Symposium

Exotic Plants as Ecosystem Dominants[1]

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Abstract: Dominant species have long been appreciated for their role in determining ecosystem attributes such as vegetation structure, successional patterns, soil characteristics, hydrology, and productivity. Exotic species may reach such high densities that they become community dominants, and it is in this role that exotics pose the greatest threat to native ecosystems. Four commonly observed patterns related to species dominance and their implications for understanding exotic invasions are discussed: the importance of scale in relationships between dominance and diversity, the positive correlation between local abundance and geographic range, the effects of dominants on ecosystem processes, and the mass effect of seed production in determining dominance. Understanding determinants of dominance will help us to better understand community invasibility.

Additional index words: Diversity, ecosystem effects, geographic range, mass effect.

INTRODUCTION

Foresters, range scientists, and plant ecologists long have recognized the central importance of dominant species in determining community and ecosystem attributes such as vegetation structure, successional patterns, soil characteristics, hydrology, and nutrient cycling processes. Ecosystem dominants are those species that, by virtue of their large biomass, high density, or extensive cover (or all) provide the context within which other species persist. Hanski (1982) considered them "core" species and noted that they were the species most likely to compete with each other. In contrast, less common "satellite" species persist within the environment created by the core species; their numbers and richness are more strongly affected by their interactions with core species than with each other. Contrasts between core and satellite species are easily appreciated by reference to a typical dominance–diversity graph shown in Figure 1, in which a few common species are orders-of-magnitude more abundant than most other species in a community. Although abundant species are not necessarily dominant species, dominant species are often also locally abundant, as are invasive exotic species. Dominant species also are often overstory species, although dominance may be shared between over- and understory species, for

example in the *Picea–Sphagnum* communities of the boreal forest.

The invasion of native plant communities by exotic species entails not only establishment and persistence of the exotic species within the existing framework of the community but sometimes the attainment of such high densities that the invader becomes the community dominant. It is this aspect of the spread of exotic species that poses the greatest threat to native ecosystems because dominants set the environmental context for the persistence of other species.

There are many similarities between invasive exotic plant species and native dominants in their effects on communities. Like native dominants, invasive exotics may become a predominant influence on light transmission, edaphic processes, disturbance regimes, and trophic structures. Although the patterns of native dominance in a landscape often have been established for centuries or millennia, dominance by exotics is often novel and rapidly changing. The consequences of this rapid change may not become fully apparent for decades. Although exotic plant invasions may reduce populations of native species, alter hydrology of watersheds, increase fire frequencies and nutrient supply, and change trophic processes (Mack et al. 2002), they do not necessarily do so; the effects of exotic plants are as diverse and complex as the effects of native dominants. Our ability to predict those consequences with reasonable confidence is central to our ability identify the worst invaders and to set priorities for control. The consequences of well-advanced invasions such as leafy spurge (*Euphorbia esula* L.) in
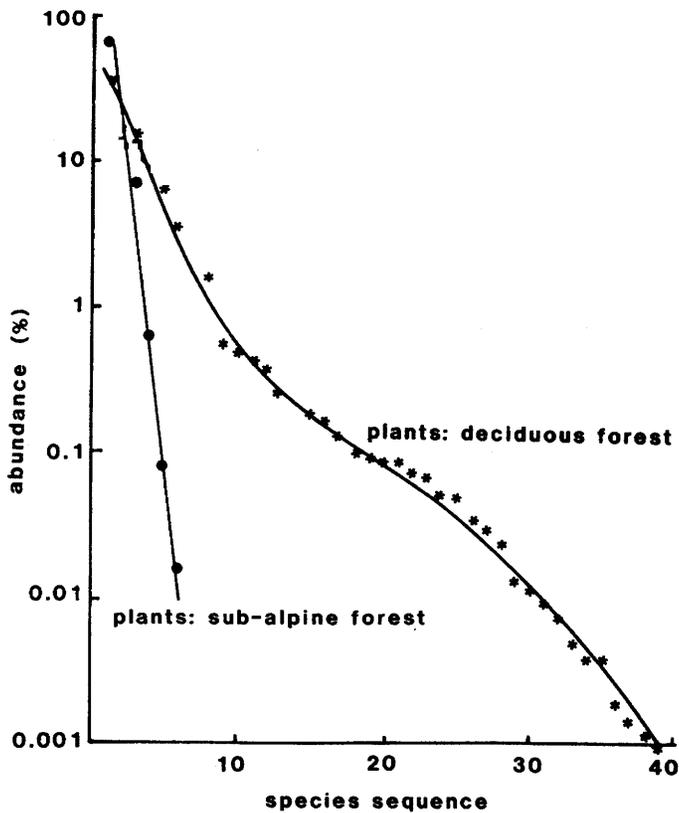
Figure 1. Dominance–diversity curves for two plant communities (adapted from Magurran 1988). Percent abundance on a log scale is plotted against the rank order of each species in the community determined by their relative abundances.

the western United States, *Melaleuca quinquenervia* (Cav.) Blake in the Florida Everglades, or *Miconia calvescens* DC in Tahiti and Hawaii are clearly apparent. Effects of other exotic species may be less obvious, particularly during early phases of their expansion.

Distinctions between native and exotic species often are blurred when expanding ranges and densities of native species become management issues. The dominance of mesquite (*Prosopis velutina* Woot.) in southwestern United States (Schade et al. 2003) and the spread of cattails (*Typha latifolia* L.) in the Everglades (Vaithiyanathan and Richardson 1999) are examples. In a longer time frame, the ranges of native species have shifted dramatically in response to climate change. The expansion of hemlock [*Tsuga canadensis* (L.) Carr.] and maple (*Acer saccharum* Marsh.) across the Eastern deciduous forest after the Pleistocene glacial retreat (Davis 1986) must have had important environmental consequences for the character of the forests they invaded.

The literature on vegetation and ecosystem patterns should provide guidance in predicting the effects of exotic invaders and lend credence to projections of the long-term consequences of their unchecked population spread. Lessons learned indicate where we should be cautious about predicting effects as well as providing a basis for extrapolations. The objective of this article is to examine some commonly observed patterns related to species abundance and dominance from the ecological literature and to discuss their implications for assessing impacts of invasive exotic species.

EFFECTS OF DOMINANTS ON SPECIES RICHNESS

Species richness often shows a negative or unimodal correlation with productivity or biomass. Huston (1979), for example, proposed that in low-productivity sites, species richness will be low because few species are able to tolerate harsh environmental conditions; whereas in high-productivity sites, high growth rates engender high rates of competitive exclusion, often attributed to one or a few species of competitive dominants. Thus, maximum species richness is expected to occur at some intermediate level of productivity where site characteristics are suitable for many species but where competitive exclusion rates are moderate. Reviews (Grace 2000; Tilman and Pacala 1993) have cited numerous examples consistent with this hypothesis. Other studies, however, suggest that these patterns are scale dependent (Gross et al. 2000; Levine and D'Antonio 1999). At a local level, high dominance is often correlated with low species diversity as Huston's hypothesis would suggest (Smith and Knapp 1999). At regional scales, however, disturbance history and regional species pools also affect local species richness (Grace 2000; Partel et al. 2000; Smith and Knapp 1999), and both native and exotic species are often more diverse in productive landscapes (Stohlgren et al. 1999). Although high densities of an invasive exotic are likely to depress the abundance of co-occurring native species, the regional effect of an exotic invasion is less easily predictable. The interactions among disturbance, dominance, and richness are complex in both native- and exotic-dominated communities. As in native-dominated communities, exotic dominants may not always decrease species diversity.

Clearly, we need a better understanding of the consequences of dominance for species richness. At what levels of dominant biomass or density does competitive exclusion affect species richness? How do productivity and vegetation physiognomy affect these critical biomass levels? Are critical biomass levels lower if the dominant also alters ecosystem processes?
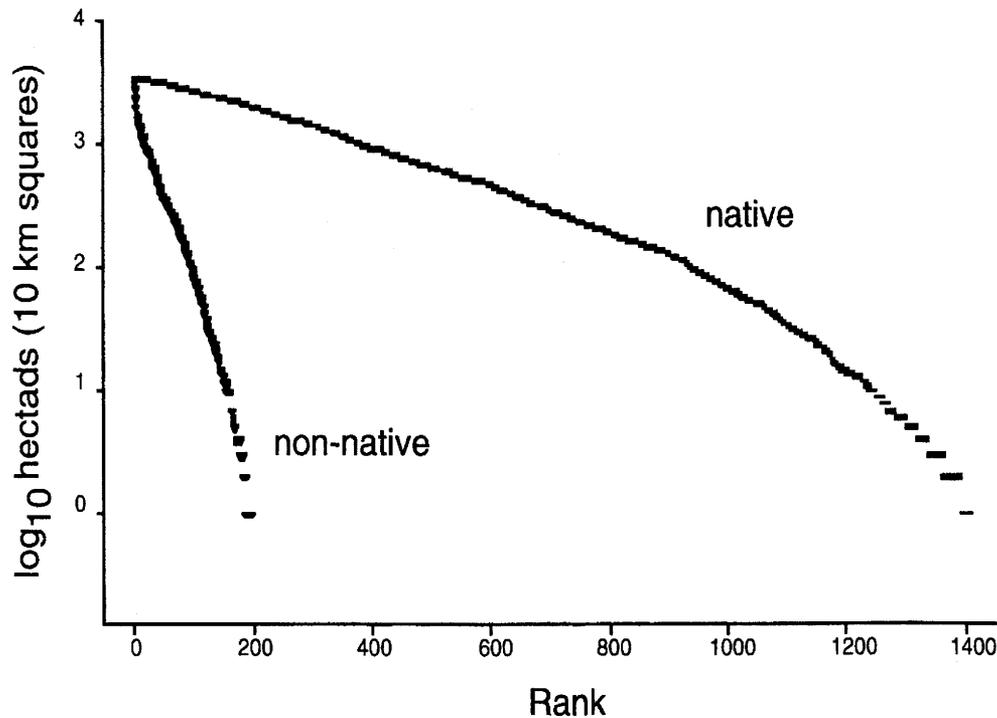
Figure 2. Area-diversity plots for native and nonnative British plants (reprinted from figure 6.3, Williamson 2002). Log of geographic range (area) of each species in Great Britain is plotted against the species rank as determined by their relative range sizes. Data are from the Ecological Flora Database.

RANGES OF EXOTIC SPECIES

Locally abundant native species are often widespread, occupying more habitats and wider ranges than locally scarce species (Collins et al. 2002; Hanski and Gyllen-berg 1997), and we expect that exotic species will follow similar patterns in their introduced ranges. Williamson (2002) found that for a given rank, the ranges of exotic species were smaller than those of natives (Figure 2). He suggested that, unlike native species, exotic species had yet to reach the extent of their potential ranges, but that, given time, should reach ranges similar to those of native species. In general we expect, then, that exotic species exhibiting high local densities likely eventually will affect many different plant communities over wide geographic ranges, whereas those that do not attain high local densities may not attain such broad ranges.

Although the relationship between range and density (or dominance) suggests fundamental differences between common and rare species, further research into the mechanisms behind the pattern are warranted. Under what circumstances might species persist at low densities across a wide range of habitats? Are the demographic vital rates that limit population growth in rare species, e.g., recruitment, seed production (Gaston 1994), the same as those that account for broad habitat tolerances in common species?

EFFECTS ON ECOSYSTEM PROCESSES

Ecosystem processes can be affected strongly by the innate characteristics of dominant species. Stand dominants modify canopy structure and light transmission to the understory, drive disturbance regimes, and influence system-wide productivity. McClaugherty et al. (1985) provided a striking example in the differences among forests on Blackhawk Island, WI, which were dominated by either sugar maple, aspen, white oak, white pine or hemlock; differences among these species in litter quality and production produced differences in the accumulation of forest floor litter mass and in nitrogen supply rates. Similarly, exotic litter production and quality will affect nutrient supply rates in invaded communities. The degree to which an exotic invader changes these processes in an invaded community depends on foliage and litter differences between the exotic and the native dominants. In Hawaii, stand-altering invasions have been described for *Myrica faya* Aiton (Vitousek et al. 1987) and, more recently, for the leguminous tree, *Falcataria moluccana* (Miguel) Barneby & Grimes (R. F. Hughes, personal communication), both of which are nitrogen-fixing trees encroaching on native *Metrosideros polymorpha* Gaud. forests. Both increase nutrient availability in young soils and alter the environmental context for all species in the community. Higher growth rates, stimu-

lated by the higher nutrient supply, not only may increase net primary productivity but also competitive interactions among native and exotic species. On young, nitrogen-poor soils of Hawaii, such changes facilitate the establishment and growth of fast-growing, physiologically plastic species, including both exotic invaders and native species. In this instance, an increase in stand productivity also may result in higher species richness as predicted by the hump-shaped productivity–diversity curves described above.

The effects of native dominants may differ across landscape gradients. Herbaceous biomass under the native mesquite declines with mesquite abundance on clay-loam soils but increases on shallow clay soils (Schade et al. 2003). In the case of exotic invasions as well, environmental context may alter invasion consequences. Lessons from the study of native dominants suggest that effects of invasive species likely will vary across heterogeneous landscapes. *Falcataria moluccana* has a greater effect on nitrogen supply in soils on 46-yr lava flows than on better-developed soils on 300-yr lava (R. F. Hughes, personal communication).

Native and exotic dominants affect disturbance regimes and regeneration processes. The course of succession often is set by the early establishment of dominance. In the Pacific Northwest United States, early site domination by the native red alder (*Alnus rubra* Bong.) can produce a stable hardwood stand in environments that more commonly support Douglas fir [*Pseudotsuga menziesii* (Mirbel) Franco] (Oliver and Larson 1996). The striking differences in stand structure, nutrient processes, and patterns of canopy turnover between communities dominated by these two species are strong evidence of the role of dominants in ecosystem and disturbance processes. In seasonally dry climates, grasses, ferns, and shrubs often provide the fuels that, with climate, drive fire frequencies, intensities, and effects. The shift in dominance caused by an exotic grass invasion can so alter fuel characteristics so as to change historic fire patterns (D'Antonio and Vitousek 1992; Tunison et al. 2001), resulting in fire-prone landscapes where fire once was rare. In seasonally dry woodlands of Hawaii, rapid postfire reestablishment by nonnative pyrophytic grasses and their coincidental monopolization of resources precludes the establishment of native woody species, altering the structure and composition of postfire plant communities (Hughes and Vitousek 1993).

MASS EFFECTS OF SEED PRODUCTION

High propagule pressure can affect successional patterns and dominance even in the face of superior competition. The red alder succession described above was due to the local abundance of alder and scarcity of Douglas fir seedlings. The abundance of red maple (*Acer rubrum* L.) in the Eastern Deciduous Forest is thought to be due in part to its high production of propagules. High seed production increases the likelihood of a red maple reaching and occupying suitable microsites ahead of competitively superior species (Beckage and Clark 2003). Because high propagule pressure contributes to the speed of many exotic invasions, management of seed rain, for example with biological control agents or creation of exotic-free buffer zones around high-value natural areas, should be central to any exotic control program.

CONCLUSIONS

These few examples suggest that a better understanding of the causes and consequences of native dominance can inform our understanding of exotic invasions and help predict the effects of such species in the early phases of establishment. It is useful to consider exotic species as special cases of otherwise common ecological phenomena, recognizing that both native and exotic species may be either core (dominant) or satellite (rare) species. Understanding the ecology of invasions within the total context of community and ecosystem ecology will provide guidelines for predicting effects and the consequences of alternative management strategies. The extraordinary densities reached by some invasive exotics suggest that quantitatively their effects may exceed those observed for many native dominants. A better understanding of the determinants of commonness and rarity among exotic species also will add to our understanding of the limits to abundance in native communities. The literature suggests that interactions among disturbance, dominance, and species richness patterns are complex in native-dominated communities. We should expect similar complexity when those communities become dominated by exotic species.

Community resistance to invasion may reside in the health, abundance, and distribution of the dominants, rather than in diversity per se. Hanski's (1982) proposition that most interspecific interactions are with or among core species, suggests that we should be paying close attention to this aspect of community structure in our attempts to understand regional patterns of invasibility and species richness. Similarly, successful plant community rehabilitation projects will seek to establish dominant species or their ecosystem functions (or both) early in the process. The selection of exotic species as

temporary dominants should be done with caution because that decision will entrain the context within which other species will establish and persist.

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