Ecology, 93(3), 2012, pp. 598–607

The natives are restless, but not often and mostly when disturbed

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Abstract. The argument that the threat posed by introduced species is overblown is often buttressed by the observation that native species sometimes also become invasive. An examination of the literature on plant invasions in the United States shows that six times more nonnative species have been termed invasive than native species, and that a member of the naturalized nonnative pool is 40 times more likely than a native species to be perceived as invasive. In the great majority of instances in which a native plant species is seen as invasive, the invasion is associated with an anthropogenic disturbance, especially changed fire or hydrological regime, livestock grazing, and changes wrought by an introduced species. These results suggest that natives are significantly less likely than nonnatives to be problematic for local ecosystems.

Key words: disturbance; fire suppression; introduced species; invasion; native invader; nonnative; succession.

. . .and there are also native American weeds, indigenous to the region, which have become strongly aggressive through changed conditions.

—George P. Marsh (1874:72)

All too familiar are those symptoms of land-illness caused by the importation of exotic diseases and pests. . . . Less familiar are the many instances in which native plants and animals, heretofore presumably 'well-behaved' citizens of the land community, have assumed all the attributes of pests.

—Aldo Leopold (1944*a*:314)

Introduction

Invasion biology is criticized by a small but vocal group of ecologists (e.g., Rosenzweig 2001, Slobodkin 2001, Sax et al. 2002, Brown and Sax 2004, Gurevitch and Padilla 2004, Sax and Gaines 2008, Davis 2009, Davis et al. 2011) who argue broadly that the threat posed by nonnative species to native species, communities, and ecosystems is often overstated.

One argument marshaled frequently (e.g., Thompson et al. 1995, Davis et al. 2000, 2001, 2005, 2011) as part of this assault is that, in terms of impacts on native species and ecosystems, there is no substantive difference between invasions by native species and invasions by nonnative species. Sagoff (1999), for example, points to invasions of the dinoflagellate *Pfiesteria piscicida* to show that native species can be every bit as harmful as nonnative ones. Following Davis and Thompson (2001), he suggests that approximately equal numbers of native plants and nonindigenous plants are expanding their ranges in the United Kingdom (Sagoff 2005). Warren (2007, 2011) notes that, in Scotland, native bracken (*Pteridium aquilinum*) and ragwort (*Senecio vulgaris*) are both damaging invasive weeds. Rotherham and Lambert (2011) list several native British plants that become problematic in certain circumstances. Head and Muir (2004) describe the plant *Pittosporum undulatum* as one of many native invaders in Australia, but they count as "native" any species native to any part of Australia, and the majority of native invaders they cite are plants that became problematic when moved to a nonnative part of their range within Australia. In the specific case of *Pittosporum undulatum*, its invasion rests on fire suppression (Gleadow and Ashton 1981). Allison (2011), working on restorations in the American Midwest, found that most of the "invasive" species were not native, but that a few species native to the region (e.g., *Rhus glabra*, *Rubus allegheniensis*, *Cornus racemosa*) had become too abundant in some projects and were thus deemed problematic. These and similar examples (e.g., Hettinger 2001) are part of the argument that there is nothing special about nonindigenous species per se, and that to the extent that much of the current interest in them is focused on damage they cause to native populations, communities, and ecosystems, it is somewhat misaimed and constitutes wasted conservation effort. Rather, according to this line of reasoning, our concern should be aimed at species that cause such damage, whether they are native or nonnative.

"Invasive" means different things to different researchers, but is most commonly taken by invasion biologists and ecologists to mean spreading from a point of introduction, often into natural or semi-natural

Manuscript received 7 July 2011; revised 8 September 2011; accepted 22 September 2011. Corresponding Editor: D. R. Strong.
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habitats, with the frequent connotation of having some sort of an impact on the recipient community (Richardson et al. 2000, Rejmánek et al. 2002). Popular science writers often refer to any established nonnative population as "invasive," while President Clinton's Executive Order 13112 ("Invasive Species") of 1999 defined an invasive species as "an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health." However, biologists working on introduced species still largely adhere to the definition of entering natural or semi-natural habitats and having some effect on the resident species, and this is how the term is used in the argument we are addressing. This is how we will use it. By "native," we mean native to a particular region rather than to a political entity. By "nonnative," we mean species transported to distant rather than contiguous regions (cf. Groves 2001).

Davis et al. (2000, 2005) note that many invasions of introduced plants resemble the replacement of one native plant species by another during succession and are driven by the same sorts of forces. It is thus unsurprising that the same terminology is occasionally used to describe species replacement during succession as is used to describe invasions, including the word "invasion" itself (see, e.g., Kaye et al. 2005). However, as the above examples show, the contention that native invaders harm native species and ecosystems in the same way that some nonnative species do is not focused on ordinary succession, although some cases may be described as the end points of a greatly displaced successional trajectory on highly disturbed sites.

The argument that, from a conservation standpoint, we should focus on damaging species or invasive species, whatever their geographic origin, may be valid (Valéry et al. 2008, Davis et al. 2011), but even if this were so, it would not automatically mean that the current explosion of interest in nonnative species does not serve conservation purposes efficiently. It could be, for example, that nonnative species are much more likely to become invasive than native species. Although substantial attention has been focused on the causes of invasion by nonnatives and on how they may relate to processes that also occur in native species (e.g., Thompson et al. 1995, Davis et al. 2000, 2005), the question of whether nonnative species are more likely than natives to become invasive seems not to have been asked. Some data suggest this might indeed be the case. For instance, approximately half of the freshwater fish, mammal, and bird species introduced from Europe to North America or vice versa have established populations, and more than half of these became invasive (Jeschke and Strayer 2005). We know of no research on what fractions of native species of any of these taxa have become invasive, but surely it would be less than this.

Perhaps Thompson et al. (1995) came closest to addressing the relative invasiveness of native and nonindigenous species. As a rough proxy for invasiveness, they sought the numbers of native and nonnative plant species in various regions that had recently expanded their ranges. For instance, for The Netherlands, they tallied ~30 nonnative species and ~160 native species falling into this category. Because they were not asking the question we are asking, they did not record the total number of plant species of each type. However, Weeda (1987) reports ~1000 native species for the Netherlands and ~220 established nonnatives that arrived after 1500, as well as ~250 species ("archaeophytes") that are either natives or nonnatives that arrived before 1500. Thus, the percentage of natives that have recently expanded their range is between 13% and 16%, while the corresponding percentage of nonnatives is between 6% and 14%, little if any difference.

Our goals are (1) to determine, for the United States, how many and what percentage of native and established nonnative plant species are recorded as invasive, and (2) to review the circumstances of invasions among the natives and perceived reasons for these invasions.

Methods

We performed two separate Web of Science literature searches, one compiling cases in which nonnative plant species were cited as invasive, and another in which native plant species were cited as invasive. In both searches we used the same list of key words ("encroachment OR range expansion OR inva*"), except that search 1 looked for nonnatives ("introduced OR alien OR exotic OR nonnative OR nonindigenous"), and search 2 looked for native species ("NOT TS = (introduced OR alien OR exotic OR nonnative OR nonindigenous)"). "NOT TS" indicates not including the subsequent terms in a search. In both literature searches, as potential sources we used 40 journals, including those focusing on basic ecology and evolution, invasion ecology, conservation biology, and management (see Appendix). Conducting the initial search in 2009, we used the dates 1900–2007 to be certain that all publications from each year were captured and to insure replicability. We then read the abstract and, when necessary, part of the body of each publication to determine whether it was relevant to our inquiry.

We limited the search to papers dealing with plants perceived as invasive in the United States and weeded out papers in which a plant was defined as invasive simply by virtue of being nonnative. In short, we required a description (whether or not supported by quantitative data and/or experiment) that the plant was actually having an impact, such as replacing a native species, affecting one or more other species, or changing an important ecosystem property.

To compare invasiveness of native and nonnative species, among the latter we focused on naturalized nonnative species. Using all nonnative plants would, for example, have entailed including many species that persist only with intensive human assistance, and often in very restricted areas. The term "naturalized," though also loosely used in popular writing, is widely employed to mean a species sustaining itself without overt human aid. Some authors require also that naturalized species be established in "nature" as opposed to anthropogenic habitats, but Richardson et al. (2000) advocate standardizing use of "naturalization" so as not to restrict it to species established in natural habitats, reserving the term "invasive" for the latter trait. This is the definition of "naturalization" we adopt in this paper.

Results

Search 1, for nonnative invasive species, yielded 825 publications, while search 2, for native invasive species, yielded 711 publications. Surprisingly, search 1, for nonnatives, which registered 538 relevant papers on "invasive" behavior by nonnatives, among these turned up 22 papers that referred also to natives that had been termed "invasive" or the equivalent. The remaining 287 papers were irrelevant (e.g., on invasions by plants outside the United States, or by animals). Search 2 registered 68 papers in which natives were perceived as invasive, and these papers did not overlap with the 22 papers found in the first search.

In the relevant papers in search 1, 323 nonnative plant species were recorded as invasive in the United States. A list just for the continental United States compiled by invasive.org at the University of Georgia and supplemented by lists of the Exotic Pest Plant Councils in the United States yielded 424 species, overlapping broadly (72%, 232 species) the list from our literature search.[4] We use 350 as a ballpark estimate of the number of invasive nonnative plant species in the United States.

By contrast, the 90 papers returned by the two searches that appeared from their titles to deal with natives perceived as invasive yielded a total of 53 native species fulfilling our criteria for being invasive (Table 1).

Discussion

There are more than six times as many nonnative invaders as native invaders. As a percentage of the species pool, which would be a far better indication of the risk of invasiveness, the disparity is even more striking (Fig. 1). The United States has >18 100 native plant species (Stein et al. 2000; T. Brooks, *personal communication*). The total number of nonnative plant species in the United States is unknown, but a very large fraction of these are found only in highly anthropogenic habitats and are often maintained by deliberate, ongoing human activity (e.g., many horticultural varieties and agricultural plants). The proper comparison group is naturalized nonnative plants, as these are the ones that, like the vast majority of native species, are established and self-perpetuating in nature. This number also is not known, but even a liberal estimate is <3000 (Kartesz 1994, Mack and Erneberg 2002). Thus, invasive species amount to at least 12% of all naturalized nonnative species. For natives, the analogous figure is <0.3%, or less than 1/40 as high a frequency as for nonnatives.

A striking finding is that invasion by the great majority of native invaders entailed some environmental change ultimately caused by humans (Table 2). In fact, 39 of the 53 species (74%) fell in this category, a figure rising to 42 species (79%) if three are included whose invasion in certain but is not attributed to anthropogenic causes at all sites. A variety of anthropogenic changes are involved, and often several changes occur together. Invasion by half (26) of these species entailed anthropogenically altered fire regimes, usually fire suppression. For 11 species, grazing by livestock was involved; in each instance, changed fire regime also played a role. The role of fire suppression and grazing in causing certain native species to become invasive has long been known. Aldo Leopold in 1924 noted the invasion of certain southwestern grasslands by native juniper and other woody species and correctly deduced the general explanation: a combination of increased grazing and fire suppression (Leopold 1924, 1944*b*). Subsequent research on grassland invasions in the West by western juniper (*Juniperus occidentalis*) (Burkhardt and Tisdale 1976), one-seed juniper (*J. monosperma*) (Johnsen 1962), white fir (*Abies concolor*) (Vale 1975), and Douglas-fir (*Pseudotsuga menziesii*; see Plate 1) (Strang and Parminter 1980, Arno and Gruell 1983, 1986) has borne him out, indicating either or both of these two causes. In Maryland and Ohio, Virginia pine (*Pinus virginiana*) invades serpentine grasslands upon fire suppression and release from grazing (Cumming and Kelly 2007, Thiet and Boerner 2007). Our search turned up similar cases. For instance, *Cornus racemosa* (gray dogwood) invaded prairie fen in Illinois after grazing and fire suppression (Bowles et al. 1996), the same circumstances under which eastern juniper (*Juniperus virginiana*) encroached on prairie fragmented by agriculture in Oklahoma (Coppedge et al. 2004).

Two native species in our searches (*Phalaris arundinacea* and *Phragmites australis*) became invasive because nonnative genotypes were introduced; perhaps these should not be tallied as native invaders. In the latter case, the invasive populations are reported to consist wholly of nonnative genotypes (Saltonstall 2002), while in the former case, the invasive genotypes arose from recombination of European varieties, but some subsequent recombination with native genotypes cannot be precluded (Lavergne and Molofsky 2007; J. Molofsky, *personal communcation*). Hybrids of two native species (*Myriophyllum sibiricum* and *Spartina foliosa*) with nonnative congeners became invasive, and these surely qualify as native invaders.

Four native species became invasive in the wake of habitat changes wrought by nonnative species, a form of invasional meltdown (Simberloff and Von Holle 1999). In Texas, Chinese tallow (*Sapium sebiferum*) invades

[4] www.se-eppc.org

grassland partly by virtue of shading native grassland plants, and the native hackberry (*Celtis laevigata*) follows in its wake (Siemann and Rogers 2003). In the high elevations of the southern Appalachians, elimination of Fraser fir (*Abies fraseri*) by the Asian balsam woolly adelgid (*Adelges piceae*) has created conditions favorable to invasion by native mountain ash (*Sorbus americana*) and fire cherry (*Prunus pensylvanica*) (Rabenold et al. 1998). Finally, native ragweed (*Ambrosia artemisiifolia*) is favored by mound-building by the red imported fire ant (*Solenopsis invicta*) in South Carolina (Seaman and Marino 2003).

Eight native species in our searches became invasive following anthropogenic changes to hydrology. For instance, in Indiana, willows (*Salix interior* and *S. nigra*) and eastern cottonwood (*Populus deltoides*) all invaded drained wetlands, and the latter also benefited from fire suppression (Choi and Bury 2003).

It is a commonplace, beginning with Elton (1958), that disturbance often favors invasion by nonnatives; many subsequent authors have elaborated on this theme (e.g., Crawley 1987, Rejmánek 1989, Lozon and MacIsaac 1997, D'Antonio et al. 1999). For instance, Lozon and MacIsaac (1997) found in a literature search that about two-thirds of all nonnative plant invasions involved some form of disturbance. Davis et al. (2000) provided an explanation for this frequent linkage, arguing that plant invasion requires a pulse of resource enrichment or release, and various disturbances are the main source of such pulses, e.g., removal of a tree canopy, increasing light for understory plants. The role of disturbance received further impetus when MacDougall and Turkington (2005) suggested that invasive plants are more often the passengers than the drivers of environmental change. In light of this emphasis on disturbance, then, aside from the small numbers of native species reported as "invasive" relative to nonnatives, one might ask if there is anything remarkable about the fact that almost all reported "native invasions" are associated with disturbance.

In fact, although disturbance is undoubtedly key to many nonnative invasions, its role is overstated, and 118 nonnative plant species invade undisturbed forests in the United States (data extracted from Martin et al. 2009). Although a few of these are well known (e.g., Norway maple [*Acer platanoides*], garlic mustard [*Alliaria petiolata*], Japanese stilt grass [*Microstegium vimeneum*]), many are not widely recognized because invasions into undisturbed forests are often slow (Von Holle et al. 2003, Martin et al. 2009). The facts that the majority of nonnative plant species that become invasive are deliberately introduced, and that most of these are fast-growing, shade-intolerant species, contribute to the false impression that disturbance is almost always a necessity for a nonnative species to become invasive (Martin et al. 2009). Yet it does almost always appear to be a necessity for native invaders.

For six species, Kaye et al. (2005) used the terms "invasion" and "encroachment" to describe what they also portray as an ordinary recurrent successional process in which native conifers move into stands of quaking aspen (*Populus tremuloides*); for three of these, no other factors were cited as inducing invasion. In fact, we expected our searches to turn up more instances of this type because of the underlying similarity of the driving forces of many successions and the plant invasions studied by invasion biologists (Davis et al. 2000, 2005). Further, we are not contesting the contention that many plant invasions could profitably be studied in a successional framework. However, many plant invasions do not fall comfortably in the framework of succession (see, e.g., Ehrenfeld 2010, Simberloff 2010, 2011), distorting the plant community in various features (e.g., physical structure, biomass) from anything remotely resembling what historical successional trajectories might have produced, and often greatly changing ecosystem properties (e.g., nutrient and fire cycles). It was analogous cases for native species that we particularly sought, in which one or more species wrought changes in the plant community that would not have been achieved by ordinary succession. As is evident from the foregoing statistics, there are very few such cases in comparison to those involving nonnatives, and the great majority are triggered by other anthropogenic activities.

The searches yielded only seven native species whose invasion was not simply successional and did not appear linked to human activity, including recent anthropogenic global climate change: *Abies procera* (Magee and Antos 1992), *Alnus* sp. (Barker et al. 2002), *Amaranthus hybridus* (Renne et al. 2006), *Baccharis pilularis* (DeSimone and Zedler 2001), *Larrea tridentata* (Hochstrasser and Peters 2004, Peters et al. 2006), *Populus tremuloides* (Andersen and Baker 2006), and *Tsuga canadensis* (Frelich et al. 1993). For one other native species, *Artemisia rothrockii*, at one site the invasion appeared natural but not simply successional (Berlow et al. 2002), while at another site the invasion seemed anthropogenic (Darrouzet-Nardi et al. 2006). For another species, *Pinus contorta*, the invasion seemed successional at one site (Kaye et al. 2005), but neither successional nor anthropogenic at another (Andersen and Baker 2006). That is, only nine native species, 0.05% of all native species, were invasive independent of human activity, aside from successional cases. Several of these native invasions were associated with historic local or regional climate events rather than current anthropogenic global warming.

The question arises whether far more nonnative than native species are reported as invasive simply because researchers are more driven to study nonnatives than natives in situations that might be called invasions. The term "invasion" would obviously be more likely to be used to describe such a study for nonnatives; this is why

TABLE 1. Native plant species perceived as invasive in the United States; see *Introduction* and *Methods* for details.

Species	Reasons	Reference
Abies grandis	global climate change	Lepofsky et al. (2003)
Abies lasiocarpa	succession	Kaye et al. (2005)
Abies procera	historic drought (1920–1940)	Magee and Antos (1992)
Acer rubrum	fire suppression plus unnamed factors	McDonald et al. (2003)
Alnus sp.†	natural flooding	Barker et al. (2002)
Amaranthus hybridus	unclear	Renne et al. (2006)
Ambrosia artemisiifolia	mound building by introduced ant	Seaman and Marino (2003)
Artemisia rothrockii	natural soil disturbance and canopy gap formation	Berlow et al. (2002)
	anthropogenic stream channel incision	Darrouzet-Nardi et al. (2006)
Asimina triloba	decreased anthropogenic fire frequency	Larimore et al. (2003)
Baccharis pilularis	small-mammal activity	DeSimone and Zedler (2001)
Celtis laevigata	shading of ground cover by introduced tree	Siemann and Rogers (2003)
Cornus drummondi	fire suppression	Lett and Knapp (2003), McCarron et al. 2003
Cornus racemosa	grazing, fire suppression	Bowles et al. (1996), Brudvig and Asbjornsen (2007)
Eriogonum fasciculatum	fire suppression	Franklin et al. (2004)
Froelichia floridana	land use change	McCauley and Ballard (2002)
Ilex glabra	fire suppression	Brewer (2002)
Juniperus ashei	livestock grazing and anthropogenically reduced fire frequency	Jessup et al. (2003)
Juniperus occidentalis	grazing, precipitation change, fire suppression	Strand et al. (2007)
Juniperus virginiana	grazing, fire suppression, agricultural fragmentation	Coppedge et al. (2004)
Larria tridentata	natural	Hochstrasser and Peters (2004), Peters et al. (2006)
Myriophyllum sibiricum	hybridization with nonnative hybrid	Moody and Les (2007)
Ostrya virginiana	altered grazing regime, fire suppression, global climate change	Brudvig and Asbjornsen (2007)
Phalaris arundinacea	introduction of nonnative genotypes	Lavergne and Molofsky (2006)
Phragmites australis	introduction of nonnative genotypes, anthropogenic habitat modification	Minchinton and Bertness (2003), Minchinton et al. (2006)
Picea engelmanii	succession	Kaye et al. (2005)
	fire suppression, grazing change, drought	Mast and Wolf (2006)
Picea glauca	global climate change	Hobbie and Chapin (1998)
Pinus aristata	fire exclusion, tree harvest, grazing	Cocke et al. (2005)
Pinus contorta	increased soil moisture after Little Ice Age	Andersen and Baker (2005)
	succession	Kaye et al. (2005)
Pinus flexilis	succession	Kaye et al. (2005)
Pinus ponderosa	succession	Kaye et al. (2005)
Pinus rigida	anthropogenically changed flooding regime	Craine and Orians (2004, 2006)
Pinus virginiana	fire suppression	Cumming and Kelly (2007)
Populus deltoides	wetland drainage, fire suppression	Choi and Bury (2003)
Populus tremuloides	increased soil moisture after Little Ice Age	Andersen and Baker (2005)
Prosopis glandulosa	overgrazing, fire suppression, global climate change	Martin et al. (2003)
	livestock grazing, fire suppression, changed rodent populations, global climate	Polley et al. (1994)
Prosopis velutina	rangeland restoration and changed grazing management	Wheeler et al. (2007)
	grazing, anthropogenic change in flood frequency, fire suppression	Potts et al. (2006)
Prunus pennsylvanicus	destruction of dominant tree by introduced adelgid	Rabenold et al. (1998)
Pseudotsuga menziesii	succession	Kaye et al. (2005)
	global climate change	Lepofsky et al. (2003)
	fire suppression, grazing change, drought	Mast and Wolf (2006)
Quercus alba	fire suppression	McClenahen and Houston (1998)
Quercus coccinea	fire suppression	Carter et al. (2006)
Quercus falcata	fire suppression	Carter et al. (2006)
Quercus macrocarpa	fire suppression	Bragg et al. (1993)
Quercus muehlenbergii	fire suppression	Bragg et al. (1993), Copenheaver et al. (2006)
Quercus stellata	fire suppression	Carter et al. (2006)
Quercus velutina	fire suppression	Carter et al. (2006)
	fire suppression, local climate change	Cole and Taylor (1995)
Quercus virginiana	livestock grazing, fire suppression	Jessup et al. (2003)
Salix interior	wetland drainage	Choi and Bury (2003)
Salix nigra	wetland drainage	Choi and Bury (2003)
Salix sp.‡	anthropogenically induced flooding	Barker et al. (2002)

TABLE 1. Continued.

Species	Reasons	Reference
Sassifras albidum	fire suppression, local climate change	Cole and Taylor (1995)
Sorbus americana	destruction of dominant tree by introduced adelgid	Rabenold et al. (1998)
Spartina foliosa hybrid	hybridization with nonnative	Levin et al. (2006)
Tsuga canadensis	natural climate change	Frelich et al. (1993)
Typha domingensis	anthropogenically altered hydrology, nutrient loads	Newman et al. (1996)

† Two species; data lacking on which are invasive.
‡ Nine species; data lacking on which are invasive.

we included the terms "encroachment" and "range expansion" in the search. The fact that our two searches turned up similar numbers of papers suggests that there was no great tendency to for researchers to neglect native species. Of course researchers are more likely to study phenomena that are viewed as problems, driven by intellectual curiosity, desire to aid society or conservation, and funding opportunities. However, this is precisely the point we are attempting to establish: many more nonnative than native species are perceived as problematic. Ordinary succession can lead to the perception of natives as invasive when humans want to maintain a nonclimax system. The several native species termed "invasive" by Kaye et al. (2005) are typical. Managers are concerned over the loss of older aspen stands to increases during the last century of conifers and browsing by elk, but this is a recurrent, long-term process involving stand-replacing fire (Kaye et al. 2005).

It is noteworthy that almost all reports of native invasions are quite local, although the phenomena believed to be triggering them in some instances are probably at least regional; the published reports, however, are from specific sites. The association of grazing and fire suppression with invasions by juniper species and Douglas-fir are examples. By contrast, many nonnative invaders are problematic over enormous areas. Kudzu (*Pueraria montana* var. *lobata*), for instance, infests ~3 000 000 ha in the United States (Mitch 2000, Forseth and Innis 2004), while cheatgrass (*Bromus tectorum*) infests at least 15 000 000 ha (Westbrooks 1998).

Finally, we can ask why nonnative species are so much more likely than natives to become invasive even without disturbance. The likely general answer was intuited by Aldo Leopold as part of his conception of

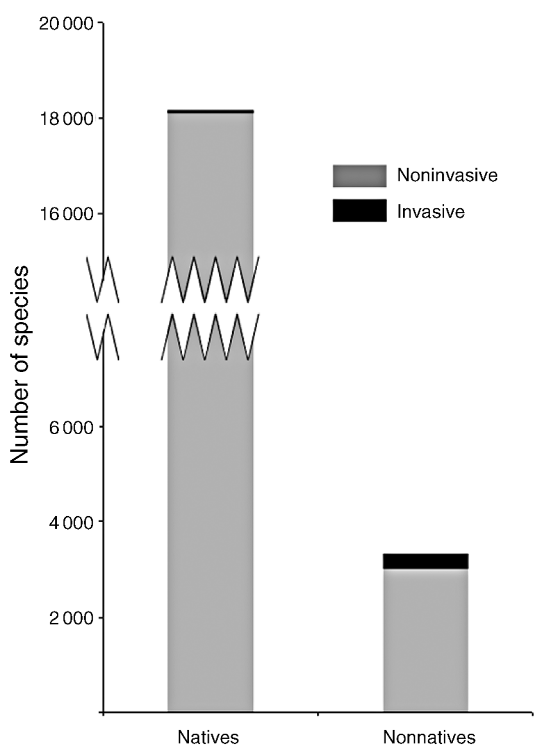

FIG. 1. The numbers of native and naturalized nonnative vascular plant species in the United States: black, invasive species; gray, noninvasive species.

TABLE 2. The stated causes for invasiveness for native species perceived as invasive; causes need not be exclusive (see *Methods*).

Cause	Number of species
Anthropogenic	
Altered fire regime	26
Grazing regime	11
Altered hydrology	8
Global climate change	5
Hybridization/introduction of nonnative genotype	4
Activity of nonnative species	4
Other anthropogenic activity	4
Natural	
Succession only	3
Other natural	7
Succession at one site, other natural at other site	1
Mixed	
Succession at one site, anthropogenic at other site	2
Other natural at one site, anthropogenic at other site	1

PLATE 1. Douglas-fir (*Pseudotsuga menziesii*), native to western North America, invading a forest on Isla Victoria, Argentina. Douglas-fir can also be invasive in its native range, particularly when fire is excluded. Photo credit: M. A. Nuñez.

land health (1942*a*, *b*): coevolution through millennia has adapted native species to one another and to their physical environment, especially the soil, and introducing nonnative species that lack a coevolutionary history with an ecosystem has a relatively high probability of disrupting large parts of the system. Leopold himself (1942*a*) admitted he could not prove this, and it is well beyond the scope of this paper to discuss all the evidence in favor of this hypothesis. Recent research by Callaway and his colleagues (e.g., Callaway and Aschehoug 2000, Callaway 2006) points in this direction.

A partial alternative hypothesis is that many of the natives were at one time invasive; however, unlike recently introduced species, they have had time to expand to their full geographical and ecological extent. This hypothesis does not differ completely from that of Leopold, in that part of that expansion, and the establishment of current geographical and ecological limits for native species, would surely have entailed coevolution with the co-occurring species and evolutionary adaptation to the physical environment.

Whatever the reason for the pattern, the fact is that nonnative plant species have proven to be far more likely than natives to be invasive in North America. The argument of Davis et al. (2011) that to manage efficiently we should ignore geographic origins is not grounded in substantial evidence.

Acknowledgments

Two anonymous referees provided useful comments on a previous draft of this manuscript.

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Supplemental Material

Appendix

List of journals included in Web of Science literature searches (*Ecological Archives* E093-053-A1).