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Biotic barriers to plant naturalization

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Abstract. The likelihood of plant naturalization is often enhanced by the immigrants' escape from their native pests (predators, grazers, parasites and competitors). Without the debilitating effects of these pests, alien species often display greater fitness and vigour than they show in their home range. Yet the advantage conferred by this escape is not universally shared; alien plants can encounter novel biotic hazards or barriers in the new range for which they lack defences. For some aliens these new barriers are so extreme as to repeatedly preclude naturalization (e.g. *Theobroma cacao* in western Africa). Despite a general awareness that such 'fortuitous biological control' can occur, it has not been comprehensively documented, even in agriculture. These barriers can be illustrated among a taxonomically diverse group of alien plants, particularly in tropical forestry. Indirect, floristic evidence further supports a role for biotic agents in thwarting naturalizations. Among state and regional floras in the United States of America, naturalized species that are members of previously unrepresented genera in these floras are often more common than naturalized congeners of natives. These distributions among genera support the contention that naturalization is enhanced for alien species that lack native relatives. Such phylogenetic distance could minimize the likelihood of host extension or shift among the native pests that have co-evolved with native plants. Our current fragmentary information for the roles of biotic barriers leads to opposing conclusions: (i) the infrequency of these cases means they are much less important than physical barriers in thwarting naturalization; or (ii) they are important but routinely overlooked because, in part, small, immigrant populations are quickly destroyed by pests in the new range.

Introduction

Plant immigrants often achieve an advantage in future naturalizations by leaving behind their debilitating native pests (predators, grazers, parasites and competitors). This principle is well-established and forms the basis for biological control because the introduction of missing pests into a new range is the object of a biological control programme (Debach and Rosen 1991). Yet the application of such deliberate control needs to be extended to only an exceedingly small fraction of the descendants of immigrants. The vast majority go extinct without ever rising to numbers that require deliberate control: lists of 'transients', 'adventives', 'waifs' and other temporary residents in new ranges greatly exceed the naturalized flora (Mack 1995). We presume these extinctions are due to any of a myriad of barriers (*sensu* Polunin 1960) in the potential new range - forces that devastated the founders or their immediate descendants, or at the very least consistently reduced their numbers so that they never reached invasive proportions.

Ironically, our knowledge of the causes of these extinctions is remarkably meagre. There are obviously invariant physical factors (photoperiod, toxic or deficient levels of soil nutrients) that would always rule against some immigrants (e.g. Huenneke *et al.* 1990). Some physical forces operate seasonally, or at least frequently, and would be effective barriers to naturalization (seasonal frost, drought, flooding) (e.g. Nilsen and Muller 1980). Other physical factors operate rarely yet could still be effective barriers to naturalization (hurricanes, fires) (Kruger 1986; Morton 1980). Of course, such factors do not act only as barriers to alien plants. Both our historical and modern understanding of plant geography is based largely on the effects of a litany of physical factors on plant abundance and distribution (e.g. Schimper 1898; Walter 1985).

Our knowledge of the enormous benefits experienced by some immigrants coincident with escape from their native pests implies that biotic agents can also strongly affect plant distribution. However, we know far less, either in specific or general terms, about biotic compared to physical barriers for plant immigrants. Naturalists and ecologists have long noted that many naturalized species grow more vigorously, are more fecund, and display much less obvious pest damage in a new range compared to their native range (Thomson 1922; Crawley 1987). Clearly, these alien plants had not acquired any significant pests from among the new range's biota. When invasive, these immigrant species have been brought under control only after their native pests were introduced (Debach and Rosen 1991). The question remains as to what fraction of local extinctions is caused by one or more novel biotic agents that attack the immigrants in the new range, i.e. pests that the alien species had never before encountered.

Based on examples, including those discussed below, I contend that these biotic barriers deserve a much more systematic and intensive scrutiny than they have received so far. An unknown fraction of immigrant extinctions may be caused by such overlooked agents.

Biotic barriers to naturalization

Insects as barriers to naturalization

Given the enormous influence of insects as phytophages, it is not surprising that the largest known group of alien plant extirpations involves these organisms. Examples span many phytophagous insect orders (e.g. Coleoptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera) and include both continental and oceanic species (Table 1). For reasons that are unclear to me, a disproportionate number of examples have been detected in tropical forestry. This frequency may stem from the early and widespread introduction of economically-important tree genera throughout the tropics (*Acacia, Eucalypts, Pinus, Prosopis, Swietenia, Tectona*) for fuel and fibre (Zobel *et al.* 1987). The strong economic incentive to cope with any pest of these plantation crops could have led to the detection of native pests.

Examples of native-insect attack on alien plants are sufficiently extensive that some categorization is possible. By far the largest group consists of insects involved in non-lethal feeding, principally grazing (*sensu* Thompson 1982) (e.g. grasshoppers and many lepidopteran larvae). A second, much smaller category, consists of insects that can kill plants, but rarely, if ever, destroy a whole immigrant population. This category obviously includes predators but also some

Table 1. Lethal attacks by native insects that prevent (or reverse) naturalizations by alien plants.

Alien plant	New range	Native pest in new range	Reference
Casuarina equisetifolia	Puerto Rico	Formicidae	Little and Wadsworth (1964)
Eucalyptus deglupta	Solomon Is.	*Amblypelta cocophaga*	Bigger (1986)
Eucalyptus saligna	Cameroon	Isopterans	Monnier (1961) in Harris (1966)
Grevillea robusta	Puerto Rico	*Asterolecanium pustulans*	Martorell (1943)
Meliaceae	Tropics	*Hypsiphyla grandella* *H. robusta*	Gray (1972)
Pinus caribaea	Philippines	*Dioryctria rubella* *Petrova cristata*	Quiniones (1986)
Schinus terebinthifolius	South Africa	*Megastigmus rhusi*	Neser (1988)
Zanthoxylum flavum	Puerto Rico	*Apion martinezi*	Martorell (1943)

parasites (*sensu* Thompson 1982). Regardless of the mode of feeding, naturalization would not be deterred by these insects acting alone. The third and smallest group of cases are composed of insects that are so recurringly devastating that the alien species cannot be maintained, except by intensive cultivation. Insects in this third category preclude naturalization.

Two lepidopteran congeners, *Hypsiphyla grandella* and *H. robusta* have repeatedly thwarted attempts to introduce alien Melastomataceae into new tropical ranges. Their joint effect is magnified because they mostly occupy allopatric home ranges: *H. grandella* is widely distributed in tropical America, while *H. robusta* occurs in Australia, southeast Asia and elsewhere around the Indian Ocean basin. Together they circumscribe a huge tropical area in which alien members of this speciose plant family cannot be cultivated (Gray 1972).

Damage by termites is usually confined to dead wood and thus presents no direct threat to plant establishment. But termites can also voraciously attack the living wood of even chemically well-defended alien eucalypts. In Cameroon, destruction of *Eucalyptus saligna* in plantations has been 100% and nearly as high for other eucalypt species. High levels of destruction have also been reported in Gambia by Mohnier (1961) (cited in Harris 1966) and southern Africa by Poynton (1979) (cited in Kruger 1986).

Examples of attacks by insects indigenous to islands are particularly interesting because comparatively depauperate island-insect-faunas would appear less likely than continental faunas to contain phytophages that are capable of host shifts or extensions. The hemipteran *Amblypelta cocophaga* however plays this role. As the name implies, this polyphagous insect feeds on coconut and has more recently attacked introduced *Eucalyptus deglupta* in the Solomon Islands. These infestations by *A. cocophaga* are sufficiently severe that *E. deglupta* has been abandoned as a plantation crop in the Solomons (Bigger 1986). A similar abandonment of an introduced timber species because of the action of native insects has occurred in the Philippines. *Pinus caribaea*, introduced from the western Caribbean, is lethally attacked by two native shoot moths, *Dioryctria rubella* and *Petrova cristata*. Both moths have undergone a host extension from the native pine congener, *P. kesiya*. Infestation rates can be 100% in plantations (Quiniones 1986).

A preponderance of examples from tropical forestry is not likely to be an accurate reflection of the relative importance of tropical native insects compared to extra-tropical insect faunas in preventing naturalizations. If only because most mid-latitude crops have a much larger introduced range than the native range of their wild progenitors (Simmonds 1979), cultivation of many temperate crops has probably involved encounters with many native pests. Well-known examples include attacks by *Leptinotarsa decemlineata* (Colorado potato beetle) on *Solanum tuberosum* (white potato) (Hare 1980) and a lepidopteran, *Pyrausta nubilalis* (the European corn borer), on introduced maize in Europe. Less well-known examples include attacks by indigenous weevils on alien woody species in both Iceland and Britain. Although feeding by a native weevil *Otiorhynchus nodosus* on introduced *Larix siberica* in Iceland does not jeopardize persistence of the alien host, its attack is intriguing (Halldorsson 1994) because Iceland has no native gymnosperms. Consequently, this weevil has undergone a substantial host-extension from native woody dicotyledons to *L. siberica*. In Britain, *Otiorhynchus singularis* and *O. sulcatus* have similarly attacked the aggressive, ericaceous alien tree *Rhododendron ponticum* (Brown 1953).

Pathogens as barriers to naturalization

The role of microbial pathogens in affecting plant growth, abundance, and survival has long been appreciated in agriculture (van der Plank 1963, and references therein). My intention here is to note the incidence and epidemiology of pathogens that are virulent to a newly-encountered host. In one sense, microbial pathogens commonly encounter new hosts because these pathogens have enormous fecundity and are readily dispersed over great distances. This great dispersibility has made assessing the opposite circumstance (an alien plant entering the native range of a pathogen) much more difficult to identify reliably. Many plant pathogens probably owe their cosmopolitan ranges to dispersal by humans. As a result, we will probably never know the original home ranges for many plant pathogens (Fenner 1977). Nevertheless, for the cases cited below the native range of the pathogen and the alien range of the plant have been reliably established (Table 2).

The destruction of *Theobroma cacao* by CSSV (cacao swollen shoot virus) in western Africa is a well-known case of an alien plant acquiring a virulent pathogen native to the new range. Cacao, a native of South America, is now widely-grown in western Africa. These plantations occur within the home ranges of native trees belonging to several closely-related families, one of which (Sterculiaceae) includes *T. cacao* (Baker 1978). Apparently, CSSV has long parasitized native members of these families without major damage (e.g. *Cola chlamydantha, Sterculia tragacantha*). In common with the epidemiology of many other plant pathogens, the spread of CSSV among hosts is aided by an insect vector, a mealybug (*Planococcoides njalensis*). Establishment of large stands of closely-spaced cacao trees would have aided the insects' movements. As a result, losses to CSSV were devastating until procedures for the prompt removal of diseased trees were implemented (Leston 1970; Posnette 1981). Clearly, cacao naturalization in western Africa remains extremely improbable because of this native virus.

More recently, another virus , rose rosette disease (RRD) has been identified as reversing the spread of multiflora rose, *Rosa multiflora,* in the United States of

Table 2. Lethal parasitism by native microorganisms that prevents (or reverses) naturalizations by alien plants. Insect vectors are in parentheses.

Alien plant	New range in new range	Native pest	Reference
Cocos nucifera	Surinam/ Guyana	*Phytomonas* sp.	Dollet (1984)
Coffea liberica	Surinam/ Guyana	*Phytomonas* sp.	Dollet (1984)
Cordia alliodora	Vanuatu	*Phellinus noxius*	Neil (1988)
Elaeis guineensis	N. South America	*Phytomonas* sp.	Dollet (1984)
Eucalyptus saligna; E. grandis	Surinam	*Diaporthe cubensis*	Anon (1979)
Pyrus communis	Eastern North America	*Erwinia amylovora*	Billing (1981)
Rosa multiflora	Eastern USA	RRD (*Phyllocoptes fructiphilus*)	Amrine and Stasny (1993)
Theobroma cacao	Western Africa	CSSV (*Planococcoides njalensis*)	Leston (1970); Posnette (1981)

America. This Asian shrub has long been used as an ornamental and 'cover' species for wildlife. It has also spread westward throughout a large new range in the eastern half of the USA, often becoming a detrimental member of pastures. Once introduced in the Great Plains for windbreaks, multiflora rose came within the native range of RRD and its native vector *Phyllocoptes fructiphilus,* a mite. RRD, a pathogen of native roses in the Rocky Mountains, can devastate *R. multiflora,* e.g. mortality reached 88% in one population in Indiana. Once in contact with *R. multiflora,* the virus moved rapidly eastward, spanning >400 km in four years (Amrine and Stasny 1993). As a result of this 'fortuitous biological control' (*sensu* Debach and Rosen 1991), the spread of multiflora rose may be curbed in a manner that could not have been foreseen.

Protozoans are well-known agents for some of the most lethal diseases in animals, including humans (e.g. malaria, African sleeping sickness, Chagas disease); their role as lethal plant pathogens is much less appreciated but may be quite important. A trio of incompletely understood but nevertheless fascinating diseases endemic to northern South America (Surinam, Guyana and northern Brazil) severely hamper, if not prohibit, the prolonged cultivation of several alien crops. The pathogens are all flagellate protozoans in the genus *Phytomonas.* Each is restricted to the host's phloem. The commercially-important crops affected (coffee, coconut and African oil palm) are infected by these *Phytomonas* species only in northern South America, strongly suggesting they are indigenous. In the remarkable case of coconut palm - one of the most widely-distributed tropical species - cultivation in Surinam is blocked completely by the attack of its protozoan pest (Dollet 1984). Given the general lack of attention to protozoans in plant pathology, the scope of their world-wide role as factors in plant distribution and abundance becomes particularly intriguing.

Evidence from naturalized floras in the USA

The likelihood that the members of an alien species will acquire pests in their new range is partially dependent on the taxonomic affinity they share with native plants. For example, alien plants entering a range with many native congeners may have a greater likelihood of acquiring pests than immigrants with no such relatives (and, in turn, no pre-adapted pests that are likely to attack it) (Strong *et al.* 1984, and references therein). The evidence relevant to this contention is not extensive but nonetheless revealing. Connor *et al.* (1980) found that both *Quercus acutissima* and *Castanea crenata* had acquired multiple leaf-miners since their introduction in eastern North America; both species have been introduced within the home range of con-subgenerics. In contrast, they cite another case in which *Quercus suber* introduced to Australia, which lacks native *Quercus* species, has acquired no native leaf-miners. Apparently, none of the native Australian leaf-miners of *Nothofagus* species (a con-familial relative) are able to feed on *Quercus* species. Similar results for *Q. acutissima* and *C. crenata* in Florida were reported by Auerbach and Simberloff (1988).

As an extension of these observations, I searched for patterns among the genera containing naturalized species within vascular plant floras. I reasoned that if alien plants often owe their naturalization to an inverse taxonomic relationship to the native flora in their new range, this link would be reflected in the proportion of genera in the flora with only naturalized species compared with the number of genera with both native and naturalized members. For such a pattern to reflect a clear advantage for the members of non-native genera, I predicted that a substantial proportion (i.e. >60%) of genera with naturalized species should also be previously unrepresented in the region's flora.

To assess this hypothesis I surveyed published floras for the USA and I restricted my tallies to floras in which it was clearly stated that the species was 'naturalized' as opposed to more equivocal terms, e.g. 'introduced,' 'adventive' or 'exotic.' I used only the most recently published flora(s) for a region or state. The results are summarized in Table 3.

The vascular plants of California may well reflect a pattern among temperate biomes. As a large coastal state (about 410000 km^2), it includes many habitats, ranging from sea-level to the alpine. Its naturalized flora (about 1000 species) is strongly represented by species with no native congeners; 279 of the genera have no native congeners. Another 147 genera have both naturalized and native members (Hickman 1993). A few of the former group also occur in plant families unrepresented in the state's native flora, e.g. the Myrtaceae, represented by the genera *Eucalyptus* (nine species), *Leptospermum* and *Luma*, the Moraceae (three species in three genera) and Tamaricaceae (five species, all in the genus *Tamarix*). Plant families with more naturalized genera (i.e. represented by naturalized species only) are more common than genera with both native and naturalized members, e.g. Apiaceae (13 and 3), Brassicaceae (28 and 8), Iridaceae (9 and 1). Species that have only con-familial relatives in the native flora may be less likely to attract any new feeders, although such host extensions do occur, e.g. the host extension of the apple maggot (*Rhagoletis pomonella*) in North America from native *Crategus* species to introduced apple (*Malus pumila*) (Metcalf and Metcalf 1993).

Also noteworthy are large plant families represented by many native and alien genera, e.g. the Asteraceae. California's flora includes 152 native composite genera. Yet another 55 genera (90 species) have been added to the state's flora through naturalization. In contrast, only 24 composite genera have both naturalized and native members (Hickman 1993). This comparison suggests a degree of specialization among the native phytophagous fauna at the genus level, such that members of previously unrepresented genera have frequently entered the state and become naturalized.

Table 3. Plant genera with naturalized species in some state and regional floras in the USA and their distribution among genera with and without native congeners.

State/ region	Genera with naturalized species only	Genera with naturalized and native congeners	Reference
California	279	147	Hickman (1993)
Florida (central)	210	120	Wunderlin (1982)
Florida (tropical)	101	70	Long and Lakela (1976)
Hawaii	433	69	Wagner *et al.* (1989)
Illinois	207	138	Mohlenbrock (1986)
New York	67	162	Mitchell (1986)

Florida has had ample opportunity to receive many alien plants, represented in particular by ornamentals, because of its generally mild climate, ranging from warm temperate in the north, to subtropical in the south. The alien floras of central- (Wunderlin 1982) and tropical- (i.e. southern) (Long and Lakela 1976) Florida reflect the naturalization of many species in subtropical, and even tropical, genera that are otherwise unrepresented in the conterminous USA. A few of these genera also represent plant families new to the USA [e.g. *Casuarina* (Casurinaceae), *Tropaeolum* (Tropaeolaceae) Long and Lakela 1976; *Cannabis* (Cannabaceae) Wunderlin 1982]. Among grasses in tropical and central Florida, genera represented only by naturalized species are twice as common as those with both native and naturalized members. Furthermore, many of the most abundant and aggressive naturalized grasses in Florida have no native congeners: e.g. *Eleusine indica, Melinis minutiflora, Hyparrhenia rufa, Rottboelia exaltata* and *Cynodon dactylon*. The prevalence of such alien grass genera is curious because, unlike most other plant families, the herbivores associated with grasses are usually generalists at the 'family-level' (W.M. Lonsdale personal communication).

The New York state flora (Mitchell 1986) is the exception among those I screened: species in only 67 genera for which there are no native congeners have become naturalized in the state. By contrast, 162 genera contain both native and naturalized members. An explanation for this distribution is problematical, although the simple lack of opportunity to immigrate, for species that could become naturalized, can never be discounted. It is nevertheless curious that all the naturalized members (six species in six genera) of the Apiaceae (Umbelliferae) occur in genera without native congeners. Perhaps the native phytophagous fauna that has co-evolved with the native species of this chemically well-defended plant family (Berenbaum 1990) has routinely prevented immigrant umbellifers within native genera from becoming naturalized.

Not surprisingly, Hawaii with its extraordinarily high level of endemism among the native flowering plants (about 89%) now supports few naturalized species with native congeners (Wagner *et al.* 1989). Only 69 genera have both native and naturalized members. In contrast, representatives of at least 433 alien genera (about 860 species) have become naturalized in Hawaii, including tropical, subtropical and temperate alien taxa that have spread to widely varying degrees among all the archipelago's habitats. New families have been added through recent immigration to an extent that has not occurred in the conterminous USA. The native flora represents only 87 flowering plant families; post-Columbian immigration has added another 59. The many genera and families represented only by naturalized species supports another plausible reason for the extraordinary vulnerability of tropical and subtropical oceanic islands: the endemic Hawaiian native flora (73 dicotyledonous and only 14 monocotyledonous families) has provided a comparatively restricted array of defences with which the insular phytophagous insect fauna has co-evolved. Consequently, this fauna, which lacks representatives of such phytophagous groups as isopterans (Zimmerman 1948), has been largely unable to attack the diverse alien flora. Even among genera with natives, the naturalized flora often rivals or exceeds the size of the native flora. Of the 15 families with the most species in the archipelago, six (Poaceae, Myrtaceae, Malvaceae, Euphorbiaceae, Solanaceae, Fabaceae) have more naturalized members than natives. In one family, the Fabaceae, 94 of the 114 species in Hawaii are naturalized (Wagner *et al.* 1989), suggesting a remarkable inability of the native legume feeders to cope with the diverse chemical defences among the aliens.

Comparisons among such counts of naturalized and native genera do not in themselves resolve how frequently naturalizations stem principally from the inability of a native phytophagous fauna to feed upon the immigrants. The pattern seen here is, however, consistent with such an explanation. Biologists have long been interested in the geographic origins of a region's naturalized flora in an attempt to predict the potential source of future naturalizations and invasions (Baker 1986; Wells *et al.* 1986). These attempts have often focused on the similarity of the alien's home range, particularly climate, to a potential new range, as a predictor of the ability to persist in the new range (Wilson *et al.* 1992). Among their shortcomings, such lists obviously reflect the opportunity for immigration as much as any intrinsic environmental explanation. It may prove more informative to examine the phylogenetic relationship among previously unrepresented genera and the native flora in a new range. It would be informative, for instance, to explore the correlation between the naturalizations among previously unrepresented genera and their phylogenetic distance from native (con-familial) genera in the new range: do members of distantly related genera have a consistently higher frequency of naturalization than those in closely related genera?

Conclusions

Assessments of the frequency, extent, and magnitude of biotic barriers to plant naturalizations and invasions are in their infancy: information with which to resolve their importance is either anecdotal (examples of the extirpation of aliens by native phytophagous fauna and microbial parasites) or circumstantial (e.g. floristic surveys of regional floras). Consequently, either of two opposite conclusions can be drawn legitimately at this time.

Firstly, biotic barriers are not as important as physical barriers. The paucity of reliable, quantified cases of recurring alien plant extirpations caused by acquired pests in a new range may mean that biotic barriers are far less important than physical barriers. Many immigrants must routinely die from physical barriers, especially those that are unvarying (e.g. photoperiod, soil texture, soil toxicity), before they can be attacked by newly-acquired pests. Furthermore, immigrant populations are usually small, and it may take some time for an effective new pest to find them, and still longer to feed upon them routinely. Before either of these occurrences, the immigrants may be destroyed by physical factors. The likelihood of an alien plant acquiring a native pest may be a function of its phylogenetic relatedness to members of the native flora in the new range. Biotic barriers would probably not be important if they were expressed mainly through the actions of narrow specialists, rather than by the actions of broad generalists.

Secondly, biotic barriers are important and pervasive but not adequately recognized. The economic incentive to look for these barriers has been highly selective - strong for crops - but almost non-existent for other alien species. Furthermore, broad-spectrum control of a crop's pests in a new range through insecticides and fungicides could destroy significant native pests without them ever being specifically identified. The role of native microbial parasites is especially difficult to assess because the ranges of these organisms have been so extensively altered by human dispersal (Fenner 1977). It is likely that some alien plants are attacked by virulent microbial parasites within the parasite's now unidentifiable home range. Perhaps most important is the small size of almost all accidental introductions and many, if not most, deliberate introductions. Small immigrant populations would go unnoticed and could vanish rapidly upon detection by new pests. No evidence of the extirpation - or even the immigration - would remain.

I contend that this topic takes on increased importance if we view plant naturalizations (and especially invasions) as being restricted or thwarted by a finite number of barriers in a potential range. Although descendants that circumvent barriers can emerge through selection (Warwick *et al.* 1984), some barriers are clearly more formidable than others. Any given immigrant population may face so many barriers that it is extraordinarily unlikely that naturalizations, much less an invasion, will occur (Mack 1995). Nevertheless, characterizing all the barriers for an immigrant species would aid in predicting which species, now merely adventive or transient in a new range, could spread rapidly once any one barrier is circumvented.

The importance of all biotic barriers, not just phytophagous fauna and microbial pathogens, but also native competitors and the absence of requisite symbionts (e.g. Rhizobiaceae, ectotrophic mycorrhizae) in the new range can only be resolved through experimentation. Even then, their importance will undoubtedly vary enormously among species and locales. Nevertheless, I contend that these well-known biotic agents (predation, competition, mutualism) form the basis for a largely neglected topic in the search for explanations of past and present plant invasions that may well allow the prediction of the course of future invasions.

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