Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL

OPINION ARTICLE

Environmental Variability and Ontogenetic Niche Shifts in Exotic Plants May Govern Reinvasion Pressure in Restorations of Invaded Ecosystems

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Abstract

When restoring ecosystems dominated by exotic plants, reinvasion pressure, or the rate of new exotic recruitment following mature exotic removal, can vary broadly between similarly invaded habitats. Reinvasion pressure strongly influences restoration costs and outcomes but is difficult to predict. Ontogenetic niche shifts (ONSs, changes in niche breadth or position during development) in exotic species paired with interannual variation in abiotic conditions may decouple pre-removal mature exotic density and average reinvasion pressure. Identifying such decouplings could improve restoration efficiency by informing site selection and management strategies, but requires estimates of average reinvasion pressure that mandate greater understanding of its principle drivers. We hypothesize that reinvasion pressure is predominantly driven by exotic propagule abundance and spatiotemporal availability of realized recruitment windows, which are periods of variable duration that permit exotic establishment from propagules. Realized recruitment windows are based on the "safe sites" concept but account for ONSs and are determined by abiotic conditions and interspecific interactions with recipient communities. Biotic resistance or facilitation may increase or decrease times required for establishment by influencing exotic growth rates or altering niche availability and may permit or preclude establishment in marginal abiotic conditions. We discuss factors influencing reinvasion pressure, basic approaches to estimate reinvasion pressure, and potential ways to increase management efficiency under different reinvasion pressure scenarios. Accurate estimates of reinvasion pressure could improve restoration efficacy, efficiency, and predictability in ecosystems dominated by exotic plants. We argue that greater theoretical and practical considerations of reinvasion pressure and ONSs are merited.

Key words: **biotic resistance, interannual variation, invasive species control, optimal management, propagule pressure, recruitment limitation, seed banks.**

Introduction

Our ability to predict outcomes of ecological restoration is limited in habitats threatened by invasive species, which degrade ecosystems and encumber restoration efforts (Kettenring & Adams 2011). Invasive species impact native communities and ecosystem functions via direct (e.g. competition) and indirect mechanisms (e.g. altered disturbance; D'Antonio & Vitousek 1992; Yelenik et al. 2007). Invasive plant management can also impact native communities, and these nontarget impacts and implications for restoration have recently received attention (e.g. Zavaleta et al. 2001; Buckley et al. 2007; Firn et al. 2008; Firn et al. 2010; Rinella et al. 2009). Impacts are predictable for specific management regimes; however, optimal management is influenced by exotic density, and management methods vary dramatically in cost (Epanchin-Niell & Hastings 2010). Exotic density also influences invader effects on communities and ecosystem functions (Grime 1998). Invader and management effects are critical early in restoration because of potential impacts on community assembly and/or succession (Suding et al. 2004). Therefore, estimating exotic density over time during restoration is crucial to predicting optimal management (which drives restoration costs) and invader and exotic management impacts (which drive restoration outcomes).

This work focuses on restoring ecosystems invaded by an exotic plant species. We assume that restoration begins with exotic removal and new exotic individuals will be removed before maturation, thus survival and fecundity of mature target exotics are negligible. Therefore, we can simplify traditional methods of estimating exotic density over time (via population models incorporating colonization, survival, and fecundity rates) by estimating reinvasion pressure. We define reinvasion pressure (Buckley et al. 2007) as abundance and performance of exotic individuals becoming established within a habitat per management horizon after removing a dominant population of conspecifics. Simplification is desirable because quantifying

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doi: 10.1111/j.1526-100X.2012.00901.x

site-specific model parameters and translating model outputs into management decisions are substantial tasks for professionals and beyond the scope of laypersons (Kettenring & Adams 2011). Most publically available management guidelines are based simply on mature exotic density in habitats of interest (e.g. The Nature Conservancy 2007). We argue that mature exotic density can poorly predict both short-term and average (long-term mean) reinvasion pressure.

We found that average reinvasion pressures varied broadly in restorations of habitats comparably invaded by Chinese tallow trees (*Triadica sebifera*). Preliminary results from experiments suggest that reinvasion pressure is correlated with soil moisture but not pre-removal mature *Triadica* density (unpublished data). The literature suggests that reinvasion pressure varies broadly in other species and systems. For example, Richardson and Kluge (2008) reported "unpredictable and sporadic" reinvasion of *Acacia* species in South Africa, and identified correlates exclude pre-removal *Acacia* density. When exotic density correlates poorly with reinvasion pressure, restoration efforts based accordingly are prone to failure if management is inadequate or inefficiency if unnecessary management is performed (Epanchin-Niell & Hastings 2010).

We provide a conceptual explanation of key factors and mechanisms governing reinvasion pressure during restorations of invaded ecosystems. We explore how predicting reinvasion pressure could enhance efficacy and efficiency of restoration projects and provide examples of particular mechanisms. Accurate estimates of reinvasion pressure would permit managers facing multiple invaded habitats to prioritize restoration efforts where costs and exotic impacts are low, which could increase overall extent of successful restoration given limited resources. To enhance our capacity to predict restoration outcomes and costs in invaded habitats, we ask: How could average reinvasion pressure be decoupled from mature exotic plant density? How might particular quantifiable or manipulatable factors influence reinvasion pressure?

We hypothesize that reinvasion pressure is decoupled from mature exotic density when abiotic tolerances of exotic plants broaden as individuals mature (ontogenetic niche expansions), and where interannual variation in abiotic conditions temporarily permits exotic recruitment in habitats typically unsuitable for recruitment. Abiotic conditions determine frequency and duration of exotic recruitment windows, which predominantly influence reinvasion pressure. Reinvasion pressure is moderated by interspecific interactions with recipient communities and is generally proportional to exotic propagule abundance. Although our examples emphasize water, our discussion of "abiotic conditions" considers climate (temperature, water, and their interactions) and resource availability, which are major factors limiting plant distributions.

Ecological Contexts of Invasion Versus Reinvasion

The literature indicates that invader establishment success depends on propagule pressure, or abundance and timing of individuals introduced (Simberloff 2009), abiotic conditions or environmental filters (e.g. Kolar & Lodge 2001), and characteristics of recipient communities (e.g. Davis et al. 2000). Spatiotemporal variation in abiotic and interspecific factors is also important, e.g. as explained by "regeneration niche" (Grubb 1977), "safe sites" (Harper 1977), "invasion windows" (Johnstone 1986), and "niche opportunity" hypotheses (Shea & Chesson 2002). Generally, abundant exotic individuals, favorable climate, weak competition or predation, and strong facilitation promote invasion success. Mechanistically, those factors influencing invasion should apply to reinvasion.

However, ecological conditions in relatively intact ecosystems as invasions begin differ from those after dominant exotic plants are removed. Ecosystems post-removal generally exhibit high resource availability, weak competition, limited native propagules, and abundant exotic propagules relative to intact ecosystems. This context and/or other positive feedbacks (Suding et al. 2004) may explain why reinvasions or novel invasions often progress rapidly after invasive plant control ceases (Kettenring & Adams 2011). Fortunately, reinvasion pressure is variable but predictable.

Decoupling Reinvasion Pressure and Exotic Density

If an exotic plant's abiotic niche broadens as individuals increase in age and/or size, populations could persist in and eventually dominate habitats where conditions are typically unsuitable for recruitment but sufficiently variable to temporarily permit germination and growth to more tolerant stages. Changes in niche breadth and/or position during development are termed ontogenetic niche shifts (ONSs) and occur in many plants (Fig. 1; Eriksson 2002). ONSs may permit coexistence (Grubb 1977) and influence species distributions (Eriksson 2002) and succession (Young et al. 2005). Herbivore

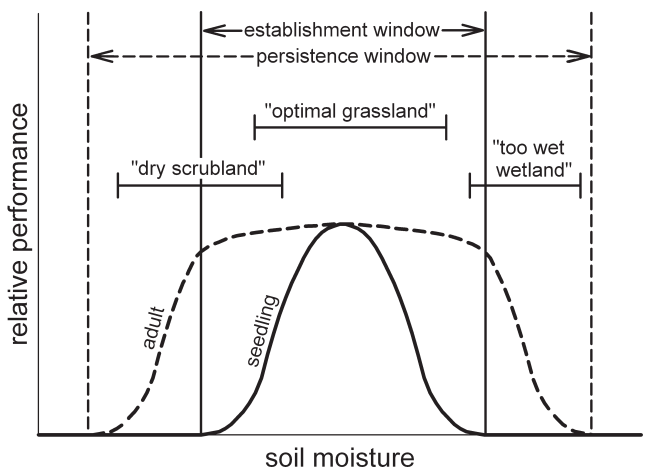

Figure 1. Adults of a hypothetical species (dashed curve) tolerate a broader range of moisture than seedlings (solid curve). Ontogenetic niche expansions like this demonstrate how adults may persist in conditions unsuitable for their establishment. Horizontal bars represent moisture ranges for three hypothetical habitats; their overlaps with the establishment window suggest that the species can colonize the wetland rarely, the scrubland occasionally, and the grassland always.

and disease resistance can also vary ontogenetically (discussed below). We emphasize niche expansions, but ONSs include niche contractions and directional shifts (Eriksson 2002). Without abiotic niche expansions, deviations from average environmental conditions could permit recruitment but not persistence in typically unsuitable habitats. Similarly, without expansions we would not expect low average reinvasion pressure where exotics dominate because conditions promoting dominance would promote recruitment.

This scenario requires abiotic conditions suitable for exotic recruitment at some times and unsuitable for recruitment yet tolerable by older exotics (Fig. 1) at other times. Interannual variation in abiotic conditions can trigger such transitions (Fig. 2a–c), cause episodic recruitment (League & Veblen 2006), and influence establishment success (Bartha et al. 2003). A key consequence is exotic-dominated habitats with low average reinvasion pressures. Thus, some habitats considered poor candidates for restoration could be restored relatively cheaply and easily. To identify these we must understand factors influencing reinvasion pressure.

Abiotic Conditions Drive Reinvasion Pressure by Defining Recruitment Windows

Plants germinate and grow in discrete ranges of abiotic conditions (recruitment niche), so when environments vary temporally there may be periods when individuals can establish (Grubb 1977; Harper 1977; Johnstone 1986; Fig. 2). These periods define "windows of opportunity" permitting recruitment. Naturally, more opportunities and time to develop broader tolerances increase establishment success. Therefore, window frequency and duration should strongly influence reinvasion pressure. Both vary by species and habitat and temporally within habitats because of interannual variation. Conditions during windows affect reinvasion pressure by influencing performance and potentially establishment success if size influences tolerances (Fig. 1). By defining frequencies and durations of recruitment windows and influencing performance, we expect that abiotic conditions drive reinvasion pressure when exotic propagules are abundant.

Recruitment windows may span entire growing seasons where abiotic conditions are highly suitable for the invader (Fig. 2b). Here, average reinvasion pressure is maximized and recruitment may fail only when interannual variation is extreme. Conversely, average reinvasion pressure is minimized where typical conditions are unsuitable for exotic recruitment (Fig. 2a). However, large deviations from average conditions (e.g. droughts or floods) may provide rare recruitment windows that permit exotics with expanding niches to germinate and reach stages or sizes tolerant of average conditions. Subsequent windows could permit dominance when propagules are limiting. We hypothesize that this mechanism underlies the strongest decouplings of average reinvasion pressure from mature exotic abundance.

Average reinvasion pressure may be moderate where typical conditions are near an exotic's limits for recruitment (Fig. 2c). In borderline conditions, interannual variation could more frequently permit or preclude recruitment, causing intermittent and possibly shorter recruitment windows. Marginal abiotic conditions could also reduce exotic performance and/or survival, potentially moderating reinvasion pressure even if windows occur annually.

Propagule Availability Fuels Reinvasion

Simberloff (2009) reviewed mounting evidence that propagule pressure is centrally important to establishment and spread phases of invasions. He suggests that increased colonizer abundances and frequencies of colonization events promote establishment by dampening effects of demographic and environmental stochasticity, respectively. Exotic propagule pressure may even supersede physical environment in determining invasion success in some systems (Von Holle & Simberloff 2005).

When restoring invaded ecosystems, initial exotic propagule abundance varies but is generally high, and propagules remain present until they die or become juveniles subject to management. Sexual invaders often produce more seeds than could establish in available space due to self-thinning, and these "supersaturated" seedbanks may fuel high reinvasion pressure for years despite recurring management (e.g. Healy & Zedler 2010). We suggest that supersaturated seedbanks are common for abundant, fecund invaders, and differences in exotic propagule abundance beyond saturation have little impact on reinvasion pressure because spatial carrying capacity likely depends more on abiotic conditions.

Nevertheless, recruits cannot exceed propagules, so propagule availability may determine reinvasion pressure when propagule density is below spatial saturation. Even if supersaturated, propagule density could affect reinvasion pressure if suboptimal abiotic conditions reduce germination or survival rates. Thus, we hypothesize that reinvasion pressure is generally proportional to propagule availability. Reinvasion pressure may decrease rapidly if exotic propagules are short lived, or if ecological conditions, e.g. seed predators (Richardson & Kluge 2008), or management, e.g. burning (Firn et al. 2008), reduce their viability. When invaders cannot store propagules, external propagule pressure likely heavily influences reinvasion pressure. Exotic propagule availability and longevity, and factors influencing propagule viability may impact reinvasion pressure.

Interspecific Interactions Moderate Reinvasion Pressure

Mack et al. (2000) suggested communities vulnerable to invasion exhibit vacant niches, few biotic constraints, low species richness, and/or disturbance. Essentially, these focus on biotic resistance—how strongly natural enemies or competitors negatively impact invaders—with niche saturation, enemy release, community structure, and reduced native abundance proposed as key mechanisms. Positive impacts of facilitation are also recognized (e.g. Maron & Connors 1996). Interactions among

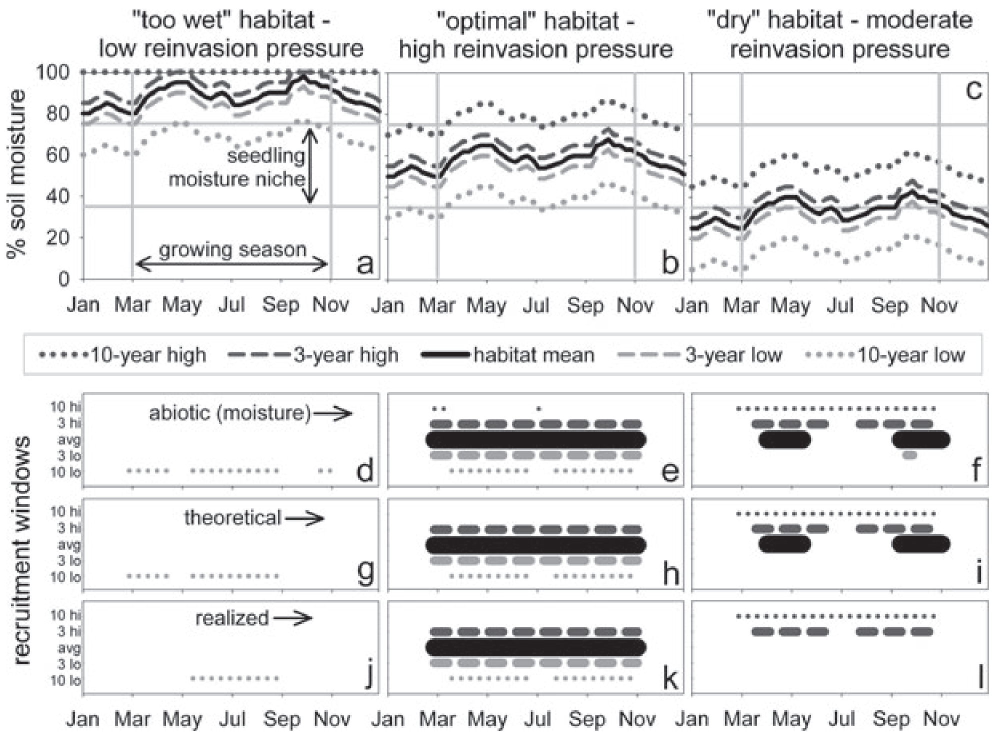

Figure 2. Contours (a–c) demonstrate ranges and frequencies of soil moisture fluctuations in three hypothetical habitats exhibiting interannual variation. Horizontal lines (d–l) represent periods, weighted by frequency, when moisture conditions could permit recruitment of a hypothetical plant species with an expanding moisture niche (recruitment windows). For simplicity, we assume that seedling performance is equal across the moisture niche, mortality is instantaneous outside the moisture niche, and interspecific interactions produce a universal net negative effect on performance. Abiotic recruitment windows (d–f) occur when abiotic conditions are suitable for germination and seedling growth—here when moisture contours (a–c) fall within the moisture niche and growing season. However, niche expansions take time. Theoretical recruitment windows (g–i) occur when abiotic windows persist long enough for seedlings to germinate and develop tolerances to subsequent conditions (to become established) based on individuals' physiological growth rates—here minimum establishment time is 6 weeks, so only abiotic windows ≥6 weeks are theoretical windows. However, biotic interactions influence seedling performance and thus establishment time. Realized recruitment windows (j–l) occur when abiotic windows are long enough to permit establishment given local abiotic and biotic conditions—here biotic resistance halves growth rate and doubles establishment time, so only abiotic windows ≥12 weeks are realized windows. In the "too wet" habitat (a), recruitment is episodic and may succeed only during 10-year lows (d, g, and j), so average reinvasion pressure is low. In the "optimal" habitat (b), recruitment is typical because suitable conditions span the growing season except during 10-year extremes (e, h, and k), so average reinvasion pressure is high. In the "dry" habitat (c), recruitment is intermittent and may succeed only in relatively wet years (f, i, and l), so average reinvasion pressure is moderate; notably, here biotic resistance precludes recruitment in average years (i vs. l).

these factors and resource availability, and their spatiotemporal variation are crucial to invasion success (Johnstone 1986; Davis et al. 2000; Shea & Chesson 2002).

In our context, one generally expects weak biotic resistance. By definition, after removal of dominant exotic plants, habitats exhibit high space and light availability, relatively low plant abundance, disturbance of some type, and often reduced species richness and niche saturation. If enemy release influenced invasion, localized exotic removal would not introduce coevolved natural enemies and should have little impact on native herbivores or pathogens. Thus, we expect that biotic resistance generally has little impact on reinvasion pressure when resources are available and competitors are scarce.

However, many restoration techniques alter characteristics of recipient communities. Introducing native competitors or biocontrol agents can bolster biotic resistance following exotic removal (Funk et al. 2008; Kettenring & Adams 2011). Introductions may not preclude reinvasion but may reduce reinvasion pressure by decreasing exotic survival or performance. Depending on abiotic conditions, reducing exotic performance could preclude establishment during some recruitment windows (discussed below).

Natural enemies may influence reinvasion pressure, particularly when exotic plants' defensive capabilities strengthen during development. A meta-analysis by Barton and Koricheva (2010) found that herbivore defenses (especially chemicals) increase through ontogeny, especially rapidly during the seedling stage. Comparably, plants are generally more susceptible to disease early in development, with pathogen resistance developing gradually or at major life cycle transitions (reviewed by Develey-Rivière & Galiana 2007). Interannual variation in natural enemy abundances paired with "windows of vulnerability" early in plant development may produce temporal variation in exotic recruitment success and could also decouple average reinvasion pressure from abundance of mature exotics not subject to enemy release.

Synthesis: Realized Recruitment Windows and "Outgrow the Stress" Hypothesis

We posit that exotic management is most efficient when planned according to timing of realized recruitment windows (Fig. 2j–l). If plant size, which is a function of age and growth rate, determines physiological tolerances (Blum et al. 1997; Kunstler et al. 2009), all factors governing growth rate during recruitment windows will influence recruitment success. Our "outgrow the stress" hypothesis holds that: (1) age and ecological conditions determine plant size, which determines a species' abiotic tolerances that ultimately limit its success during recruitment windows when its propagules are abundant, and (2) availabilities of propagules and realized recruitment windows determine recruitment success over time, which determines reinvasion pressure.

Caveat: Net positive interspecific effects could reduce establishment times (unlike Fig. 2g–l). We doubt this is common and note most modes of facilitation are considered elsewhere in our model: pollination and dispersal influence propagule availability, and theoretical recruitment windows consider microclimates produced by nurse plants. Very strong facilitation, e.g. via mycorrhizae, could void this assumption.

Conclusions and Recommendations

Our conceptual model explains potential mechanisms underlying variable reinvasion pressure in restorations of habitats dominated by exotic plants. Average reinvasion pressure may be decoupled from mature exotic density when interannual variation in abiotic conditions (Fig. 2a–c) permits exotics exhibiting ontogenetic niche expansions (Fig. 1) to dominate habitats where their average recruitment success is relatively low. Abiotic conditions drive reinvasion pressure by defining availability of recruitment windows (Fig. 2d–i) and influencing exotic performance. Reinvasion pressure is generally proportional to exotic propagule abundance, but may plateau at spatial saturation. Practitioners can most control biotic resistance, which moderates reinvasion pressure by influencing exotic survival and performance, and may preclude exotic recruitment in some situations (Fig. 2j–l). Ultimately, spatiotemporal availability of exotic propagules and realized recruitment windows determine reinvasion pressure.

Without reliable predictors, sound estimates of average reinvasion pressure require sizeable but attainable amounts of data. Basic knowledge of the target exotic plant's abiotic and functional niches; capacity for niche shifts; germination, growth and reproductive rates and strategies; phenology; propagule longevity; natural enemies; and responses to particular exotic control methods is essential. For problematic and well-studied invaders, this information is likely common knowledge among average managers or attainable via agricultural extension. For less studied invaders, sufficient information for rudimentary estimates is likely attainable through agricultural extension. Necessary information may be unavailable for emerging invaders, but data on closely related species may be suitable. If not, we suggest estimates via repeated surveys or pilot studies (see below), and adaptive management where estimates are unattainable or unreliable.

Data on environmental conditions, interannual variability, disturbance regime, and natural enemies within candidate habitats are also necessary. This could come from historic climate and/or disturbance records, soil maps, experience, or could be inferred from extant species' requirements. One could estimate average reinvasion pressure directly via repeated surveys of exotic germination, survival and performance in candidate restoration sites, or preferably via pilot experiments under environmental conditions expected following exotic removal.

Where invaders are well-studied or resources permit in situ research, reliable estimates of reinvasion pressure are highly realistic and practical. Where invaders are less studied and research capacity is low, coarser estimates are still realistic but may only be practical if existing management methods or decision-making tools are deficient. Developing estimates is likely impractical for independent managers without substantial pre-existing data for their system (e.g. in understudied regions) or access to it (e.g. in developing regions). Reliable estimates of average reinvasion pressure can guide management to enhance restoration efficacy and efficiency (see Implications for Practice). Reinvasion pressure is a general, quantifiable metric that provides a useful decision-making context and may guide management strategies and site selection wherever invasion has already occurred.

Implications for Practice

- Where average reinvasion pressure is high: Emphasize management that reduces exotic propagule abundance or viability. Avoid native introductions until need for destructive management diminishes.
- Where moderate: Avoid destructive management and increase biotic resistance early via native introductions. Reduce exotic propagule abundance only when inexpensive or seedbanks are long lived.
- Where low: Utilize management strategies responsive to episodic recruitment pulses rather than annual management. Prioritize these habitats.
- Generally: Utilize adaptive management strategies that accommodate fluctuations in exotic recruitment to ensure exotic control is always commensurate with reinvasion pressure.

Acknowledgments

This work was supported by US-NSF (DEB-0910361), Garden Club of America (Fellowship in Ecological Restoration), Society of Wetland Scientists (Student Research Grant), Native Plant Society of Texas (A.M. Gonzalez Grant), Wintermann Research Fund, and Lodieska Stockbridge Vaughn, Houston Livestock Show and Rodeo and Wray-Todd Fellowships.

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