Research

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Propagule pressure hypothesis not supported by an 80-year experiment on woody species invasion

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Ecological filters and availability of propagules play key roles structuring natural communities. Propagule pressure has recently been suggested to be a fundamental factor explaining the success or failure of biological introductions. We tested this hypothesis with a remarkable data set on trees introduced to Isla Victoria, Nahuel Huapi National Park, Argentina. More than 130 species of woody plants, many known to be highly invasive elsewhere, were introduced to this island early in the 20th century, as part of an experiment to test their suitability as commercial forestry trees for this region. We obtained detailed data on three estimates of propagule pressure (number of introduced individuals, number of areas where introduced, and number of years during which the species was planted) for 18 exotic woody species. We matched these data with a survey of the species and number of individuals currently invading the island. None of the three estimates of propagule pressure predicted the current pattern of invasion. We suggest that other factors, such as biotic resistance, may be operating to determine the observed pattern of invasion, and that propagule pressure may play a relatively minor role in explaining at least some observed patterns of invasion success and failure.

What limits the establishment of plant species in a community is a perennial question in ecology. The role of ecological filters versus that of availability of propagules has been the focus of substantial research, showing that species response may depend strongly on local biotic and abiotic factors (Turnbull et al. 2000, Clark et al. 2007, Poulsen et al. 2007, Myers and Harms 2009). However, these articles show that propagule limitation seems to be a fundamental factor explaining species presence and abundance. This result pertains not only to native species; several studies suggest that both native and exotic species can be affected by propagule availability (Lockwood et al. 2005, Simberloff 2009).

Historically, the study of biological invasions has been focused on two aspects believed to be the key to understanding success or failure of introduced species, but that are unrelated to propagule availability. These are 1) the intrinsic characteristics of the introduced species and 2) the characteristics of the community or environment where it was introduced (Elton 1958, Baker 1965, Mooney and Drake 1986, Drake et al. 1989). These two features – the "invasiveness" of species and "invasibility" of communities – were highlighted in the SCOPE (Scientific Committee on Problems of the Environment) program that triggered modern invasion biology in the 1980s (Simberloff 2009), and during the 1980s and 1990s most studies on invasion were based on these two factors and a number of hypotheses associated with them (Richardson and Pyšek 2006). Only recently has propagule pressure been proposed to be crucial to explain the success or failure of exotic species (Lockwood et al. 2005, Simberloff 2009).

Propagule pressure – that is, propagule size (number of introduced individuals), number of distinct introduction events (each with its own propagule), and/or the spatial and temporal patterns of propagule arrival – has been claimed to be most frequently the key factor explaining success or failure of invasions (Cassey et al. 2004, Colautti et al. 2006, Lockwood et al. 2005, 2007, Reaser et al. 2008). For example, Lockwood et al. (2009) stated that "it is now widely appreciated that the primary determinant of establishment success is propagule pressure or the number of individuals introduced." A few detailed studies on experimental systems with information on propagule pressure and success rate offer support for this hypothesis (Memmott et al. 2005, Von Holle and Simberloff 2005, Maron 2006). However, most studies with long historical records (decades) of successes or failures of introductions have relied on indirect measurements of propagule pressure (like sales records from plant nurseries) or on non-experimental systems (e.g. bird introductions by acclimatization societies); this reliance may lead to biases (Simberloff 2009). For example, confounding factors are usually associated with propagule pressure (Lockwood et al. 2007), and it may be that a species prone to succeed (e.g. found to have succeeded elsewhere) would have been introduced in larger numbers than species with lower chances of success by land managers or acclimatization societies (Simberloff 2009). Also, given the characteristics of some of the historical data (some more than 100 years old), they may be prone to misinterpretation (Moulton et al. 2010).

We conducted this study on Isla Victoria, Nahuel Huapi National Park, Argentina. On this island at the beginning of the last century hundreds of thousands of woody plants from many non-indigenous species were planted to determine which species would thrive in the region (Simberloff et al. 2002, 2003). We know now that many of them have often invaded natural ecosystems elsewhere (Rejmánek and Richardson 1996, Richardson and Rejmánek 2004; Table 1). This area provides an excellent opportunity to test the role of propagule pressure because we have detailed information on both the current extent of colonization by each exotic woody species on the island and direct measures of propagule pressure during the introduction process.

Methods

The study site

Isla Victoria, Nahuel Huapi National Park, Argentina (40°58'S, 71°32'W) has an area of ca 3710 ha. Starting ca 1925, more than 130 species of exotic woody species were planted on this island. In the late 1940s the systematic introduction of exotic species stopped, and by 1960 all activities associated with planting exotic trees and cattle ranching were cancelled, as this area was part of a national park. For many of the species that were planted detailed information is available on the number of planted individuals and the timing and locations of the planting. This island is part of a protected area and the plantations have been left untouched for many decades. Currently, the island is mostly covered by two dominant native trees, *Nothofagus dombeyi* (coihue) and *Austrocedrus chilensis* (ciprés), but several roads, old fields, and facilities of the national parks administration remain (Simberloff et al. 2002).

Invasion survey

Studies of seed dispersal in pines show that a number of seeds can be dispersed long distances, hundreds or thousands of meters (Greene and Johnson 1989, Nathan et al. 2000), and long-distance dispersal has been shown to be extremely important for pine invasion (Higgins and Richardson 1999). Pine colonization in North America after Quaternary

Table 1. Studied species, common names, regions of origin, whether invasive or naturalized elsewhere, and whether predicted to be invasive by the method of Rejmánek and Richardson (1996) (species with positive Z-scores are expected to be invasive). Code for countries: ARG = Argentina, Australia = AU, Austria = AUS, Belorussia = BRU, Brazil = BR, Bulgaria = BU, Canada = CA, Chile = CH, Czech Republic = CR, France = FR, Germany = GE, Georgia (former USSR) = GA, Great Britain = GB, Hawaii = HA, Hungary = HU, Ireland = IR, Kenya = KE, Lithuania = LI, Malawi = MA, New Zealand = NZ, Norway = NOR, Puerto Rico = PR, South Africa = SA, Poland = PO, Russia = RU, Spain = SP, Sweden = SW, Tanzania = TA, Ukraine = UKR. Codes for states and regions in North America: California = CAL, Missouri = MS, Michigan = MIC, New York = NY, Ontario = ON, southeast = SE, northeast = NE.

Species	Common name	Region of origin	Invasive elsewhere[a]	Naturalized elsewhere[a]	Predicted to invade based on its traits[b]. Z-scores in parenthesis
Acer pseudoplatanus	sycamore	Europe, Asia	NOR	N/A	N/A
Araucaria araucana	monkey-puzzle	South America	GB	N/A	no (<0)
Cupressus sp[c]	cypress	North America	N/A	AU, BR, GA, KE, MA, PR, TA, AU, GB, IR, NZ	yes (5.5 to 5.7)
Juniperus communis	common juniper	North America, Asia and Europe	N/A	N/A	yes (5.6)
Larix decidua	European larch	Europe	CR, GB, NZ	CA, IR, LI, NZ, USA (NE and NY)	yes (5.2)
Pinus contorta	lodgepole pine	North America	AU, GB, NZ, CH, IR, SW	ARG, CH, RU	yes (11.41)
Pinus lambertiana	sugar pine	North America	N/A	N/A	no (–12.35)
Pinus monticola	western white pine	North America	N/A	ARG	yes (1.7)
Pinus mugo	mountain pine	Europe	NZ	GB, LI, USA (NE), RU	N/A
Pinus nigra	black pine, Austrian pine	Europe, Asia	AU, FR GB, HU, NZ, USA (Mic)	CR, LI, RU, USA (NE)	yes (1.33)
Pinus ponderosa	ponderosa pine	North America	ARG, AU, CH, NZ	RU	yes (0.29)
Pinus strobus	eastern white pine	North America	CR, HU, NZ	BRU, BU, GE, GB, PO, RU, UKR	yes (3.46)
Pinus sylvestris	Scots pine	Europe, Asia	CA (ON), CH, NZ	ARG, IR, USA (NE, SE, NY)	yes (7.12)
Pinus wallichiana	Himalayan pine	Asia	N/A	N/A	yes (0.66)
Pseudotsuga menziesii	Douglas fir	North America	ARG, AUS, BU, CH, GER, GB, NZ	CR, IR, USA (NY)	yes (5.6)
Sequoia sempervirens	redwood	North America	N/A	GB, NZ	yes (11.9)
Sequoiadendron giganteum	giant sequoia	North America	N/A	UKR	yes (3)
Tsuga candadensis	eastern hemlock	North America	N/A	GA, PO, USA (MS)	yes (2.3)

[a] based on: Fremstad and Elven 1996, Richardson and Higgins 1998, Simberloff et al. 2002, Richardson and Rejmánek 2004, Bustamante and Simonetti 2005, Richardson 2006, Peña et al. 2008, Simberloff et al. 2010.
[b] based on Rejmánek and Richardson 1996, Richardson and Rejmánek 2004.
[c] these are two species we could not differentiate in the field, *Cupressus macrocarpa* and *Cupressus lusitanica*.

glaciations offers a good example; the average rates of northward migration were 400 m yr^{-1} for *Pinus banksiana* in eastern North America and 670 m yr^{-1} for *P. contorta* in coastal Canada and Alaska (Macdonald et al. 1998). Both of these species were planted on Isla Victoria without becoming invasive, although they invade elsewhere.

A detailed survey of all the individual non-native trees in the vicinity of the two main areas of planting on Isla Victoria (south from the Puerto Pampa plantations and north and south from the central area plantations) was conducted in 2001 (Simberloff et al. 2002). Transects, 10 m wide parallel to the plantations starting 100 m away from them and placed every 100 m after that, were established to find the colonizing individuals inside the native communities. The total length for all transects was 28.73 km (area equal to 28.73 ha). In this study all individuals (of any size, from seedlings to adults) of every exotic non-native tree species were recorded. Consult Simberloff et al. (2002) for a detailed explanation of surveying methods. Before this survey, plantations were not removed in the study areas and there was no systematic attempt to remove or control exotics outside plantations, so the results of this study accurately depict the natural colonization of the island by these introduced plant species.

Planting surveys

We gathered data on the introductions from publications and internal records that still remain from the era when planting of exotic trees was underway. We used Lebedeff (1932, 1942), Koutché (1942), and Barrett (1952), as well as many internal reports in the Parque Nacional Nahuel Huapi archives. These records include detailed information on variables such as growth rates, survival, sizes, cone production, and other measurements that interested the foresters responsible for the plantations. Because all species used in our study survived on the island, we were able to check ambiguous records by determining the current presence of the species. We were able to collect propagule pressure information for 18 introduced species (Table 1). All are currently present in the plantations, and individuals of all these species have attained large sizes. Seven of the 18 species for which we have propagule pressure data were never found outside their plantations by Simberloff et al. (2002): *Sequoiadendron giganteum*, *Pinus mugo*, *P. nigra, P. strobus*, *P. wallichiana*, *P. lambertiana* and *Tsuga canadensis*. Many other species were planted on the island and are still present, but for them the introduction records were not as detailed as those of the 18 species we used. The specific geographic origins of the propagules for the 18 studied species are unclear. All species were planted as seedlings in the forestry plantations, and the internal documents suggest that many were brought into the area as seeds and a few as seedlings, but often the specific origin was unrecorded and the number of different sources cannot be determined. We examined the relationship between the number of individuals of the studied exotic species established in the study areas outside the plantations and three variables representing propagule pressure: 1) no. of introduced individuals (i.e. no. of planted seedlings), 2) no. of sites (plantation areas that occupy tens of hectares and are at least 1000 m apart from each other) to which they were introduced in the vicinity of the areas surveyed by Simberloff et al. (2002), and 3) no. of times the species were introduced (i.e. no. of years during which the species were planted).

Data analyses

We analyzed the association between the number of individuals of 18 exotic species established outside plantations and three variables for propagule pressure. We used multiple and simple linear regressions to seek a relationship among variables. The variable "number of individuals found outside plantations" was log-transformed to achieve the required assumptions for linear regression analyses (natural logarithm, ln, of the value plus one, since some values were zero). We conducted a multiple regression analysis with the studied variables using stepwise variable selection to detect if these variables in combination were associated with invasion success. Because we expected high correlation among the independent variables, we performed correlation analysis to detect which variables were highly correlated. All analyses were conducted with SAS 9. We also conducted generalized linear models (GLMs) with the assumption of a Poisson distribution with a log–link function also using SAS to seek a relationship among the studied variables to corroborate if different analyses would produce the same results.

Results

None of the multiple or single regression analyses for the three estimators of propagule pressure and the natural logarithm of the number of individuals subsequently established were significant (Fig. 1). There was no relationship between the number of individuals found invading in the forest and the number of planted individuals ($F = 2.99$, $p = 0.11$, $R^2 = 0.16$, $n = 18$), the number of areas where they were planted ($F = 0.69$, $p = 0.42$, $R^2 = 0.04$, $n = 18$), or the number of times they were introduced ($F = 3.04$, $p = 0.10$, $R^2 = 0.16$, $n = 18$). In sum, it is clear from the examination of the untransformed data (Fig. 1) and the statistical tests on the log-transformed data that there is no relationship between the dependent variable and any of the three independent variables. Analyses using generalized linear models with the assumption of a Poisson distribution yielded the same results: none of the estimators of propagule pressure and the number of individuals subsequently established were significant.

There was a significant correlation between two of the independent variables (number of introduced individuals and number of years they were planted), with a Pearson's correlation coefficient of $r = 0.65$ ($p = 0.004$). The correlations for the number of introduced individuals and number of years they were planted versus the number of areas where they were planted were not significant, with $r = 0.40$ ($p = 0.11$) and $r = 0.39$ ($p = 0.12$), respectively. The stepwise procedure among the variables that were not significantly correlated did not produce a best model, because no variable met the $p = 0.10$ significance level criterion for staying in the model.

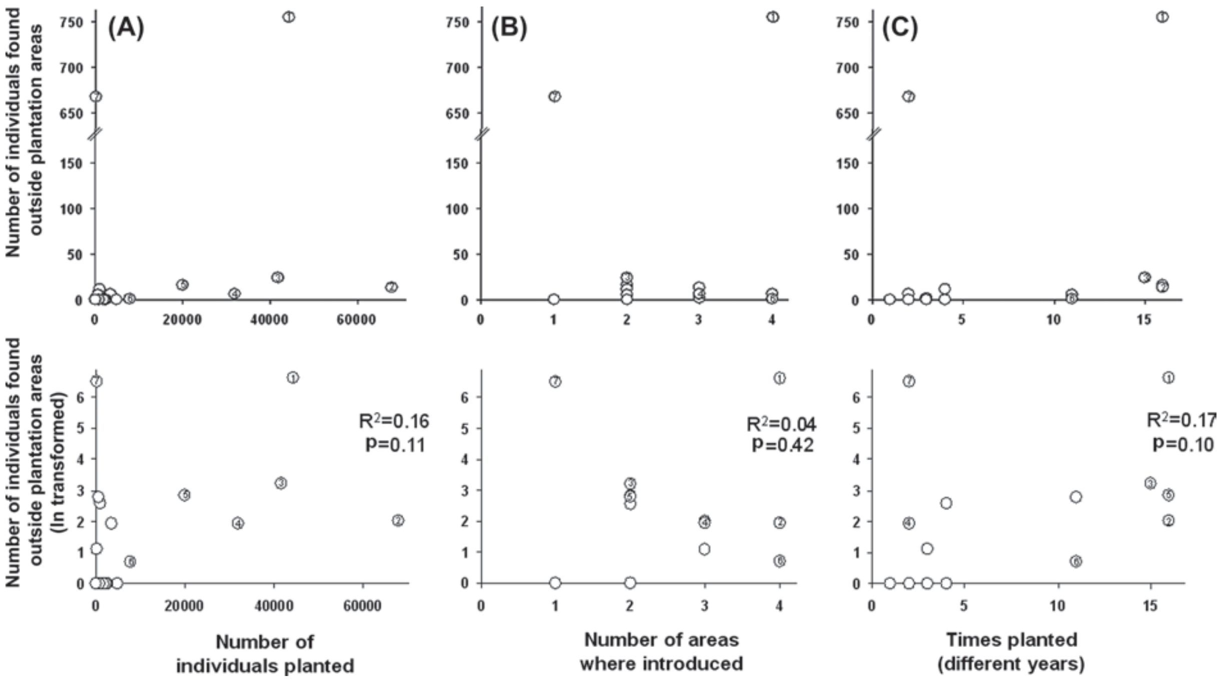

Figure 1. Relationships between three different estimators of propagule pressure and the actual amount of invasion in the study area. Relationship of individuals observed invading (top row) and the natural logarithm of the individuals observed invading (bottom row) versus: (A) number of areas where the species was introduced, (B) number of planted individuals, and (C) number of times (different years) the species was planted. Numbers inside the circles in the graphs denote seven noteworthy species. 1 = *Pseudotsuga menziesii*, 2 = *Pinus sylvestris*, 3 = *Pinus contorta*, 4 = *Acer pseudoplatanus*, 5 = *Pinus ponderosa*, 6 = *Larix decidua*, 7 = *Juniperus communis*.

Discussion

We found no support for the hypothesis that propagule pressure is determining the fate of introduced woody species to our study system. The lack of support for the hypothesis, which contrasts with previous studies on many other systems, could be due to the scale at which we conducted this study. General reviews on the topic of propagule pressure that have found strong support for the hypothesis have largely been based on studies using two approaches for testing the hypothesis (Cassey et al. 2004, Lockwood et al. 2005, Colautti et al. 2006). One approach is based on small experimental plots over short time periods, where propagule densities and degree of invasion can be measured in detail. The other approach is to use large-scale observational studies (regional or continental level) over long time periods where the propagule size is obtained from indirect estimates, and where invasion is usually described as a categorical variable (i.e. successful vs unsuccessful). Our study was over a long time (ca 80 years) and at a relatively large scale (hundreds of hectares), on long-lived plant species, and we used direct measures of propagule pressure (no. of planted individuals) and of the degree of plant invasion found in the area (no. of individuals found outside plantations), so it could be argued that this study differs fundamentally from others on propagule pressure. Nevertheless, we believe that despite our unexpected results, the analysis performed at the landscape level, with detailed information on both propagule pressure and invasion records, provides a strong test of the hypothesis for the studied species. Moreover, it has been suggested that the effect of propagule pressure may be taxon-specific and that for some groups like Pinaceae, to which many of the studied species belong, it may have less explanatory power than for other groups, although this hypothesis requires further testing (Rejmánek et al. 2005).

There could be a threshold number of individuals that greatly increases the chances of success for some of the analyzed species, but that could be much larger than the introduced numbers in our study area. Simberloff et al. (2010) found that the first records of invasion by exotic conifers in the Southern Hemisphere were closely related to the time when large-scale plantations for forestry started, even when smaller introductions for other purposes (e.g. wind barriers, ornamental) had occurred much earlier. Observational studies on woody species have found support for the propagule pressure hypothesis, but at a much larger spatial scale (regional or larger) and with higher levels of propagules (e.g. hundreds of hectares of exotics used as invasion foci, or tens or hundreds of areas where introduced) (Rouget and Richardson 2003, Krivanek et al. 2006, Bucharova and van Kleunen 2009). Therefore, it could be that millions of individuals planted in hundreds of different places may trigger invasion, rather than thousands of individuals planted in a few places. A global review of the topic may be needed to address this issue.

This study has limitations. For example, only two species – Douglas fir and common juniper – have successfully invaded the area so far (i.e. are commonly found outside plantations, sometimes in large densities; Simberloff et al 2002), and the "experiment" has been running only about 80 years. Nevertheless, most of these species would have been predicted to invade based on their traits – small seed mass, short length of juvenile period, and/or small intervals between large seed crops (Rejmánek and Richardson 1996, Richardson and Rejmánek 2004), with some species having notably high intrinsic invasiveness (i.e. high Z-score based on the methods of Rejmánek and Richardson (1996), e.g. *Pinus contorta*, Table 1); and they have been shown to be invasive elsewhere (Table 1). Also, many were planted in large quantities (more than 1000 individuals for 12 of the 18 species). Those that did not trigger an invasion (all species but Douglas fir and juniper) were planted with a range of numbers from tens to almost 70 000 individuals, and the two successful invaders are near the ends of this gradient, from fewer than 100 individuals for juniper to almost 45 000 individuals for Douglas fir. Data on other successful invaders would have added valuable information, but surprisingly, despite the large colonization pressure (sensu Lockwood et al. 2009), only two of the 130 + species introduced successfully colonized the area.

It could be that this system, because it is now mostly covered by forests of *Nothofagus dombeyi* and *Austrocedrus chilensis*, has strong biological inertia, and 60 to 80 years may not be long enough to detect the effect of propagule pressure (Von Holle et al. 2003, Martin et al. 2009). However, the island has many open areas where the exotics could have established (e.g. roadsides, old farms, forest gaps), many of them near or adjacent to plantations, and the exotics are absent from there (expect for Douglas fir and juniper). Time lags between arrival and invasion are expected to occur for many of the studied species in the region (Richardson et al. 2008, Simberloff et al. 2010), but the time during which they have been present may be considered to be sufficient, assuming that propagule pressure is the key factor. In support of this idea, Richardson et al. (2000) suggested a threshold of 50 years to determine if trees could become invasive or not (i.e. if they did not invade an area in 50 years or more they can be labeled as non-invasive). It is important to note that most of these species reach reproductive maturity before 10 years of age.

We lack information on different propagule numbers for a given species (i.e. replication per species), and there is evidence that various traits may make a species benefit more or less from enhanced propagule pressure (Blackburn et al. 2009). For example, it could be hypothesized that wind-dispersed species (such as many species in the Pinaceae) might be more sensitive to low propagule pressure owing to their limited dispersal ability far from parent plants, whereas animal-dispersed species (such as juniper) may be less sensitive. In fact, we have argued that at least part of the reason that juniper has invaded on Isla Victoria is how readily it is dispersed by birds and mammals (Simberloff et al. 2002). Half of the studied species belong to one genus (*Pinus*), and most of the studied species belong to a single family (Pinaceae), which limits our ability to analyze the effect of phylogeny or to control for its impact on the observed results. Propagule pressure can be more or less important for different families with different dispersal syndromes.

It is possible that, even if propagule pressure is huge, invasion may be halted by other factors (Wilson et al. 2007). Previous studies on the island have suggested that biotic factors, such as lack of mycorrhizal fungi, deer herbivory, and seed predation, may play roles in determining which species invade (Nuñez et al. 2008a, b, 2009, Relva et al. 2010). This is clearly the case for *Pinus sylvestris* (the most heavily planted species on the island with ca 67 900 individuals planted, in three areas, for 16 years), which rarely establishes on Isla Victoria because the introduced aphid *Pineus pini* (Hemiptera: Adelgidae) is present. This insect has been shown to severely affect *Pinus sylvestris* elsewhere, and the few observed individuals of this pine on the island were ravaged by the aphid (Simberloff et al. 2002).

In our study system ecological filters seem to be more important than propagule pressure, as has been reported elsewhere for other systems (Clark et al. 2007). Our results suggest that propagule pressure may not be a key factor explaining invasion of exotic trees in our study system. However, it is still unclear which factors can trigger invasion in the area. Multiple factors appear to be operating to determine which species invade and which do not. It is also noteworthy that the threshold for conifer invasion may be higher than the amount of pressure generated by the plantations on Isla Victoria to overwhelm the role of other factors, such as biotic resistance (above; Von Holle and Simberloff 2005, Simberloff et al. 2010). Therefore, propagule pressure may still play a role in conifer invasion but at a scale at which experimental tests – like the one reported here – are notably challenging.

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