

## How relevant are ecologically equivalent species and vacant niches to the invasive potential of introduced woody plants?

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### Abstract

The widespread occurrence of invasive woody plants as well as their ability to displace native vegetation on oceanic islands would suggest that species disharmony, the flora's lack of competitive ability or the existence of vacant niches may explain, at least to some degree, islands' susceptibility to invasions. A review of the known instances of invasive woody plants in both island and continental settings does not provide a firm answer to the relevance of ecological equivalence and vacant niches to invasion failure or success.

### Introduction

Throughout the world, but on oceanic islands in particular, introduced woody plants are increasingly invading disturbed, semi-natural and natural plant communities (Cronk & Fuller 1995, Binggeli 1996). However, only a fraction of introduced species are actually spreading while the majority of exotics appear to pose no threat to native vegetation (Williamson 1996). Thus the two main questions relating not just to invasive woody plants, but to all invasive organisms, are:

- a) what set of attributes make a species invasive and/or a particular ecosystem/community susceptible to invasions, and
- b) can we predict which species will be invasive and/or which ecosystem/community will be invaded.

To-date limited progress has been made in trying to answer either question (e.g. Crawley 1987, but see Rejmanek & Richardson 1996 for their prediction of invasibility in the genus *Pinus*), although the conservation of biodiversity in many parts of the world depends on a satisfactory answer to both of them. In order to answer the second question progress must be made with the first one and here evidence relating to invasive tropical woody plants is reviewed.

### Reasons for the invasive success of woody plants

The ability of invasive woody plants to displace native vegetation, and this is particularly true on oceanic islands,

would suggest that species disharmony, the flora's lack of competitive ability or the existence of vacant niches may explain, at least to some degree, islands' susceptibility to invasions. The successes achieved with biological control programmes in controlling a number of invasive species in many parts of the world (Julien 1992) suggest that in many instances predator escape is also a major factor in the successful spread of introduced species, although failures would indicate that this is not always the case.

The idea of vacant niches in invaded regions has been proposed as a reason for the success of introduced species (e.g. Simberloff 1981). Although the niche concept is fundamental to ecology, its meaning has varied widely through time and major differences in interpretations have been expressed by scientists with a botanical or zoological backgrounds (Schoener 1989). As far as plants are concerned Grubb (1977) has argued that the following four components of a plant's niche can be recognized: habitat, phenology, life-form and regeneration. The modern theory of the niche, as understood by zoologists (Schoener 1989), focuses chiefly on resource competition (excluding the life-form and regeneration components of a plant's niche) and the niche is viewed as a property of the individual as opposed to the habitat as formerly understood. As a result vacant niches can not exist. However, by focusing on basic resources which are essential to all plants, this modern definition of the niche is too narrow to be of much help to explain the process of invasion by woody plants.

If one assumes that a plant's niche does include attributes such as life-form and life history, it is then important to

determine whether a successful invader does have similar species in the invaded region, that is ecologically equivalent species.

## Ecological equivalent species

Ecologically equivalent species should exhibit great similarities in species attributes (e.g. life-form, size, lifespan, fruit type, dispersal agent, etc), in site and climatic requirements as well as in successional status. Generally, only detailed investigations can differentiate ecologically equivalent species, thus inferences can only be drawn from a limited number of examples as the autecology of invasive and native plants is usually lacking.

A good example of ecologically equivalent species is provided by the two European timber trees *Acer pseudoplatanus* L. and *Fraxinus excelsior* L. both native to Europe, with the former being invasive in many parts of

the world. Their autecology is markedly similar but they differ mainly in terms of duration in seed dormancy, tolerance to flooding, susceptibility to grass competition and variation in latitudinal and altitudinal distributions (Binggeli 1992).

## Ecological equivalence in the tropics

A review of the literature of well-documented invasive woody species in the tropics (for detailed cases histories see [species accounts](#)) shows that in only one case is the existence of an ecologically equivalent species a possibility (Table 1). In tropical Africa the introduced *Cecropia peltata* is difficult to differentiate from the native *Musanga cecropioides* from a morphological and autecological point of view. However, the former species has been reported as displacing the latter. In all other cases the existence of ecologically equivalent species in the invaded region is wanting.

**Table 1.** Occurrence of ecologically equivalent species in the flora of tropical ecosystems invaded by well reported invasive woody plants. (LF = life-form, T = tree, sT = small tree, S = shrub, V = vine) (information extracted from detailed [species accounts](#)).

Species	LF	Invaded regions	Habitat invaded	Existence of ecologically equivalent species in the invaded region and main differences	
<i>Acacia nilotica</i>	T	Australia, Indonesia	grassland	No	Life-form hitherto absent
<i>Cecropia peltata</i>	T	Africa, Asia	disturbed areas, and forest gaps	Yes	Competing with a morphologically ecologically similar species
<i>Chromolaena odorata</i>	S	Africa, Asia	fallow, logged forest	No	Grows faster
<i>Clidemia hirta</i>	S	Oceanic islands	disturbed areas, forest	No	Unique life-history
<i>Lantana camara</i>	S	Tropics	pasture, plantations	No	Allelopathy, fire tolerance, fast growth rates, and great variability
<i>Leucaena leucocephala</i>	sT	Pacific islands	disturbed areas	No	
<i>Maesopsis eminii</i>	T	East Africa	natural & secondary forest	No	Unique reproductive cycle
<i>Melaleuca quinquenervia</i>	T	Florida	swamp	No	Different water requirements
<i>Miconia calvescens</i>	sT	Pacific islands	forest	No	Unique life-history
<i>Mimosa pigra</i>	sT	Australia, Thailand	flood plain	No	Life-form hitherto absent
<i>Myrica faya</i>	sT	Hawaii	lava flows	No	Mycorrhizal associations and growth rates
<i>Passiflora mollissima</i>	V	Hawaii	forest	No	
<i>Pinus patula</i>	T	East Africa	forest, grassland	No	No <i>Pinus</i> species
<i>Pittosporum undulatum</i>	T	Jamaica	forest	No	Rooting system and response to hurricane
<i>Psidium guajava</i>	sT	Pacific islands	pasture, forest	No	Mycorrhizal associations
<i>Schinus terebinthifolius</i>	sT	Florida	disturbed areas, grassland	No	Mycorrhizal associations and reproductive phenology
<i>Syzygium jambos</i>	T	Oceanic islands	forest, old field	No	Shade tolerant and large fleshy fruits
<i>Ulex europaeus</i>	S	Montane regions	pasture	No?	No clear comparative species identified

A number of introduced species appear to possess attributes not found in the local flora, such as mycorrhizal associations and life-history characteristics or have life-forms not encountered at all (Table 1). These unique characteristics must provide the invasive species with some competitive advantage over native species, although this has yet to be demonstrated.

### **Can we predict which woody species will become invasive using species characteristics only?**

Although the evidence presented above clearly suggests that most introduced species, which have become highly successful invaders, do not have ecologically equivalent species in the flora of the invaded region, ecosystem characteristics are nevertheless important if not determinant to the success of an invader. The majority of species reported in Table 1 exhibit a time-lag between their introduction and their subsequent spread. Major changes in a biotic factor (e.g. grazing, pollinator, seed disperser) or an abiotic (e.g. fire, wind, flood, logging) factor determine the duration of time-lag (Binggeli 1995).

For instance the phenomenal spread of *Miconia calvescens* in French Polynesia is probably a result of a number of factors including unique species attributes and introduced bird species as efficient dispersers (Meyer 1994), but the vegetation structure of the native vegetation is likely to have had a predominant role. The forests of the Society Island are relatively small in stature and *Miconia* rapidly reaches canopy height, but not the height of emergent trees, to usurp native woody plants. Being a small tree of around 15 m, *Miconia* would be unable to have such an impact in forests with canopies reaching greater heights (25-40 m).

### **Conclusion**

Instances of invasive woody plants presented above do not provide a firm answer to the relevance of ecological equivalence and vacant niches to invasion failure or success. The evidence indicates that no single factor or concept is sufficient to explain the wide array of examples which are known in some detail. Further progress, particularly in relation to prediction of invasiveness, will only be made when a good understanding of the invasive species' autecology in both the native and invaded regions and the ecology of invaded communities will be known for a larger number of instances. Much will also be gained by looking at introduced species which have failed to spread. Many of the generalisations regarding biological invasions have been based on theoretical studies and a dearth of basic field data. It is now essential that data on wide array of species and ecosystem attributes should be collected in a systematic fashion. This requires a concerted effort by all scientists concerned.

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### **Article history**

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