, M.D. Smith, T.J. Stohlgren, D. Tillman, and B. Von Holle. 2007. The invasion paradox: reconciling pattern and process in species invasions. Ecology 88, 3–17

Fargione, J. E., and D. Tilman. 2005. Diversity decreases invasion via both sampling and complementarity effects. Ecology Letters 8:604-611

Gilbert B, and J.M. Lechowicz. 2005. Invasibility and Abiotic Gradients: The Positive Correlation Between Native and Exotic Plant Diversity. Ecology 86:1848–1855.

Keane, R. M. and J.M. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. 17: 164-170.

Kennedy, T. A., S. Naeem, K. Howe, J. M. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature 417:636–638.

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

Levine, J. M. and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87: 15-26.

Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854.

Levine, J. M. 2001. Local interactions, dispersal and native and exotic plant diversity along a California stream. Oikos 95:397–408.

Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 10:975-989

Martin, P.H., C.D.Canham, and P.L.Marks. 2008. Why forests appear resistant to exotic plant invasions: intentional introductions stand dynamics, and the role of shade tolerance. Frontiers in Ecology and the Environment 7(3): 142–149.

McLane, C.R., L.L. Battaglia, D.J. Gibson, and J.W. Groniger. 2012. Succession of exotic and native species assemblages within restored floodplain forest: a test of the parallel dynamics hypothesis. Restoration Ecology 20(2):202-210

Meiners, S. J., S.T.A. Pickett and M.L .Cadenasso. 2002. Exotic plant invasions over 40 years of old field successions: community patterns and associations. Ecography 25:215–223.

Meiners, S. J. 2007. Native and exotic plant species exhibit similar population dynamics during succession. Ecology 88:1098–1104.

Naeem, S., J. M. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97–108.

Ortega, Y. K., and D. E. Pearson. 2005. Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. Ecological Applications 15:651–661.

Pfeil, E. K.; N. Casacchia; G. J. Kerns; T. P. Diggins. 2007. Distribution, Composition, and Orientation of Down Deadwood in Riparian Old-growthWoodlands of Zoar ValleyCanyon, western New York State, USA. Forest Ecology and Management 239: 159-168.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273-288.

Rejmánek M., D.M. Richardson, and P. Pyšek. Plant invasions and invasibility of plant communities. In: E. van der Maarel, ed. :Vegetation Ecology, p. 332-355 Blackwell, Oxford, 2005

Renne I.J., B.F. Tracy, I.A. Colonna. 2006. Shifts in grassland invasibility: Effects of soil resources, disturbance, composition, and invader size. Ecology 87:2264-2277

Sax, D. F., J. J. Stachowicz, J. H. Brown, J. F. Bruno, M. N. Dawson, S. D. Gaines, R. K. Grosberg, A. Hastings, R. D. Holt, M. M. Mayfield, M. I. O'Connor, and W. R. Rice. 2007. Ecological and evolutionary insights from species invasions. Trends in Ecology and Evolution 22:465-471.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17:170–176.

Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1:21-32.

Sinn, B.T., E.K. Pfeil, T.P. Diggins, and C.F. Chuey. 2007. Pteridophyte assemblage composition and richness as a reflection of woodland maturity. Poster presented at the 2007 Ecological Society of America meeting.

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

Stohlgren, T. J., D. Binkley, G. Chong. 1999. Exotic plant species invade hot spots of native plant diversity. Ecol. Monogr. 69:25–46.

Stohlgren, T. J., D. T. Barnett, and J. T. Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. Front. Ecol. Environ. 1:11–14.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81–92.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences 101:10854-10861.

USDA. 2012. United States Department of Agriculture Plant Database. Accessed 2012. http://plants.usda.gov

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997, Human domination of Earth's ecosystems. Science 277, 494-499.