

Mechanisms Underlying Nonindigenous Plant Impacts: A Review of Recent Experimental Research

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Nonindigenous plant species (NIS) can affect individuals, communities, and ecosystems through numerous direct and indirect mechanisms. To synthesize the current understanding of how NIS cause impacts, we reviewed experimental research from the past decade. We found alteration of the microenvironment, such as incident light and air and soil temperature, was much more often a mechanism underlying NIS impacts than competition for soil water and nutrients. NIS litter frequently caused the alteration of microenvironments, and litter effects were often of greater consequence than the effects of live NIS plants. Results supported altered soil microbial communities and mycorrhizal associations as mechanisms underlying NIS impacts on native plant growth, community structure, and nutrient cycling. Impacts often could not be attributed to a single mechanism, highlighting the need for multi-factor studies that identify and distinguish between multiple, concurrently operating mechanisms. Overall, our synthesis indicates that effective management will require attention to legacy effects of NIS, that removing live NIS may not ameliorate impacts, and that removal of dead NIS biomass may be necessary for native species' survival. Furthermore, rehabilitating soil microbial and mycorrhizal communities may be crucial for successful post-NIS management revegetation.

Key words: Competition; ecological impacts; exotic plants; invasive plant species; synthesis.

Nonindigenous plant species (NIS) establishment has led to undesirable ecological changes worldwide. Recent reviews and meta-analyses have found several general trends in NIS impacts: invasions typically reduce the fitness and growth of native plant species, reduce the fitness and abundance of animal species, and alter plant community structure by decreasing plant species' abundance and diversity (Pyšek et al. 2012; Vilà et al. 2011). Additionally, NIS tend to increase aboveground net primary production, above- and belowground carbon (C) and nitrogen (N) pools, soil C, soil N, and rates of litter decomposition, N mineralization, and nitrification (Ehrenfeld 2010; Liao et al. 2008). Responding to NIS impacts is motivated by the desire to restore and maintain native populations, quality habitat, and functional ecosystems. Critical to these efforts, as well as to predicting the response of communities to future invasions, is an understanding of the mechanisms,

or processes, underlying NIS impacts (Levine et al. 2003; Seabloom et al. 2003).

The most common mechanism by which NIS are thought to cause impacts is competition for resources, such as water, nutrients, and light (Levine et al. 2003). Differences in morphological, chemical, and physiological traits between native species and NIS can lead to changes in ecosystem properties or processes, such as water availability, nutrient cycling, and litter decomposition (Ehrenfeld 2010). NIS can affect native plant populations by altering pollinator activity and disrupting pollinator networks (Levine et al. 2003; Traveset and Richardson 2006). Other potential mechanisms of NIS impacts include allelopathy, whereby NIS release secondary chemical compounds that are detrimental to neighboring plants and soil microbial communities, and chemical alteration of the soil through salt accumulation (Hierro and Callaway 2003). Additionally, NIS can affect the individual fitness and population dynamics of other organisms by increasing predation, herbivory, or disease, an effect known as "apparent competition" (White et al. 2006), as well as by modifying the microenvironment (e.g., moisture, temperature, light, space) (Crooks 2002; Strayer et al. 2006).

Nonindigenous plant impacts, and the potential mechanisms underlying these impacts, have been the focus of a

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Management Implications

The primary objective of most nonindigenous plant species (NIS) management is to reduce or eradicate live NIS plants using herbicides and manual removal. While this often is a sensible approach, it does not always achieve the desired outcome of reestablishing native plant cover. Through a review of experimental NIS impact studies, we found that consideration of the mechanisms, or ways, by which NIS cause impacts, may improve general approaches to NIS management. It is often assumed that the primary way NIS impact native plants is by robbing them of necessary resources, such as water and nutrients. However, the experimental research we reviewed shows that this often is not the underlying cause and that NIS impacts are more often traced to alterations of microenvironments, belowground communities, and plant-pollinator interactions. Additionally, many NIS impacts are attributable to NIS litter rather than live plants. Reducing NIS impacts and reestablishing native plant cover may be more successful if some resources typically spent on direct NIS treatment (i.e. spraying, pulling) are diverted to removal of NIS litter and applying mycorrhizal and microbial inoculations to improve or rebuild belowground communities. These communities are thought to be an important component of revegetation success. Another alternative management approach based on impact mechanisms is NIS flower removal, particularly when whole plant removal or chemical treatment is not feasible. Removing NIS flowers prevents native plant-pollinator interactions from being altered, increasing the chances of successful native plant reproduction. NIS flower removal has the additional benefit of eliminating NIS seed production, thereby lowering or stabilizing population growth rate. Our synthesis shows that fine-tuning management to address the mechanisms underlying NIS impacts will likely improve NIS control and increase the success of native revegetation.

substantial body of research. However, previous reviews have found that mechanism studies, and NIS impact studies more generally, are often observational or anecdotal, leaving considerable uncertainty about cause-and-effect relationships between NIS invasion and ecological impacts (Didham et al. 2005; Levine et al. 2003). This lack of experimental evidence is considered a critical shortcoming of invasion ecology research and has led to appeals for more experimental work (Byers et al. 2002; Didham et al. 2005; Ehrenfeld 2003). Our objective was to assess the current understanding of mechanisms underlying NIS impacts based on studies that experimentally tested potential mechanisms. We compare our findings with those of Levine et al. (2003), identifying areas that have advanced and areas where more research is needed.

In this review, we synthesize experimental findings for the impact mechanisms that have been examined. Although many studies tested for multiple potential mechanisms, other mechanisms may play a role in NIS impacts but have yet to be studied. Additionally, few experimental studies assess whether and to what degree NIS impacts and impact mechanisms vary as a function of other factors, such as NIS abundance, habitat type, and natural or anthropogenic

disturbance. Thus, we are presenting the current state of knowledge of an ever advancing field of research. As with any review, we can only include published studies, which may bias conclusions toward significant results since these are more likely to be published. Furthermore, some mechanisms have been examined to a greater extent than others so their relative importance may change as more research becomes available (Hulme et al. 2013). While the number of studies examining mechanisms of NIS impacts has increased over the past decade, it is still only a small proportion of the total number of impact studies. Consequently, there is not yet a large enough body of research to conduct a robust meta-analysis. Nevertheless, we see value in synthesizing the existing data, examining what has been learned during the past decade, and highlighting priority areas for future research. Awareness of the mechanisms underlying NIS impacts can improve our understanding of the variability of impacts and improve NIS management strategies.

Methods

We searched for NIS impacts research published in English on the ISI Web of Knowledge (<http://www.webofknowledge.com/>) database using the following search term combinations: (alien OR exotic OR introduced OR invas* OR non-indigenous OR non-native OR NIS) AND (alter OR effect OR impact OR influence) AND (forb OR grass OR plant* OR shrub OR tree). To establish a more comprehensive search, we also examined references within the publications located through the electronic search. We focused on studies published from 2001 onwards to assess advances made since the mechanisms review by Levine et al. (2003).

Each publication was examined for potential inclusion in this review. Our primary selection criterion was that an experimental approach was used to explicitly test a potential mechanism (or mechanisms) underlying NIS impacts. A prerequisite to this was that the study tested for the occurrence and statistical significance of some type of NIS impact (or impacts), such as a change in native plant abundance or plant community richness. We focused solely on terrestrial NIS, but we put no restrictions on species or growth forms, impact metrics, study locations, or ecosystem types. We included studies that examined impacts of multiple NIS species, as well as those that assessed impacts on multiple response variables (e.g., abundance and richness), multiple target species, or both. We included allelopathic studies if impacts of the whole NIS plant were examined, reflecting in-situ conditions. Our focus was the findings of experimental studies (e.g., species removals, additions) that examined potential mechanisms underlying NIS impacts; therefore, we did not include observational site comparisons (invaded vs. uninvaded sites), theoretical studies, or purely modeling-based studies.

Results and Discussion

Of the 131 experimental NIS impact studies published between 2001 and April 2013 that fit our criteria, we identified 68 (52%) that explicitly tested mechanisms of NIS impacts (Supplemental Data 1). From the larger pool of 512 NIS impact studies generated by our initial search, 70% were observational site comparisons—essentially the same percentage as with impact studies published prior to 2001 (Levine et al. 2003). Thus, despite a marked increase in the total number of impact studies conducted annually (Hulme et al. 2013), the proportion of experimental studies remains relatively low.

From our pool of 68 studies, NIS impacts on individual plant species were examined in 52 and were typically quantified by changes in native plant germination, growth, reproduction, and survival. Impacts on community structure, such as abundance, richness, diversity, and composition, were examined in 16 studies—11 focused on plant communities, four on arthropod communities, and one on soil microbial communities. Potential mechanisms underlying impacts on ecosystem properties and processes such as nutrient concentrations, N mineralization, and soil temperature were examined in seven studies.

Among the 68 reviewed studies, 50 NIS were examined, 18 of which were in multiple studies (Table 1, Supplemental Data 2). Only four N-fixing species were studied and only three in relation to impacts on soil nutrient cycling and availability, indicating there has not been a disproportionate focus on N-fixing NIS species, as was the case in earlier mechanisms research (Levine et al. 2003). We identified 13 mechanisms of impact, none of which are mutually exclusive (Table 1). Thirty-one studies (46%) examined multiple potential mechanisms of NIS impacts. In the following sections, we consider each mechanism and the impacts with which they were associated, and synthesize the experimental findings.

Altered Plant–Pollinator Interactions. During the past decade, alteration of native plant–pollinator interactions was the most frequently investigated mechanism of NIS impacts, examined in 21 experimental studies (Table 1, Supplemental Data 1). This is a major increase in focus in recent years. From over 150 NIS impact studies conducted between 1969 and 2001, only three examined changes to plant–pollinator relationships (Levine et al. 2003). There are two potential pathways of impact associated with altered plant–pollinator interactions. First, pollinator visits to native plants can be reduced if NIS are more attractive or rewarding than native plants (pollinator siphoning) (Ratchke 1983). Second, successful pollination of native flowers can be reduced if NIS presence leads to the transfer of less conspecific pollen or more heterospecific pollen to native plant stigmas (reproductive interference) (Waser and

Fugate 1986). Reduced native seed set, reduced native plant population growth, and changes in native plant genetic structure are potential consequences of these altered plant–pollinator relationships (Bjerknes et al. 2007; Traveset and Richardson 2006).

Results of studies examining altered plant–pollinator interactions as a mechanism of NIS impacts varied widely, reflecting the variability that has been observed of NIS impacts more generally (Vilà et al. 2011). Of the 14 studies that examined the effect of NIS on pollinator visitation to native plants, visits decreased in seven, increased in three, and had no effect in the remaining four (Table 1). Reduced pollinator visits led to significant reductions in native plant seed set in all seven cases. Thus, NIS reduced native plant reproduction through pollinator siphoning 50% of the time. Of the eight studies that examined reproductive interference (i.e., decreased conspecific or increased heterospecific pollen, or both) as a mechanism of NIS impacts, six found that manual application of NIS pollen to native flowers caused a significant reduction in native seed set (Table 1). However, five studies found that the quantity of NIS pollen required for interference was not found on native flowers under typical field conditions, concluding that a significant impact on native plant reproduction in these invaded populations was unlikely (i.e., natives were not pollen-limited).

In some cases, NIS can act as “magnet” species, attracting more pollinators to an area, which can increase pollinator visits to native plants (Bjerknes et al. 2007). The effect this has on native seed production is context-dependent. For example, Nielsen et al. (2008) found significantly more pollinator visits to the native seep monkeyflower (*Mimulus guttatus* DC.) when planted in stands of invasive perennial giant hogweed (*Heracleum mantegazzianum* Sommier & Levier); however, this had no effect on *M. guttatus* seed set. Conversely, the nonindigenous perennial forb purple loosestrife (*Lythrum salicaria* L.) caused an increase in pollinator visits to the coflowering native Allegheny monkeyflower (*Mimulus ringens* L.), but *M. ringens* seed set was significantly reduced (Flanagan et al. 2010). This indicates *L. salicaria* affected native reproduction by decreasing conspecific or increasing heterospecific pollen deposition (or both) on native flowers (reproductive interference). Nielsen et al. (2008) suggest that the presence of *H. mantegazzianum* may counteract the general decline of pollinator populations, particularly in abandoned grasslands, but more needs to be known about which species were increasing (e.g., generalists vs. specialists), and whether other pollinator populations were affected by these increases, to determine whether this is an ecologically desirable outcome.

The outcomes of plant–pollinator interaction studies varied widely sometimes even among studies examining the same NIS. For example, three studies examined impacts of

Table 1. Mechanisms of nonindigenous plant species (NIS) impacts and results of experimental studies (2001–April 2013). Mechanisms are not mutually exclusive; many studies examined multiple potential mechanisms. Scientific species names with taxonomic authorities and common names are provided in Supplemental Data 2.

NIS ^a species, life form, and study reference numbers (Supplemental Data 1)	NIS impact type	Mechanism and count of studies (no.) that examined this mechanism				
		Plant–pollinator interactions		Microenvironment		
		Pollinator visits (14)	Reproductive Interference ^b (8)	Light availability (16)	Litter (9)	Air or soil temperature (4)
% of studies with significant support for mechanism		50	75 ^d	81	100	75
Grasses						
Annual						
<i>Avena barbata</i> , <i>Bromus diandrus</i> , <i>Bromus hordeaceus</i> (36)	I-P				1 ^e	
<i>Bromus madritensis</i> subsp. <i>rubens</i> (16)	I-P					
<i>A. barbata</i> , <i>Brachypodium distachyon</i> , <i>B. madritensis</i> subsp. <i>rubens</i> (67)	I-P, C-A				1	
<i>A. barbata</i> , <i>B. diandrus</i> , <i>B. hordeaceus</i> , <i>B. madritensis</i> (12)	C-P				1	
<i>A. barbata</i> , <i>B. hordeaceus</i> (24)	EPP					
<i>Microstegium vimineum</i> (3)	I-P					
<i>M. vimineum</i> (18, 57)	C-A, C-P			0		
<i>M. vimineum</i> (31)	EPP					
Perennial						
<i>Agropyron cristatum</i> , <i>Bromus inermis</i> , <i>Euphorbia esula</i> (28)	I-P					
<i>Ammophila arenaria</i> (14)	I-P					
<i>Andropogon virginicus</i> , <i>Melinis minutiflora</i> , <i>Schizachyrium condensatum</i> (39)	EPP				1	1
<i>B. inermis</i> , <i>Phleum pratense</i> , <i>Poa pratensis</i> (15)	I-P			0		
<i>Dactylis glomerata</i> , <i>P. pratensis</i> (38)	C-P			1		
<i>Holcus lanatus</i> (4)	I-P					
<i>Phragmites australis</i> (44)	I-P			1	1	
<i>Typha</i> × <i>glauca</i> (34)	I-P, C-P			1	1	
<i>T. × glauca</i> (20)	C-P, EPP			1	1	
Forbs						
Annual						
<i>Alliaria petiolata</i> (10, 32, 33, 60, 66)	I-P					
<i>A. petiolata</i> (59)	C-P			1		1
<i>Brassica nigra</i> (52)	I-P					
<i>Cakile maritima</i> , <i>Carpobrotus</i> spp. (1)	I-P	0				
<i>Impatiens glandulifera</i> (2, 9, 37)	I-P	0, 1(–)				
<i>Phacelia tanacetifolia</i> (62)	I-P	0(–)				
Annual/perennial						
<i>Centaurea diffusa</i> (61)	I-P					
<i>Medicago polymorpha</i> ^N (35)	I-P					
<i>Melilotus officinalis</i> ^N (58)	I-P			1		
<i>M. officinalis</i> ^N (19)	C-P			1		
Perennial						
<i>Carduus nutans</i> (7)	I-P	0				
<i>Centaurea stoebe</i> (8, 54)	I-P					
<i>E. esula</i> (45)	I-P		1 ^d			

Table 1. Extended.

Mechanism and count of studies (no.) that examined this mechanism							
Resource competition		Belowground communities					
Nutrient availability (12)	Soil water (10)	Soil microbes (7 ^c)	Mycorrhizal associations (5)	Allelopathy (11)	Apparent competition (6)	Nutrient cycle (2)	Other mechanisms (11)
17	40	71	80	82	83	50	91
							1
	0						
	1						
	0						1
0		1					
		0					
		1					
		1					
					1		
0	1						
0	0						
			1				1
0							
		1	1	1,1,1,1			1,1,0
	0						
					1		
0							
					1		1
0	1						
					1, 1		

Table 1. Continued.

NIS ^a species, life form, and study reference numbers (Supplemental Data 1)	NIS impact type	Mechanism and count of studies (no.) that examined this mechanism				
		Plant–pollinator interactions		Microenvironment		
		Pollinator visits (14)	Reproductive Interference ^b (8)	Light availability (16)	Litter (9)	Air or soil temperature (4)
<i>Heracleum mantegazzianum</i> (50)	I-P	0 (+)	1 ^d			
<i>Ipomoea hildebrandtii</i> (50)	C-P, EPP					
<i>Lythrum salicaria</i> (6, 13, 21, 23)	I-P	1(–), 1(+) ^f	1 ^{d,g}	1		
<i>L. salicaria</i> (25)	C-P			0		
<i>Psidium cattleianum</i> (29)	I-P	0				
<i>Ranunculus ficaria</i> (11)	I-P					
<i>Solanum elaeagnifolium</i> (63, 64)	I-P	1(–)	1 ^c			
<i>Solidago gigantea</i> (55)	C-M					
<i>Tamarix</i> sp. (43)	I-P					
<i>Taraxacum officinale</i> (30, 40, 47, 51)	I-P	1(–), 1(–)	1, 0			
Vines						
<i>Hedera helix</i> (5)	I-P					
Shrubs						
<i>Berberis thunbergii</i> (31)	EPP					
<i>Carpobrotus</i> spp. (27, 46)	I-P		1, ^d 0			
<i>Cytisus scoparius</i> ^N (56)	I-P, EPP					
<i>Lonicera maackii</i> (10, 41, 42)	I-P	1(–)		1		
<i>Polygonum × bohemicum</i> (48, 65)	I-P			1		
Trees						
<i>Acacia saligna</i> (68)	C-P, EPP				1	0
<i>Ailanthus altissima</i> (22)	I-P					
<i>Cinchona pubescens</i> (26 ^g)	C-P			1		1
<i>Pinus contorta</i> , <i>Pseudotsuga menziesii</i> (17)	I-P, C-A			1	1	
<i>Pinus nigra</i> (53)	C-A			1		

^a Abbreviations: NIS, nonindigenous plant species; I-P, individual plant species; C-P, plant community; C-A, arthropod community; C-M, microbial community; EPP, ecological properties or processes (e.g., nitrogen pools, nitrogen mineralization).

^b Reproductive interference tested by applying NIS pollen to native flowers.

^c One study, Kourtev et al. (2003), was counted twice because they examined the mechanisms of impacts of two different NIS.

^d Of the six studies in which seed set was reduced when NIS pollen was manually applied to native flowers, five found that the quantity of NIS pollen required for this impact was not found on native flowers under normal field conditions.

^e Results symbols: 0, results did not support mechanism ($P > 0.05$); 1, at least one experiment within a study supported mechanism ($P < 0.05$). Pollinator visits: 0, NIS presence did not affect pollinator visits or native seed set; 0(+) or 0(–), NIS presence increased (+) or decreased (–) pollinator visits to natives, but native seed set was not affected; 1(+) or 1(–), NIS presence increased (+) or decreased (–) pollinator visits to natives and native seed set was significantly reduced. Reproductive interference: 1, NIS pollen significantly reduced native plant seed set.

^f Pollinator visits increased, but seed set was reduced due to pollen quality (interference from NIS pollen).

^g Quantified impacts over 7 yr as NIS invaded study area (increased in abundance over time).

Table 1. Extended Continued.

Mechanism and count of studies (no.) that examined this mechanism							
Resource competition		Belowground communities					
Nutrient availability (12)	Soil water (10)	Soil microbes (7 ^c)	Mycorrhizal associations (5)	Allelopathy (11)	Apparent competition (6)	Nutrient cycle (2)	Other mechanisms (11)
0	0					0	
							1
0				1			
1			1				
					0		
		0					
0					0	1	1
			1		1		1
1							
				1			1
0	1	1	0				
	0						

the nonindigenous annual forb ornamental jewelweed (*Impatiens glandulifera* Royle), all hypothesizing altered plant–pollinator interactions as a mechanism, and outcomes varied among all three. In one case there was no effect on pollinator visits to, or reproduction of, a co-occurring native forb (Bartomeus et al. 2010). In another, those same variables were significantly reduced for a different co-occurring native forb (Chittka and Schurkens 2001) and in a third case, pollinator abundance, richness, and visits to co-occurring natives all increased in the presence of *I. glandulifera* (Lopezaraiza-Mikel et al. 2007). Impacts of nonindigenous common dandelion (*Taraxacum officinale* F.H. Wigg.) through reproductive interference also varied depending on the focal native plant species (Kandori et al. 2009; Matsumoto et al. 2010). In addition

to native species identity, other sources of variability were distance between natives and NIS, NIS density, and pollinator identity, with visitation rates to native plants altered for some pollinator species but not others.

Altered Microenvironment. Another primary means by which NIS cause impacts is by altering the microenvironment (Crooks 2002). The physical traits and spatial distribution of NIS can affect light availability, air and soil temperature, and quantity and quality of litter, all of which can affect native species survival and fitness, community structure, and ecosystem processes (e.g., nutrient cycling, decomposition). Results from recent experimental research strongly support alteration of the microenvironment as a mechanism underlying NIS

impacts on individual species, communities, and ecosystem processes (Table 1).

In their review of NIS impact mechanisms, Levine et al. (2003) described several studies that suggested reduced light availability as a mechanism, but noted that more experimental work was needed. Experimental evidence quantifying the effect of altered light availability by NIS has increased substantially over the past decade. Altered light availability as a mechanism of NIS impacts was examined in 16 reviewed studies, of which 81% found significant experimental support (Table 1). NIS associated with this mechanism were perennial grass, shrub, and tree species with large or spreading growth forms, effective at blocking light from the understory. Decreased access to incident light significantly ($P < 0.05$) reduced native plant emergence, growth, abundance, and diversity. Several studies examined the effect of altered light availability on multiple native plant species and found early seral species experienced greater negative impacts than late seral species (Spellman and Wurtz 2011; Urgenson et al. 2012). In most cases, altered light availability impacted native plants directly by limiting a resource necessary for growth; however, impacts from altered light availability can arise indirectly as well. For example, the overstory shading created by the invasive shrub Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder] altered pollinator behavior, which led to reduced pollinator visits and, consequently, reduced seed set in native forbs (McKinney and Goodell 2010).

Results of reviewed studies also strongly supported litter effects as a common mechanism underlying NIS impacts—all nine studies that examined this mechanism found significant support (Table 1). Many NIS produce litter in much greater quantities, and often with different qualities, such as the C : N and lignin : N ratios, than native plants (Evans et al. 2001; Levine et al. 2003). The introduced litter can inhibit germination and establishment of native plants, promote fungal pathogens, and alter nutrient cycling to the detriment of native species (Belnap and Phillips 2001; Evans et al. 2001). The majority of studies that examined litter effects were focused on nonindigenous grasses, which characteristically produce abundant biomass and litter. NIS litter was shown to reduce native plant growth and survival through simple physical obstruction or interference in some cases (e.g., Lenz et al. 2003), but in other cases litter altered light availability or soil temperature, which ultimately caused the impact (Farrer and Goldberg 2009; Larkin et al. 2012). In several cases multiple mechanisms were operating concurrently. For example, nonindigenous perennial common reed [*Phragmites australis* (Cav.) Trin. ex Steud.] reduced native forb establishment and survival through both light limitation and physical interference by shoots and litter (Minchinton et al. 2006).

In some cases, the effect of NIS on the microenvironment can lead to increased native species growth and

abundance. In a xeric coastal-scrub habitat of southern California, Wolkovich (2010) found that litter of nonindigenous annual grasses increased soil moisture, which increased native shrub growth, which, in turn, led to an increase in arthropod richness and abundance. Whether an increase in a response variable is a desirable change is generally a subjective assessment and will depend on the ecological context.

In addition to impacts on plant growth and community structure, NIS litter can also be a mechanism underlying impacts on ecosystem processes and nutrient availability. Mack and D'Antonio (2003) found significantly reduced N mineralization rates in Hawaiian woodlands invaded by nonindigenous perennial C₄ grasses. They showed this impact was driven by litter induced changes to the microclimate—higher soil moisture and lower soil temperature—and increased C : N ratio of soil organic matter (SOM). In a different case, N mineralization rates increased significantly in response to the quantity and quality of NIS litter (hybrid cattail [*Typha* × *glaucua* Godr.]) (Farrer and Goldberg 2009), underscoring that the direction of NIS impacts is often context-dependent (Pyšek et al. 2012).

Many recent litter effects studies examined nonindigenous annual grasses that have invaded woodlands and shrublands where, prior to NIS establishment, species that rapidly produce large quantities of biomass and litter were absent. Thus, these cases support the idea that NIS with traits markedly different from those of resident native species are likely to cause significant impacts (Ehrenfeld 2010; Vitousek 1990).

Resource Competition vs. Indirect Effects. In their review of earlier NIS impact studies, Levine et al. (2003) reported that competition was frequently hypothesized to underlie impacts on plant community structure, but that there was rarely supporting experimental evidence. The past decade has seen an increase in experimental work testing the assumption of resource competition as a mechanism underlying NIS impacts. In our review, 12 studies examined altered soil nutrient availability, which, in most cases, could be attributed to direct resource competition. Only 17% of these studies found experimental evidence of competition for soil nutrients as a mechanism underlying NIS impacts. Competition for soil water was more strongly supported—10 studies examined this mechanism and 40% found significant support (Table 1).

Understanding of competitive effects of NIS has advanced considerably in recent years, in part, because of studies that differentiate impacts caused by direct competition for soil resources, such as water and nutrients, from those caused by indirect effects, such as physical interference from litter, shading, or altered soil temperature. These

studies used experimental approaches that allowed them to differentiate between these potential mechanisms. For example, Coleman and Levine (2007) conducted factorial removals of live NIS and NIS litter and crossed both treatments with water addition. They found that both the removal of live nonindigenous grasses and the removal of nonindigenous grass litter resulted in significant increases in native forb cover. However, the responses did not change with the addition of water, indicating that the nonindigenous grasses were not competing with natives for water. Rather, shading by live plants and physical interference from litter caused the reduction in native plant growth (Coleman and Levine 2007). Of the six studies that distinguished resource competition from indirect effects, all six found support for indirect effects, but only one found evidence of resource competition (Table 1, Supplemental Data 1). Both Farrer and Goldberg (2009) and Larkin et al. (2012) found that litter effects, specifically light reduction and physical obstruction, were the mechanisms driving *T. × glauca* impacts on native plant growth and diversity, rather than direct competition from live *Typha*.

While there is a need to continue building the body of experimental evidence, the results of recent studies indicate that direct competition for soil resources as a mechanism underlying NIS impacts is less common than previously assumed. Based on the current state of knowledge, impacts on native species and community structure are much more likely to derive from the effects of altered microenvironments.

Altered Belowground Communities. At the time of their review, Levine et al. (2003) found alteration of belowground communities as a mechanism of NIS impacts was just beginning to be explored, noting several observational studies showing different soil communities under NIS stands compared with native plant stands. As with altered plant–pollinator interactions, studies examining altered belowground communities and mutualisms as a mechanism of NIS impacts have increased markedly in recent years. NIS can promote soil microbes such as bacteria and fungi, as well as larger soil fauna such as nematodes and arthropods, that are structurally and functionally distinct from those supported by native plants. This shift in composition can alter nutrient cycling and availability, cause a loss of mutualisms beneficial to native plants, and subsequently reduce native species growth and abundance (van der Putten et al. 2007; Wolfe and Klironomos 2005). Seven studies in our review examined altered soil microbial communities as a mechanism of NIS impacts; 71% found experimental support (Table 1). The impacts that resulted from altered microbial communities included reduced native plant growth, reduced nematode abundance and diversity, altered nutrient cycling, and increased soil pH and SOM. NIS life forms that caused impacts by altering

soil microbial communities were trees, annual forbs, and annual and perennial grasses.

Another species interaction that NIS can disrupt is that between plants and soil mycorrhizae. Many native plant species form mutualistic associations with arbuscular mycorrhizal and ectomycorrhizal fungi, which promote native plant growth by facilitating nutrient acquisition (Wolfe and Klironomos 2005). Five reviewed studies tested alteration of mycorrhizal associations as a potential mechanism of impact and 80% had supporting results (Table 1). Impacts from nonindigenous perennial grass, annual forb, perennial forb, and tree species developed through this pathway; the impact in all cases was reduced native plant growth.

Although based on a relatively small sample size, recent experimental evidence indicates that altered soil microbial communities, mutualisms, and mycorrhizal associations can be an important mechanism by which NIS affect individual species, as well as ecosystem properties and processes. The findings suggest that plant–soil feedbacks may be particularly sensitive to NIS establishment and highlight the need for research that spans multiple trophic levels.

Allelopathy. A common alternative hypothesis to direct competition for resources as a mechanism of NIS impacts is allelopathy, whereby NIS produce secondary compounds that injure neighboring plants and the soil community through direct toxicity or by altering the chemical environment of the soil (Hierro and Callaway 2003; Wardle et al. 1998). Allelopathic effects are typically quantified based on the response to activated C (AC) additions.

Because of its high affinity for organic compounds, AC is added to experimental soils to reduce potential allelopathic effects by adsorbing inhibitory compounds (Callaway and Aschehoug 2000). If allelopathy is a significant mechanism of NIS impact, native plant growth, fitness, or both should improve in AC treatments. An improvement in native plant growth in AC treatments less than that seen when native plants are grown alone indicates that NIS are exerting inhibitory effects other than, or in addition to, allelopathy (Mahall and Callaway 1992).

Of the 11 studies that experimentally tested allelopathy as a mechanism of NIS impacts, 82% found reductions in native plant growth were, at least in part, attributable to this mechanism (Table 1). As with many impacts, the occurrence and strength of allelopathic effects were often context-dependent. Sources of variability in outcomes included density and spatial distribution of NIS, target species life form, and target species identity. For example, Gomez-Aparicio and Canham (2008) examined potential allelopathic effects of the nonindigenous tree of heaven [*Ailanthus altissima* (Mill.) Swingle] on three native tree

species: red maple, sugar maple, and northern red oak (*Acer rubrum* L., *Acer saccharum* Marshall, and *Quercus rubra* L.) in temperate forests of the northeastern United States. In a seed-sowing/seedling transplant experiment, they found that addition of AC shifted the impact of *A. altissima* on seedling growth from neutral or slightly positive to very positive for *A. rubrum*, from negative to positive for *A. saccharum*, but had no effect on the consistently negative interaction between *A. altissima* and *Q. rubra*.

Allelopathy studies provided additional evidence that NIS impacts often arise from multiple mechanisms. Six studies tested for, and attempted to distinguish between, allelopathic and non allelopathic effects of NIS. The results from five showed that some other unidentified mechanism was operating concurrently with allelopathy to affect native plant growth (Table 1).

Concerns have been raised that the addition of AC can alter soil nutrient availability, thereby confounding interpretation of allelopathic effects (Inderjit and Callaway 2003, Lau et al. 2008). The results of several reviewed studies substantiated this concern, showing that AC affected native plant growth regardless of the presence of NIS (Cipollini et al. 2008, Wixted and McGraw 2010). In another study, a direct effect of AC could not be ruled out (Murrell et al. 2011), which may also be the case in other studies but was not measured. Clearly, more research is needed on the effects of AC on soil conditions and plant growth and to what degree these effects bias interpretations of chemical inhibition by NIS.

Apparent Competition. In addition to allelopathy, another indirect mechanism by which NIS can affect native plants is through shared predators or herbivores. Consumers may be drawn to areas where NIS have established because the plants offer an additional food source, habitat, or refuge. The elevated consumer abundance can increase consumer pressure on native plants, driving down individual fitness, population growth rates, or both, an effect known as apparent competition (Connell 1990; White et al. 2006). Six reviewed studies tested whether apparent competition was responsible for NIS impacts and 83% found at least some support (Table 1). In general, NIS increased the availability of food and habitat for native consumers, which led to significantly ($P < 0.05$) increased predation of native seed and, therefore, reduced native plant populations. For example, in a California grassland, Lau and Strauss (2005) tested whether the nonindigenous forb California burclover (*Medicago polymorpha* L.) affected the fitness of a co-occurring native forb directly through competition or indirectly by increasing herbivory by several insects known to feed on both plant species. The results from factorial NIS and insect removals indicated that *M. polymorpha* reduced native forb reproduction through increased herbivory as well as through some other, unidentified, mechanism. Impacts

varied between years depending on herbivore abundance, highlighting temporal variability of NIS impacts, particularly those involving other organisms with fluctuating population dynamics.

Apparent competition may be particularly detrimental for rare native plant species, as Dangremond et al. (2010) demonstrated with Tidestrom's lupine (*Lupinus tidestromii* Greene), an endangered, coastal dune forb. When grown in close proximity to nonindigenous European beachgrass (*Ammophila arenaria* L.), *L. tidestromii* experienced high levels of seed consumption by native rodents, which led to a significantly reduced *L. tidestromii* population growth rate. Projection models indicated that the reduced growth rate was likely to cause some populations to decline toward extinction under the NIS-mediated consumption levels (Dangremond et al. 2010).

Overall, experimental evidence supports apparent competition as an important mechanism of NIS impacts; however, the available research is quite limited at this point. Additional research involving other species and environments will help determine the prevalence of this mechanism and will be particularly insightful if designed to test for, and distinguish between, apparent competition and other co-occurring mechanisms of NIS impact.

Nutrient Cycling. It is well established that some NIS can alter ecosystem processes, particularly soil nutrient cycling (Ehrenfeld 2010; Vitousek et al. 1987). Given the ubiquity of plant-soil feedbacks and multi-trophic interactions, altered soil nutrient dynamics can generate widespread effects for individual species, communities, and ecosystems (Mack et al. 2000; Wolfe and Klironomos 2005). Levine et al. (2003) emphasized that while many earlier impact studies had shown NIS could alter ecosystem processes, particularly nutrient cycling, the consequences of this for community structure were largely unknown and untested. A recent meta-analysis of NIS impacts found causal links between ecosystem impacts and community effects remain largely unexplored (Vilà et al. 2011). We found this to be the case as well in recent experimental research. Only a few studies examined altered nutrient cycling or changes in other ecosystem processes as mechanisms of NIS impacts. One study found that the nonindigenous annual grass, Mary's-grass or Nepalese browntop [*Microstegium vimineum* (Trin.) A. Camus] altered nutrient cycling and that this was likely contributing to impacts on plant community structure (DeMeester and Richter 2010). Several other studies clearly showed that NIS altered nutrient dynamics, such as the reduction in N mineralization rates by nonindigenous perennial C_4 grasses in Hawaiian woodlands (Mack and D'Antonio 2003); however, it is unknown whether these changes in ecosystem processes ultimately affected other organisms or community properties. Some of the impacts associated with NIS litter may

have been the result of altered nutrient cycling. Thus, there remains a need for experimental research examining the consequences of altered ecosystem processes for individuals, populations, and communities.

Multiple Concurrent Mechanisms. There is much yet to be learned about the processes underlying the impacts of NIS. This is demonstrated by the 10 studies that found evidence of other, unidentified mechanisms in addition to those explicitly tested (Table 1, “Other mechanisms” column). Furthermore, evidence of multiple impact mechanisms operating concurrently was found in 71% of studies that tested for this possibility (22 of 31 studies). Thus, while significant advances have been made in understanding the mechanisms that have been explicitly tested, in many cases, these mechanisms are not working in isolation and others that are untested or undertested may prove to be important. The use of multi-factor experimental approaches has increased in the last several years. Continuation of this trend will be necessary for a more complete understanding of NIS impacts and the variability in magnitude and direction of these impacts.

In summary, a great deal of progress has been made during the last decade toward understanding the mechanisms underlying NIS impacts. The review by Levine et al. (2003) found that numerous observational studies had compared community structure and ecosystem processes in areas with and without NIS, but that only a small fraction experimentally tested for NIS impacts and potential underlying mechanisms. Although still only composing approximately 30% of NIS impact studies overall, the body of experimental research is now much more robust. Many of the NIS impact mechanisms that had been hypothesized based on observations have been explicitly tested. From our synthesis of this research, we found that alteration of microenvironments was much more often a mechanism underlying NIS impacts than direct competition for soil water and nutrients. This understanding has come, in part, from multi-factor studies that tested for and distinguished between impacts caused by direct competition and those caused by indirect effects, such as altered growing conditions. Evidence indicates that NIS litter is a significant driver of changes to the microenvironment, and that litter effects are often of greater consequence than the effects of live NIS plants.

The alteration of plant–pollinator interactions and soil communities by NIS has been the focus of numerous recent mechanism studies. Results support altered soil microbial communities and mycorrhizal associations as important factors driving NIS impacts on native plant growth, community structure, and nutrient cycling. As with NIS impacts more generally, the outcomes of mechanism studies were often context-dependent, varying as a function of NIS density, native species identity,

seral stage of native vegetation, and spatial distribution of NIS.

Recent experimental research also indicates that NIS impacts often cannot be attributed to a single mechanism. For example, NIS impacted individuals and populations through allelopathy and apparent competition; however, in most cases, other, unidentified mechanisms also contributed to the impacts. This highlights the need for multi-factor studies that can identify and distinguish between multiple, concurrently operating mechanisms. Progress toward understanding the consequences of altered nutrient cycling and other ecosystem processes for individuals and communities has been limited despite past recognition of this knowledge gap. We are beginning to see an increase in research spanning multiple ecological levels, which will be crucial to understanding the ecosystem consequences of NIS establishment.

Effective and efficient NIS control and ecosystem restoration require understanding the processes driving NIS impacts. The results of this review indicate that effective management will require attention to legacy effects such as litter, altered soil properties, and changes in belowground communities. The fact that impacts often arise from NIS litter means that removing live NIS plants may not ameliorate impacts and that removal of dead biomass will be necessary to restore conditions in which native species can thrive. Rehabilitating soil microbial and mycorrhizal communities may be crucial to the success of post-NIS management revegetation efforts.

This review details the current trends in experimental research and provides a synthesis of some of the most prevalent mechanisms of NIS impacts. As a cumulative process, our review builds on the framework developed by Levine et al. (2003), and future studies will further contribute to a more complete picture of the processes underlying NIS impacts. This continued attention will not only benefit natural resource management, but will also help address broader questions about the drivers of undesirable ecological change.

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