

Frontiers in Ecology and the Environment

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Front Ecol Environ 2008; 6, doi:10.1890/070096

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Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance

Patrick H Martin^{1*}, Charles D Canham², and Peter L Marks³

Invasion ecology has traditionally focused on exotic plant species with early successional life-history traits, adapted to colonize areas following disturbance. However, the ecological importance of these traits may be overstated, in part because most invasive plants originate from intentional introductions. Furthermore, this focus neglects the types of plants most likely to invade established communities, particularly forests – namely shade-tolerant, late-successional species. In invasion ecology, it is generally assumed that undisturbed forests are highly resistant to plant invasions. Our review reveals that this assumption is not justified: in temperate and tropical regions around the world, at least 139 exotic plant species are known to have invaded deeply shaded forest understories that have not undergone substantial disturbance. These exotics present a particular management challenge, as they often increase in abundance during succession. While forest invasions may develop comparatively slowly under natural disturbance regimes, anthropogenic processes, including the spread of exotic pests and pathogens, can be expected to accelerate the rate of invasion.

Front Ecol Environ 2008; 6, doi:10.1890/070096

Since Elton's landmark work, *The ecology of invasions by animals and plants* (1958), invasion ecology has emphasized the central role of disturbance in facilitating exotic plant invasions (Crawley 1987; Rejmánek 1989; Lodge 1993) and plant species with early successional life histories adapted to colonize under such conditions (Bazzaz 1986; Rejmánek and Richardson 1996; Grotkopp *et al.* 2002). An important implication of this paradigm is that "intact" (ie undisturbed) plant communities are assumed to strongly resist or repel exotic invasions, a community attribute known as biotic resistance (see Levine *et al.* 2004). Indeed, if early successional traits and adaptation to disturbance are intrinsic elements of most plant invasions, it follows that

invasions will be rare in undisturbed communities, where life-history traits favoring competitive ability predominate. Closed-canopy forests, in particular, have long been cited as highly resistant to invasion (Cavers and Harper 1967; Crawley 1987; Rejmánek 1989; Von Holle *et al.* 2003).

While the scope of invasion ecology has continued to expand (incorporating, for example, evolutionary factors and enemy release), its fundamental emphasis on early successional and disturbance-adapted species has remained unchallenged, leaving important questions about invasions in intact communities – particularly forests – largely unaddressed. Are forests effectively immune to invasion, even by exotic plants with late successional life-history traits, especially shade tolerance? Are late-successional plants essentially non-invasive, suggesting a fundamental trade-off between invasive and competitive life-history traits? Although they are relatively few, some recent studies have begun to address these questions (Gilbert and Lechowicz 2005; Martin and Marks 2006) and offer evidence that an important subset of forest invasives is neither dependent on disturbance nor restricted to early successional life-history strategies (Figures 1, 2, 3, and 4).

Here, we focus on invasion dynamics in closed-canopy forests, where conditions support the development of an essentially contiguous canopy of tree foliage. We begin by evaluating the limitations of traditional theories of invasion ecology in addressing forest invasions. Next, we analyze the influence of intentional introductions and horticultural practices on the pool of available exotic flora. Finally, we review the incidence of shade-tolerant exotic invasives worldwide, and consider the processes by which forest invasions develop.

In a nutshell:

- The vast majority of invasive exotic plant species originate from intentional introductions, most of which are fast-growing, shade-intolerant species
- The number of shade-tolerant species that have been deliberately introduced is much lower, but a very high percentage of these shade-tolerant exotics invade deeply shaded forests
- Forests are not immune to invasion; while the rate of invasion by these shade-tolerant species may be comparatively slow, many shade-tolerant invasives have detrimental and long-term impacts on forest ecosystems worldwide

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Figure 1. Norway maple (*Acer platanoides*) is one of the few well studied exotic invasive tree species. A very common street and yard tree in the US, it frequently dominates the seedling layer of invaded understories, as shown here.

■ The early successional dominance of invasion ecology theory: is it overstated?

Early successional species continue to attract most of the attention of invasion ecologists. Numerous studies have concluded that early successional traits best explain invasiveness, especially long-distance dispersal and high fecundity (Bazzaz 1986; Lodge 1993; Rejmánek and Richardson 1996; Williamson and Fitter 1996; Reichard and Hamilton 1997). Other traits considered invasive include short generation time, long fruiting period, small seed size, and prolonged seed viability (eg Rejmánek and Richardson 1996; Mehrhoff 1998). In general, early successional species are typified by rapid growth, poor shade tolerance, early reproduction, and a short life span (Bazzaz 1979). Rejmánek and Richardson (1996) concluded that most invasive species occur on the *r*-selected end of the *r*-*K* selection continuum.

Despite the prominence of this view, we feel that the importance of early successional species in invasions is overstated, at least for conceptualizing the spread of exotic species in forests. The study of invasions has traditionally relied on retrospective methods and the study of exotics already recognized as invasive (Reichard and Hamilton 1997; Grotkopp *et al.* 2002). This post-hoc approach is inherently biased toward exotic species which invade rapidly or were introduced earlier. In forests, “rapid” invasions can unfold comparatively slowly (at least in human terms; Von Holle *et al.* 2003; Martin and Marks 2006) and, hence, may be underestimated. Retrospective studies also typically focus on areas where exotic invasives are already established or widespread. These are often sites that have been highly disturbed or

stressed by human activities, and may not be indicative of broader invasiveness, as many exotics were intentionally introduced to thrive in unusual environments (eg high pollution tolerance; Bassuk 1985). In such settings, sources of exotic species seed may be greater than those of native species seed (Martin 1999), and resistance mechanisms of the plant community may be highly altered (eg very high populations of herbivores and seed predators; Nupp and Swihart 1998).

Theories of plant invasions were also developed almost exclusively in grasslands or herbaceous communities. Levine *et al.* (2004) conducted a comprehensive literature review of experimental studies on biotic resistance to exotic plant invasion: 42 of the 53 studies covered by the review were conducted in grasslands or grass-like communities, while only six studies were conducted in forests or shrub-

lands. Moreover, 61 of the 71 exotic species were annual or perennial grasses and forbs, while only four exotic tree and seven exotic shrub species were included (Figure 1). The applicability of such research for forests is questionable. For example, 97% of all annuals and biennials in the US are intolerant of deep shade (Sutherland 2004), and while early successional traits and an adaptation to frequent disturbance (especially grazing and fire) may make *r*-selected species invasive in grasslands, environmental conditions and disturbance regimes are very different in forests. Indeed, Lozon and MacIsaac’s (1997) review of disturbance and invasions found that 79% of disturbance-facilitated invasions occurred in grasslands, but that such invasions were very rare in all forest types. Finally, most theories which explain invasiveness – why an exotic species has an advantage over natives (eg “enemy escape”, “novel weapons”) – are applied in the context of early successional species and disturbed habitats (Blumenthal 2006).

■ Intentional introductions, horticulture, and invasive plants

Patterns of plant introductions provide further reason to reconsider the dominance of early successional, disturbance-dependent species in invasion ecology theory. Trends in life-history traits of invaders may simply reflect human priorities, as most exotic species in many regions were intentionally introduced. A recent, highly comprehensive, global compilation of exotic plants “strongly invasive in natural areas” by Weber (2003) – considered to be by far the most complete overview of invasive plant species (Pyšek 2004) – found that 354 of the 427 (81%)

species originated from intentional introductions. For woody plants, these patterns are even more pronounced: in North America, 99% of all naturalized exotic woody plants were intentionally introduced, 85% for the landscape trade (both ornamental and functional plants) and 14% for agriculture or production forestry (Reichard and Hamilton 1997). Certainly, many exotic species that invade grasslands and agricultural areas arrive via accidental introductions, but even 66% of exotic invasive herbs and grasses originate from intentional introductions (Weber 2003). Accidentally introduced species are also likely to be adapted to human-dominated and disturbed environments, as these species grow in and around settlements and are most likely to be transported accidentally by humans (Crawley 1987). Of course, no source is without its limitations; Weber's (2003) list may underrepresent accidental introductions, particularly in some agricultural and rangeland regions (M Rejmánek pers comm). Furthermore, intentional introductions are less important in countries where horticulture and related activities, such as forestry, have not been widespread (Arroyo *et al.* 2000).

By itself, this pattern of intentional introductions raises questions about the validity of post-hoc generalizations about invasive life-history traits, at least for woody plants. Indeed, the life-history traits of intentionally introduced plants are decidedly non-random, as the vast majority of these introductions have early successional life histories (Reichard and Hamilton 1997; Grotkopp *et al.* 2002). An examination of horticultural practices indicates why intentional introductions are predominately *r*-selected or early successional. Most importantly, these species are selected for their ability to thrive in human-modified environments, which tend to be highly disturbed or altered (eg highly fragmented, polluted). Introduced plants are typically chosen for ease of propagation, low maintenance, vigor, and lack of obvious diseases. In horticulture, a premium is also placed on species with rapid growth rates, especially for tree species (Willet 1990). The vast majority of plantation and forestry tree species are also fast-growing, shade-intolerant species such as pines, acacias, and eucalypts (Weber 2003). We compiled evidence from standard references in the horticultural literature that detail the pervasiveness of early successional introductions:

(1) Flint's (1983) comprehensive compendium of exotic and native ornamental plants in the eastern US includes 1500 plant species of all life-forms, and our tally of this list found that 93% are classified as fast growing and intolerant of shade and that fewer than 1% of the shade-tolerant species are trees.



Courtesy of L.J. Weithoff

Figure 2. Many shade-tolerant invaders are capable of invading both disturbed and undisturbed habitats. Japanese stilt grass (*Microstegium vimineum*), an exotic annual grass, is highly shade tolerant and invades both sunny areas and shady forest understories.

- (2) Dirr's (1997) compendium of woody landscape plants includes 491 exotic and native trees, shrubs, and woody vines; 68% of that total are shade intolerant, as are 85% of tree species.
- (3) A widely used guide for urban–suburban trees (Bassuk *et al.* 2003) recommends 106 tree species (47 exotics), of which 81% require full sun and 76% are fast growing, while only 10% are slow growing and fewer than 2% tolerate full shade.

Furthermore, Bassuk *et al.* (2003) strongly recommend mesophytic exotic tree species: 97% of recommended species are adapted to a neutral or alkaline soil pH, while only 11% are adapted to prolonged drought and only 3% are adapted to saturated soils. It appears that horticulture has generally recommended fast-growing, shade-intolerant trees that thrive in base-rich, mesic sites.

■ The role of shade tolerance in exotic plant invasions of forests

In light of the horticultural influence on exotic flora, there can be little doubt that the pool of *available* exotic flora is dominated by early successional species with little or no shade tolerance. Shade intolerant exotics generally do not invade forests, even those experiencing common small-scale disturbances, such as canopy gaps (Howard *et al.* 2004; Gilbert and Lechowicz 2005). Rather, the common trait of most forest invasives is shade tolerance. Despite their reputation for invasion resistance, evidence showing that temperate and tropical forests are readily invaded by shade-tolerant exotics continues to grow (Webb and Kaunzinger 1993; Woods 1993; Meyer and Florence 1996;

Rejmánek 1996; Martin 1999; Martin *et al.* 2004; Gilbert and Lechowicz 2005; Martin and Marks 2006). The scope of forest invasions by shade-tolerant exotics is unknown, however, as there have been no efforts to date to gather a comprehensive list of such invasions (NRC 2002).

We addressed this knowledge gap by compiling all available reports and publications on shade-tolerant invasives from a database of scientific literature (Web of Science), an internet search engine (Google), and additional references in these sources, searching with keyword combinations of “shade tolerant, shade tolerance, invasive, invader, and invasion”. Only exotic invasives explicitly considered tolerant of “full” or “deep” shade were tallied. Occasionally, sources differed on the degree of shade tolerance; we included a species if it was considered unambiguously shade tolerant by at least one source. This search is not completely comprehensive; however, it is sufficiently thorough to offer a robust estimation of the pervasiveness of shade-tolerant forest invasives. Some sources cited in our search define a species as invasive if it has, at a minimum, established self-sustaining populations in its introduced range. While this does not focus exclusively on highly aggressive invasives, such a criterion excludes approximately 90% of all introduced species (Williamson and Fitter 1996). Over time, this list will undoubtedly increase as information on life-history attributes of invasive species improves. We have developed a website so that additional species can be added to this database of shade-tolerant forest invasives (http://landscapeecology.agsci.colostate.edu/research/invasives/forest_invaders/forestinvasives.html).

Our search identified 139 exotic invasive plant species considered tolerant of shade (Table 1). This list includes species that also invade disturbed ecosystems and have

other traits typically considered early successional (Figure 2), as such traits can co-occur with shade tolerance. Many forest invaders in this list also exploit gaps and other small-scale disturbances common in forests, such as hiking trails. Yet, all of the species listed have the capacity to invade deeply shaded forest understories. Thus, while it may facilitate or accelerate invasion, disturbance is not obligatory for any of these species to invade a shaded understory. More importantly, the evidence indicates that shade-tolerant exotics comprise the majority of invasives in forests (Table 2), even though this tabulation includes data from forest ecosystems that are highly disturbed by human activities. For example, consider the evidence compiled by the Invasive Plant Atlas of New England (IPANE; Mehrhoff *et al.* 2006), a comprehensive survey of invasive and potentially invasive exotic plants in New England. We tallied IPANE's species invading both disturbed and undisturbed terrestrial upland habitats (a total of 80 species): even when including the invasives of comparatively open grassland and meadow habitats, 49% of New England's invasive exotics are very shade tolerant and 6% are partially shade tolerant. The degree of invasiveness of forest invasives also appears to be linked to shade tolerance; in Virginia, a statewide survey of terrestrial upland habitats (disturbed and undisturbed) reported that 68% of “highly invasive” plant species tolerate full shade and 91% tolerate partial shade; 33% of “moderately invasive” species tolerate full shade and 81% tolerate partial shade; and only 14% of “occasionally invasive” species tolerate full shade, while 86% tolerate partial shade. In addition, 100% of the species in all three categories invade only mesic habitats (DCR 2003).

Our keyword search indicates that plant life-form may also play an important role in the patterns of shade-tolerant invasives: herbs (35%) and shrubs (28%) were the most common life-forms, while trees and vines comprised 21% and 17% of the total, respectively (Table 1). A broader inspection of plant life-form and invasiveness using Weber (2003; Table 2) shows 36% of vines, 27% of shrubs, 23% of trees, and 6% of herbs are shade tolerant. However, these percentages are for all habitat types. In New England, where natural areas are predominantly forested, the proportion of exotic invasives that are shade tolerant is much higher: 81% of shrubs, 76% of vines, 50% of trees, and 39% of herbs and grasses (Mehrhoff *et al.* 2006; Table 2). In the eastern US alone, we found evidence of at least 23 exotic shrubs capable of invading deeply shaded forest understories (Table 1; Figure 3). These life-form patterns may be partially attributable to the history of intentional plant introductions. Dirr's (1997) compendium of woody landscape plants lists 121 of 271 shrub species as shade tolerant, while only 29 of 196 tree species are shade tolerant. In Flint's (1983) compendium of ornamental plants, 105 exotic species can tolerate full shade: 41 are shrubs, 39 are herbs, 22 are vines, and 3 are trees. What is not clear is whether certain life-forms – shrubs in particular – are inherently more inva-

Table 1. Summary of shade-tolerant exotic plant invaders

Life-form	Number of species
Herbs	
Temperate	31
Tropical	17
Total	48
Shrubs	
Temperate	26
Tropical	13
Total	39
Trees	
Temperate	9
Tropical	20
Total	29
Vines	
Temperate	14
Tropical	9
Total	23
Total species	139

Notes: This list was compiled from peer-reviewed and online publications by searching keywords in Web of Science and Google, and references in these publications. Keywords included combinations of: shade tolerant, shade tolerance, invasive, invader, and invasion. Only exotic invasives explicitly considered tolerant of “full” or “deep” shade were tallied. See WebTable 1 for the full species list.

sive in forests or merely include more intentionally introduced species with traits appropriate for invading forests.

■ Exotic invasions and forest dynamics

Forest invasions are best viewed in the context of existing theories and models of forest dynamics, particularly successional patterns (Davis *et al.* 2001). Understory light levels in most closed-canopy forests are consistently low, typically 5% to < 2% of incident solar radiation (Canham *et al.* 1990). In such a low-light environment, shade tolerance drives succession, both as interspecific differences in shade cast by adults (Canham *et al.* 1994) and shade tolerance of juveniles (eg Kobe *et al.* 1995). The basis of this dynamic is a well known trade-off between high survivorship under low light versus rapid growth under high light (see Crawley 1997). The scarcity of shade-tolerant, mid- to late-successional exotic tree species (Table 2) means that all but highly disturbed forests appear resistant to exotic tree invasion, and that exotic trees are disproportionately dependent on disturbance. However, unlike forest understories, competition in a forest canopy is effectively a zero-sum game, as all potential canopy space is occupied by mature trees; thus, invasion by an exotic tree comes at the expense of the abundance of other (typically native) tree species.

Small canopy gaps, as the most common disturbance in forests (Platt and Strong 1989), play a central role in forest dynamics. Stand-replacing disturbances which reset succession are important, but these events are over 500 times less frequent than small gaps (Lorimer 1989). The role that canopy gaps play in invasion dynamics is limited, however, since the vast majority of gaps are small enough to be filled by the lateral crown expansion of adjacent canopy trees (Canham 1985) or by the height growth of previously suppressed saplings and sub-canopy trees. This means that native and exotic tree species must be sufficiently shade tolerant to survive repeated periods of suppression before canopy recruitment (Canham 1985). Nevertheless, the very low light levels in forests make the rate of canopy recruitment by even shade-tolerant tree species strongly dependent on gaps, to the extent that a temporary scarcity of gaps could create a "lag phase" in invasions by shade-tolerant exotics. For example, the

Table 2. Life-form, shade tolerance, and disturbance-dependence percentages of exotic invasive plants

Invasives database	Number of species	Life-form	Shade tolerant	Disturbance dependent
Global¹				
Trees	81	19%	23%	49%
Shrubs	107	24%	27%	50%
Vines	33	8%	36%	48%
Herbs, grasses, and succulents	216	49%	6%	85%
Total	437	100%	17%	67%
Global²				
Trees	41	23%	38%	
Shrubs	41	23%	49%	
Vines (woody and herbaceous)	25	14%	48%	
Grasses	26	15%	29%	
Herbs (non-climbing)	42	24%	36%	
Total	175	100%	40%	
North America³				
Trees	21	27%	38%	
Shrubs	29	37%	83%	
Vines	9	12%	44%	
Herbs and perennials	13	17%	23%	
Grasses	6	8%	16%	
Total	78	100%	52%	
New England⁴				
Trees	8	10%	50%	
Shrubs	21	26%	81%	
Woody vines	8	10%	76%	
Herbs and grasses	43	54%	39%	
Total	80	100%	63%	
Southern forests, US⁵				
Trees	13	22%	15%	
Shrubs	17	29%	82%	
Woody vines	14	24%	79%	
Herbs	6	10%	33%	
Grasses	8	14%	13%	
Total	58	100%	52%	

Notes: This compilation of invasive species patterns was limited to sources that were globally or regionally comprehensive and that included detailed information on species life-history traits. All of these sources used strict definitions of what constitutes an invasive (described below). In databases for which life-form categories were not mutually exclusive, the dominant growth form of the species was used to categorize life-form. ¹Weber (2003): global in scope; a comprehensive list of species considered seriously invasive in all types of natural areas (grasslands, forests, savannas, alpine and wetlands); ²Global Invasive Species Database (2005): global in scope; a searchable database of invasive alien species "that most threaten native biodiversity...in all ecosystems types". We confined our search to plant species that invade uplands, including "coastlands, riparian zones, disturbed areas, planted forests, natural forests, scrub/shrublands, and range/grasslands"; ³Randall and Marinelli (1996): a list of the 80 worst invasive plants of horticultural origin in the US; ⁴Mehrhoff *et al.* (2006): a comprehensive list of invasive or potentially invasive exotics in New England. We did not include any species from this list that exclusively invade wetland and aquatic habitats. ⁵Miller (2003): lists the non-native plants invading US southern forests "at an alarming rate".

seedlings of Norway maple, a highly shade-tolerant exotic tree species, appear to remain as a "seedling bank", suppressed for decades in deep shade until light levels increase (Martin and Marks 2006). Another exotic tree species, tree of heaven (*Ailanthus altissima*), appears to represent an exception to this rule. While not considered shade tolerant in any traditional sense, the rapid height growth rates of its saplings under the relatively low light levels of even single-tree gaps may allow individuals to reach the canopy before the canopy recloses as a result of lateral crown expansion (Knapp and Canham 2000).



Figure 3. Exotic shrubs are invading forest understories throughout the eastern US. Here, the understory of a sugar maple stand is dominated by the exotic shrub, burning bush (*Euonymus alata*). Introduced to the US from Asia in the 1860s, burning bush is widely planted for its bright red autumn foliage. It tolerates very deep shade and spreads rapidly by root suckers and bird-dispersed seeds.

However, even in the case of a species as remarkable for its potential invasiveness as the tree of heaven, the rate of invasion will generally appear slow, and controlled by the rate of canopy tree turnover.

Forest understories will be more prone to invasion than forest canopies, as most do not appear saturated in terms of either biomass or species diversity (see Gilbert and Lechowicz 2005). This is particularly true in forests of the northeastern US, where agricultural land-use histories have depleted understories of native species of shrubs and herbs (Flynn and Vellend 2005). Furthermore, the larger pool of shade-tolerant invasive herbs (eg Japanese knotweed, *Polygonum cuspidatum*; Figure 4) and shrub species (Table 1) and their comparatively short life cycles suggest that invasions of forest understories may be more common and rapid. Invasions of unsaturated understories may also be primarily limited in the short term by the dispersal ability of exotic species and in the long term by inherent limitations on growth rates in low-light environments. Where forest understories are unsaturated, however, invasion by a non-native herb or shrub may not decrease the absolute abundance of native occupants of the understory.

Several life-history trade-offs may slow the spread of forest invasives. In general, there is a positive relationship between shade tolerance and large-seeded species of all life-forms (Hewitt 1998). While large seeds may confer shade tolerance to propagules, large-seeded species tend to have highly localized dispersal (Ribbens *et al.* 1994). Conversely, there is a strongly negative relationship between seed size and fecundity (Henary and Westoby

2001). If applicable to most shade-tolerant exotics, these trade-offs suggest that many forest invasions will be limited by dispersal. Species with faunal dispersal vectors – which are much more common in tropical forests for both native and exotic woody species (Rejmánek 1996) – will not necessarily be held to these patterns, and such trade-offs are not absolute; for example, some gymnosperms are both small seeded and shade tolerant (eg *Tsuga canadensis*).

As is the case with successful invaders in high-light environments, many successful shade-tolerant invaders have demographic rates that are high compared to native shade-tolerant competitors (Martin and Marks 2006), possibly resulting from a wide range of mechanisms that include release from natural enemies (Mitchell and Power 2003), and allelopathy and novel weapons (Callaway and Ridenour 2004). Such mechanisms may also make some species typically considered light demanding in their native range shade tolerant in their introduced range. For example, DeWalt *et al.* (2004) report

that herbivores and fungal pathogens eliminate the shrub *Clidemia hirta* from shaded habitats in its native range, but a lack of enemy pressure in its introduced range allows it to invade shady forest understories. Shade tolerance is also a relative trait – introduced species may have a greater effective shade tolerance in forests that have few native shade-tolerant species, which may be the case on tropical islands, where invasions of intact forests are much more common (Rejmánek 1996).

Patterns of forest invasions will potentially be influenced by the species richness of the native community, as theory predicts that species-rich communities should be more resistant to invasion (Levine and D'Antonio 1999). While a few studies support this theory (Tilman 1997), a host of recent studies report a positive relationship between native and exotic diversity at both fine and coarse scales (Lonsdale 1999; Stohlgren *et al.* 1999; Gilbert and Lechowicz 2005). This positive relationship has been attributed to an indirect relationship between diversity and resource availability (Levine and D'Antonio 1999; Stohlgren *et al.* 1999). Indeed, evidence of positive associations between exotic plant richness and abundance with measures of soil fertility, particularly soil pH, continues to increase (Howard *et al.* 2004; Gilbert and Lechowicz 2005; Martin and Marks 2005). In forests, environmental conditions associated with higher native diversity – usually mesic and fertile soils (Peet *et al.* 2003) – are also correlated with increased invasion by shade-tolerant exotics (Howard *et al.* 2004). These patterns may also reflect the influence of intentional introductions that have favored mesophytic species, many of which originated from a European flora

rich in species adapted to base-rich or limestone-derived soils (Peet *et al.* 2003).

While invasion of forests by shade-tolerant exotics may be a slower process than the establishment of exotic species in disturbed or open ecosystems, the long-term effects are likely to be just as pervasive. For instance, a study in Puerto Rico found that the abundance of shade-intolerant invasives, such as the African tulip tree (*Spathodea campanulata*) and guava (*Psidium guajava*), declined rapidly 40 years after land abandonment, while the shade-tolerant rose apple (*Syzygium jambos*) persisted or increased in abundance (Lugo 2004). Shade-tolerant exotic species are also the most likely to invade protected natural areas (Howard *et al.* 2004; Gilbert and Lechowicz 2005). A few studies of shade-tolerant exotics indicate that they can have strong impacts on native understory diversity and structure. These include *Acer platanoides* (Martin 1999), *Lonicera tatarica* (Woods 1993), and *Miconia calvescens* (Meyer and Florence 1996). Unlike the vast majority of invaders that never reach high abundance or exert large impacts (Williamson and Fitter 1996), these shade-tolerant invasives are more likely to be problematic because they persist or increase during succession. The same traits that make native, late successional species dominant – competitive ability, longevity, and casting deep shade (Canham *et al.* 1994) – confer on shade-tolerant invasives the ability to profoundly impact native communities.

■ Conclusions

Resistance to invasion is fundamentally a quantitative, not a categorical, property of a community (Levine *et al.* 2004). Measured in absolute terms and relative to human time scales, rates of invasion by shade-tolerant, exotic species in forests may indeed be slower than for the more widely studied early successional and disturbance-dependent species that invade grassland, savanna, and desert ecosystems, but the appearance of forest resistance to invasion seems to be largely a function of long turnover times for canopy tree species. Our assessment of shade-tolerant exotics suggests that they are not less invasive, but that the pool of such invaders is relatively small because most invasive woody species, in particular, were deliberately introduced and chosen purposefully for their early successional life-history traits. Of the shade-tolerant exotic species introduced into forested regions, however, a surprisingly high percentage become invasive. The slower absolute rate of invasion by these species may have lulled us into ignoring their potentially severe and long-term impacts on forest ecosystems worldwide.



Figure 4. The exotic herbaceous perennial, Japanese knotweed (*Polygonum cuspidatum*). In its introduced range in Europe and the US, it spreads exclusively by vegetative reproduction, aggressively invading both sunny and shady habitats.

■ Acknowledgements

This work was supported by a grant from the USDA Biology of Weedy and Invasive Plants Program (2003-35320-13583). This paper is a contribution to the program of the Institute of Ecosystem Studies.

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WebTable 1. Compilation of documented shade-tolerant exotic plant invaders

Scientific name	Life form	Geography	Source
<i>Aegopodium podagraria</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Ajuga reptans</i>	Herb	Temperate	Society for Ecological Restoration, Ontario Chapter, Canada (2002)
<i>Alliaria petiolata</i>	Herb	Temperate	Nuzzo (1999)
<i>Asparagus densiflorus</i>	Herb	Tropical/temperate	Global Invasive Species Database (2005)
<i>Asparagus scandens</i>	Herb	Tropical/temperate	Global Invasive Species Database (2005)
<i>Blechnum occidentale</i>	Herb	Temperate	Rejmánek (1996)
<i>Cardamine impatiens</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Dieffenbachia sequine</i>	Herb	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Duchesnea indica</i>	Herb	Temperate	TNC Global Invasive Species Initiative (2006)
<i>Epipactis helleborine</i>	Herb	Temperate	Gilbert and Lechowicz (2005)
<i>Polygonum cuspidatum</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Geranium robertianum</i>	Herb	Temperate	Seattle Urban Nature Project (2006)
<i>Glechoma hederacea</i>	Herb	Temperate	DCR (2003)
<i>Hedychium flavescens</i>	Herb	Tropical	Global Invasive Species Database (2005)
<i>Hedychium gardnerianum</i>	Herb	Tropical	Global Invasive Species Database (2005)
<i>Hemigraphis alternata</i>	Herb	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Heracleum mantegazzianum</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Hesperis matronalis</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Hieracium lepidulum</i>	Herb	Temperate	Wiser et al. (1998)
<i>Impatiens glandulifera</i>	Herb	Temperate	Society for Ecological Restoration, Ontario Chapter, Canada (2002)
<i>Lamium amplexicaule</i>	Herb	Temperate	Southeast Exotic Pest Plant Council (2003)
<i>Lamium purpureum</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Lysimachia nummularia</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Mentha spicata</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Myosotis scorpioides</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Polygonum caespitosum</i>	Herb	Temperate	Mehrhoff et al. (2006)
<i>Pteris cretica</i>	Herb	Tropical	Rejmánek (1996)
<i>Ranunculus ficaria</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Ranunculus repens</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Sedum telephium</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Sphagneticola trilobata</i>	Herb	Tropical	Global Invasive Species Database (2005)
<i>Tradescantia fluminensis</i>	Herb	Tropical/temperate	Global Invasive Species Database (2005)
<i>Tradescantia spathacea</i>	Herb	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Tradescantia zebrina</i>	Herb	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Tussilago farfara</i>	Herb	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Urtica dioica</i> ssp <i>dioica</i>	Herb	Temperate	Society for Ecological Restoration, Ontario Chapter, Canada (2002)
<i>Vinca major</i>	Herb	Temperate	Miller (2003)
<i>Vinca minor</i>	Herb	Temperate	Miller (2003)
<i>Arthraxon hispidus</i>	Herb (grass)	Temperate	DCR (2003)
<i>Ehrharta stipoides</i>	Herb (grass)	Tropical	Denslow et al. (2006)
<i>Imperata cylindrica</i>	Herb (grass)	Tropical/temperate	Global Invasive Species Database (2005)
<i>Microstegium vimineum</i>	Herb (grass)	Temperate	Leicht et al. (2005)
<i>Neyraudia reynaudiana</i>	Herb (grass)	Tropical	Global Invasive Species Database (2005)
<i>Oplismenus compositus</i>	Herb (grass)	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Oplismenus hirtellus</i>	Herb (grass)	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Olyra latifolia</i>	Herb (grass)	Tropical	Rejmánek (1996)
<i>Panicum maximum</i>	Herb (grass)	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Paspalum conjugatum</i>	Herb (grass)	Tropical	Rejmánek (1996)
<i>Ardisia crenata</i>	Shrub	Tropical	Rejmánek (1996)
<i>Berberis darwinii</i>	Shrub	Temperate	McAlpine and Jesson (2007)
<i>Berberis thunbergii</i>	Shrub	Temperate	Silander and Klepeis (1999)
<i>Berberis vulgaris</i>	Shrub	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Clerodendrum chinense</i>	Shrub	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Clidemia hirta</i>	Shrub	Tropical	DeWalt et al. (2004)
<i>Cotoneaster franchetti</i>	Shrub	Temperate	US National Park Service (2006)
<i>Cotoneaster pannosa</i>	Shrub	Temperate	US National Park Service (2006)

(Continued)

WebTable 1. Compilation of documented shade-tolerant exotic plant invaders – *Continued*

Scientific name	Life form	Geography	Source
<i>Elaeagnus pungens</i>	Shrub	Temperate	Miller (2003)
<i>Elaeagnus umbellata</i>	Shrub	Temperate	Edgin and Ebinger (2001)
<i>Eugenia uniflora</i>	Shrub	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Euonymus alata</i>	Shrub	Temperate	Randall and Marinelli (1996)
<i>Euonymus atropurpureus</i>	Shrub	Temperate	Howard <i>et al.</i> (2004)
<i>Fuchsia arborescens</i>	Shrub	Tropical	Rejmánek (1996)
<i>Lespedeza bicolor</i>	Shrub	Temperate	Southeast Exotic Pest Plant Council (2003)
<i>Ligustrum amurense</i>	Shrub	Temperate	TNC Global Invasive Species Initiative (2006)
<i>Ligustrum japonicum</i>	Shrub	Temperate	Southeast Exotic Pest Plant Council (2003)
<i>Ligustrum lucidum</i>	Shrub	Tropical/temperate	Aragon and Groom (2003)
<i>Ligustrum obtusifolium</i>	Shrub	Temperate	TNC Global Invasive Species Initiative (2006)
<i>Ligustrum ovalifolium</i>	Shrub	Tropical	TNC Global Invasive Species Initiative (2006)
<i>Ligustrum robustum</i>	Shrub	Tropical	Global Invasive Species Database (2005)
<i>Ligustrum sinense</i>	Shrub	Temperate	Global Invasive Species Database (2005)
<i>Ligustrum vulgare</i>	Shrub	Temperate	TNC Global Invasive Species Initiative (2006)
<i>Lonicera maackii</i>	Shrub	Temperate	Mehrhoff <i>et al.</i> (2006)
<i>Lonicera morrowii</i>	Shrub	Temperate	Mehrhoff <i>et al.</i> (2006)
<i>Lonicera standishii</i>	Shrub	Temperate	DCR (2003)
<i>Lonicera tatarica</i>	Shrub	Temperate	Woods (1993)
<i>Lonicera xylosteum</i>	Shrub	Temperate	Mehrhoff <i>et al.</i> (2006)
<i>Melastoma candidum</i>	Shrub	Tropical	Rejmánek (1996)
<i>Nandina domestica</i>	Shrub	Temperate	Miller (2003)
<i>Odontonema tubaeforme</i>	Shrub	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Ossaea marginata</i>	Shrub	Tropical	Rejmánek (1996)
<i>Rhamnus cathartica</i>	Shrub	Temperate	Randall and Marinelli (1996)
<i>Rhamnus frangula</i>	Shrub	Temperate	Randall and Marinelli (1996)
<i>Rhododendron ponticum</i>	Shrub	Temperate	Niinemets <i>et al.</i> (2003)
<i>Rubus phoenicolasius</i>	Shrub	Temperate	DCR (2003)
<i>Rubus rosifolius</i>	Shrub	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Spiraea japonica</i>	Shrub	Temperate	DCR (2003)
<i>Wikstroemia indica</i>	Shrub	Tropical	Rejmánek (1996)
<i>Acer ginnala</i>	Tree	Temperate	Mehrhoff <i>et al.</i> (2006)
<i>Acer platanoides</i>	Tree	Temperate	Webb <i>et al.</i> 1993; Martin (1999)
<i>Acer pseudoplatanus</i>	Tree	Temperate	Mehrhoff <i>et al.</i> (2006)
<i>Adenantha pavonia</i>	Tree	Tropical	Green <i>et al.</i> (2004)
<i>Ardisia elliptica</i>	Tree	Tropical	Global Invasive Species Database (2005)
<i>Bischofia javanica</i>	Tree	Tropical	Yamashita <i>et al.</i> (2003)
<i>Castilla elastica</i>	Tree	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Chrysophyllum cainito</i>	Tree	Tropical	Rejmánek (1996)
<i>Cinnamomum verum</i>	Tree	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Clausena excavata</i>	Tree	Tropical	Green <i>et al.</i> (2004)
<i>Cupaniopsis anacardioides</i>	Tree	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Cyathea cooperi</i>	Tree	Tropical	Rejmánek (1996)
<i>Ilex aquifolium</i>	Tree	Temperate	Gray (2005)
<i>Litsea glutinosa</i>	Tree	Tropical	Rejmánek 1996
<i>Miconia calvescens</i>	Tree	Tropical	Meyer and Florence (1996)
<i>Pentadesma butyracea</i>	Tree	Tropical	Kueffer <i>et al.</i> (2007)
<i>Phellodendron amurense</i>	Tree	Temperate	Massachusetts Invasive Plant Advisory Group (2005)
<i>Pittosporum undulatum</i>	Tree	Tropical/temperate	Rose and Fairweather (1997)
<i>Prunus laurocerasus</i>	Tree	Temperate	Seattle Urban Nature Project (2006)
<i>Prunus serotina</i>	Tree	Temperate	Closset-Kopp <i>et al.</i> (2007)
<i>Psidium cattleianum</i>	Tree	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Sapium sebiferum</i>	Tree	Temperate	Bruce <i>et al.</i> (1997)
<i>Schefflera actinophylla</i>	Tree	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Schinus terebinthifolius</i>	Tree	Tropical	Global Invasive Species Database (2005)
<i>Sorbus aucuparia</i>	Tree	Temperate	Society for Ecological Restoration, Ontario Chapter, Canada (2002)

(Continued)

WebTable 1. Compilation of documented shade-tolerant exotic plant invaders – Continued

Scientific name	Life form	Geography	Source
<i>Sphaeropteris cooperi</i>	Tree	Tropical	Durand and Goldstein (2001)
<i>Syzygium jambos</i>	Tree	Tropical	Martin <i>et al.</i> (2004)
<i>Syzygium malaccensis</i>	Tree	Tropical	Rejmánek (1996)
<i>Waterhousea floribunda</i>	Tree	Tropical	Global Invasive Species Database (2005)
<i>Cynanchum nigrum</i>	Vine (herbaceous)	Temperate	Society for Ecological Restoration, Ontario Chapter, Canada (2002)
<i>Cynanchum rossicum</i>	Vine (herbaceous)	Temperate	Society for Ecological Restoration, Ontario Chapter, Canada (2002)
<i>Dioscorea alata</i>	Vine (herbaceous)	Tropical	Rejmánek (1996)
<i>Dioscorea bulbifera</i>	Vine (herbaceous)	Tropical	Horvitz and Koop (2001)
<i>Dioscorea oppositifolia</i>	Vine (herbaceous)	Tropical/temperate	Global Invasive Species Database (2005)
<i>Dioscorea sansibarensis</i>	Vine (herbaceous)	Tropical	Rejmánek (1996)
<i>Humulus japonicus</i>	Vine (herbaceous)	Temperate	DCR (2002)
<i>Mikania micrantha</i>	Vine (herbaceous)	Tropical	Global Invasive Species Database (2005)
<i>Solanum dulcamara</i>	Vine (herbaceous)	Temperate	Hunter and Mattice (2002)
<i>Syngonium angustatum</i>	Vine (herbaceous)	Tropical	Institute of Pacific Islands Forestry (2006)
<i>Akebia quinata</i>	Vine (woody)	Temperate	Global Invasive Species Database (2005)
<i>Ampelopsis brevipedunculata</i>	Vine (woody)	Temperate	Mehrhoff <i>et al.</i> (2006)
<i>Celastrus orbiculatus</i>	Vine (woody)	Temperate	Greenberg <i>et al.</i> (2001)
<i>Euonymus fortunei</i>	Vine (woody)	Temperate	Global Invasive Species Database (2005)
<i>Hedera helix</i>	Vine (woody)	Temperate	Gray (2005)
<i>Jasminum dichotomum</i>	Vine (woody)	Tropical	Horvitz and Koop (2001)
<i>Jasminum fluminense</i>	Vine (woody)	Tropical	Horvitz and Koop (2001)
<i>Lonicera japonica</i>	Vine (woody)	Temperate	Mehrhoff <i>et al.</i> (2006)
<i>Lygodium japonicum</i>	Vine (woody)	Temperate	Global Invasive Species Database (2005)
<i>Lygodium microphyllum</i>	Vine (woody)	Tropical/temperate	Global Invasive Species Database (2005)
<i>Thunbergia grandiflora</i>	Vine (woody)	Tropical	Rejmánek (1996)
<i>Wisteria floribunda</i>	Vine (woody)	Temperate	Global Invasive Species Database (2005)
<i>Wisteria sinensis</i>	Vine (woody)	Temperate	Global Invasive Species Database (2005)

Notes: Species in this list were compiled from peer-reviewed and online publications by searching keywords in Web of Science and Google, and references in these publications. Keywords included combinations of: shade tolerant, shade tolerance, invasive, invader, and invasion. Only exotic invasives explicitly considered tolerant of “full” or “deep” shade are listed. While the degree of invasiveness varies in these species, a species was listed if at least one source considered it invasive. Many of these species can also be invasive in disturbed and open areas, and some are not highly shade tolerant in their native range. Nomenclature and life-form listed are from the cited source. Full citations for sources are listed below.

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WebTable 1. Compilation of documented shade-tolerant exotic plant invaders – Continued

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