
The Horticultural Trade and Ornamental Plant Invasions in Britain

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Abstract: *Ornamental horticulture has been recognized as the main pathway for plant invasions worldwide. We examined the link between propagule pressure created by the presence of ornamental plants in the market and their ability to escape from cultivation and establish in the wild. A random sample of 534 non-native ornamental species on sale in nineteenth century Britain showed that 27% of these species were recorded growing outside cultivation and 30% of those were established. Species that had escaped from cultivation were more frequently on sale both in the nineteenth century and today than nonescaping species. We used logit regression models to identify biological and socioeconomic variables that affect species' abilities to escape cultivation and become established. Frequencies in the market in the nineteenth century and today were good explanatory variables that distinguished escaping from nonescaping species, whereas for the transition from casual to established status these two socioeconomic variables were either absent or only of weak significance. Biological characteristics that increased the probability that a species would escape from cultivation were species height, a European native range, and being an annual. Climbing plants and species intolerant of low temperatures were less likely to escape. In contrast, the establishment probability was greater if the species belonged to a genus native to Britain and increased as the number of continents in a plant's native range increased. Annual plants had a reduced probability of establishment. Market presence, prices, and the date of introduction are among the socioeconomic factors that have had important effects on the observed course of invasions.*

Keywords: casual alien plants, established alien plants, market presence, plant nursery catalogs, propagule pressure

El Comercio Horticultural y la Invasión de Plantas Ornamentales en Gran Bretaña

Resumen: *Mundialmente, la horticultura ornamental ha sido reconocida como la principal vía para la invasión de plantas. Examinamos la relación entre la presión de propágulos creada por la presencia de plantas ornamentales en el mercado y su capacidad de escapar del cultivo y establecerse en el medio silvestre. Una muestra aleatoria de 534 especies de plantas ornamentales no nativas en venta en Gran Bretaña en el siglo XIX mostró que 27% de estas especies fueron registradas fuera de cultivos y 30% de ellas estaba establecido. Las especies que escaparon del cultivo estuvieron en el mercado más frecuentemente, tanto en el siglo XIX como actualmente, que las especies que no escaparon. Utilizamos modelos de regresión logística para identificar variables biológicas y socioeconómicas que afectan las capacidades de las especies para escapar al cultivo y establecerse. La frecuencia en el mercado en el siglo XIX y actualmente fueron buenas variables explicativas que distinguieron entre especies que escapan y no escapan, mientras que estas dos variables socioeconómicas estuvieron ausentes o tuvieron baja significancia para la transición de estatus casual a establecido. Las características biológicas que incrementaron la probabilidad de que una especie escape del cultivo fueron la*

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altura de la especie, un rango nativo europeo y que fuera una especie anual. Las plantas trepadoras y especies intolerantes a bajas temperaturas tuvieron menor probabilidad de escapar. En contraste, la probabilidad de establecimiento fue mayor si la especie pertenecía a un género nativo de Gran Bretaña e incrementó a medida que aumentó el número de continentes en el rango nativo de la especie. Las plantas anuales tuvieron una probabilidad de establecimiento reducida. La presencia de mercados, los precios y la fecha de introducción son algunos de los factores socioeconómicos que tuvieron efectos importantes sobre el curso de las invasiones observado.

Palabras Clave: catálogos de plantas de vivero, plantas invasoras casuales, plantas invasoras establecidas, presencia de mercado, presión de propágulos

Introduction

The dominant proximate cause of the increase of biological invasions is the growth and development of world markets (Perrings et al. 2000). The development of new trade routes has opened up new pathways for introducing species, and growth of trade along existing routes has increased the frequency of introductions. Changes in the technology of transport and travel have enhanced the survival prospects of both deliberately introduced and passenger species. By better understanding the properties of particular markets, one may better understand why particular species invade and why particular systems are invaded. Ecological determinants of invasions are important, but there is another set of determinants that are largely economic and particularly important in the early stages of invasion (Mack 2003; Williamson 2006).

We considered one market: that involved in the ornamental horticultural trade. This market is the means by which large numbers of non-native plant species are introduced and distributed into new areas. Indeed, it is the most important pathway for plant invasions in many areas (Groves 1998; Reichard & White 2001). In the Czech Republic 53% of deliberately introduced non-native plants were first brought in as ornamentals (Pyšek et al. 2002). In Australia 65% of plant species that became established between 1971 and 1995 were introduced as ornamentals (Groves 1998). In Germany 50% of the alien flora consists of deliberately introduced species, and more than half of these came in as ornamentals (Kühn & Klotz 2002).

Trade is associated with both repeated introductions of popular exotic species in many systems and with secondary releases through cultivation (Mack 2000; Kowarik 2003, 2005). Little information is currently available on the proportion of ornamental cultivated plants that become at least casual aliens. Here we examined the role of the market for ornamentals in Britain in selecting for and promoting species that can invade and in distributing such species within the range that can be invaded. The demand for ornamental plants is driven by consumers in search of good garden subjects whose attributes often predispose them to become invasive. The horticultural industry seeks to meet this demand by importing or breeding plants with the appropriate attributes.

Plant invasions involve a number of stages (Clement & Foster 1994; Williamson 1996, 2000, 2006; Richardson et al. 2000): introduction, existence as a casual alien, permanent establishment (sometimes called naturalization), and spread. We considered only the earlier stages of invasion: introduction, casual status, and establishment.

Ecologically, the marketing of exotic species matters because it affects propagule pressure, still the best explanation of invasion success (Williamson 1996, 1999; Lockwood et al. 2005). Variation in the invasion success of pet animals shows that trade volumes may be a good proxy for propagule pressure. The volume of trade in parrot species is a significant factor in the probability of their establishment (Cassey et al. 2004), and fish species sold in high volumes in the aquarium trade are more likely to be sighted in the wild (Semmens et al. 2004; Duggan et al. 2006). Where there are no data on trade volumes, other proxies of market activity may be useful. In southeastern Australia, actively marketed exotic tree species (those included in nursery catalogs) are more often found naturalized than exotic species not so marketed (Mulaney 2001). We used a similar proxy for the volume of trade in ornamental plants.

Methods

To test the relation between our indirect trade proxy for propagule pressure, the marketing of plants, we considered a random sample of species introduced and distributed by the horticultural industry. We examined the link between propagule pressure created by the presence of the plants in the market and their ability to escape to and establish in the wild in two ways. First, we considered the frequency with which species in nursery catalogs reached different stages of the invasion process. Second, we considered how the likelihood that an individual species will escape and establish depends on market presence and species traits.

Given the long time scales over which invasion processes take place, we drew our sample from ornamental species that were on sale and actively advertised in nursery catalogs in the middle of the nineteenth century. We

Table 1. Nineteenth century nursery catalogs used to select a sample of ornamental species for analysis.

<i>Nursery, location</i>	<i>Catalog</i>	<i>Year</i>
James Backhouse & Son, York	nursery stock	1867
Barr & Sugden, London	seeds	1861
E. G. Henderson & Son, London	seeds	1867
Jackman & Son, Surrey	nursery stock	1865
William Knight, Sussex	nursery stock	1867/1868
Peter Lawson & Son, Edinburgh	nursery stock and seeds	1854/1855
William Thompson, Ipswich	seeds	1869
James Veitch Junior, Royal Exotic Nursery, London	nursery stock	1862 and 1866

chose eight nurseries that were among the leading companies of the time (Hadfield 1960) and that were located in different parts of Britain (Table 1). To cover the full spectrum of plants available in the market at that time, three of the catalogs we considered were seed catalogs and five were nursery-stock catalogs that included ornamental shrubs and trees. These catalogs were printed between 1854 and 1869. Excluding horticultural varieties and cultivars, these catalogs contained 5701 plant species. Out of this number, we randomly selected a sample of 600 species, a reasonably sized yet manageable number.

We checked for synonyms of plant names in different databases (Germplasm Resources Information Network [GRIN, <http://www.ars-grin.gov/npgs/aboutgrin.html>], electronic plant information center at Kew [<http://www.kew.org/epic>], Integrated Taxonomic Information System [ITIS, <http://www.itis.usda.gov>], Missouri Botanical Garden's VAST [VAScular Tropicos nomenclatural database, <http://mobot.mobot.org/W3T/Search/vast.html>], Encke et al. [1993] and Brickell [1996]). We found 17 synonyms and reduced the sample by that number.

We considered a species to be native if it has or had native occurrences anywhere in Britain (rather than in Britain and Ireland as in floras). We removed 49 species from our sample because they were native by this definition, including *Maianthemum bifolium* (L.) F.W. Schmidt, *Homogyne alpina* (L.) Cass., and *Pinguicula alpina* L., all doubtfully native. The result was a sample of 534 ornamental, non-native species.

We refer to species known outside cultivation as *escaping* and categorized them as *casual* (i.e., not persisting in Britain without reintroduction, unlikely to be permanent, and including the "persistent" class of Clement & Foster [1994]) or *established* (likely to remain permanent, even if only in one place in Britain) based on listings in Clement and Foster (1994) and Ryves et al. (1996) and in a few cases in Preston et al. (2002). All the species we studied were therefore designated as "not escaping," "casual," or "established" even though the distinctions are often subjective. Only one species, *Heracleum mantegazzianum* Sommier & Levier, is commonly regarded as a pest.

We considered a species present in the market in the mid-nineteenth century if it was listed in one of the eight catalogs selected from that period. We considered a species present in the market today if it was listed in the *Plant Finder*, an annual Royal Horticultural Society publication, from 1987 to 2004. The 2004 edition of *Plant Finder* lists around 73,000 plant species and cultivars available in the horticultural market in the United Kingdom and around 760 nurseries offering them (Lord 1987; Royal Horticultural Society 2004). Our proxy for trade volume, and hence propagule pressure, was the number of nurseries offering a species in our nineteenth century list (Table 1) and as given in the latest edition of *Plant Finder* in which the plant appears.

The biological traits recorded were life form (annual, perennial, shrub, tree, climber), plant height, minimum temperature tolerated, recommended propagation method (seeds, cuttings, root cuttings, layering, division, offsets), native range of species (Africa, America, Asia, Australia, Europe), native range of genus (whether native to Britain or not), and garden origin. These were selected to reflect the fact that we were studying the horticultural trade. Dichotomous variables were coded as 1 (present) and 0 (absent). Additional data included the date of introduction and the date of the first record in the wild (for escaping species). Data on plant traits came primarily from Klotz et al. (2002), Preston et al. (2002), Brickell (1996), Lord (2003), and D. Pearman (personal communication).

We used nonparametric tests (chi-square, Mann-Whitney) to compare the frequency of ornamental plants escaping with those not escaping and for those that escape to compare the frequency of casual with established. We used two logit regressions to test for economic and ecological characteristics that might explain these two transitions. These models assumed that the probability of escaping or establishing depends on a continuous latent variable that is modeled as a function of a set of explanatory variables (e.g., market presence and plant traits). The logistic function gives the predicted probability

$$P(y) = \exp(x_i\beta) / [1 + \exp(x_i\beta)],$$

where β is a vector of k unknown parameters and x_i is a vector of independent variables. We checked for misspecification of the model with a regression specification error test (RESET) and calculated marginal effects (Long & Freese 2003).

Results

Escape and Market Presence

Of our sample of 534 species, 142 have been recorded outside cultivation in Britain (i.e., escaping) (Table 2). Several tests show that the probability of a species escaping is related to its presence in the market. Two hundred

Table 2. Invasion success of the 142 escaping species in the random sample of 534 ornamental plant species.

Status	Number of species	Percentage of escaping species (n = 142)	Percentage of total sample (n = 534)
Old casualties (pre-1930 records only)*	14	9.8	2.6
Casual	86	60.6	16.1
Established	42	29.6	7.9
Total	142	100	26.6

*Clement & Foster 1994.

thirteen of the nonescaping species (54%) are no longer on sale compared with 30 (21%) of the escaping species ($\chi^2 = 46.36$, $df = 1$, $p < 0.001$). In the nineteenth century catalogs, escaping and nonescaping species were found on average in 1.9 and 1.4 catalogs, respectively (Mann-Whitney, $p < 0.001$). From the *Plant Finder*, 14.4 nurseries now, on average, sell escaping species, and 9.1 sell nonescaping species (Mann-Whitney, $p = 0.014$).

There was a significant difference in the frequencies with which species occurred in nineteenth century catalogs (Fig. 1) ($\chi^2 = 38.36$, $df = 3$, $p < 0.001$). Two hundred

seventy-five nonescaping species (70%) appeared in only one catalog, whereas there were only 10 (3%) nonescaping species compared with 16 (11%) escaping (Table 3) in more than three catalogs. The current market was similar: the frequencies of escaping and nonescaping species were significantly different (Fig. 1, Table 4) ($\chi^2 = 58.79$, $df = 4$, $p < 0.001$; excluding those not on sale, $\chi^2 = 10.25$, $df = 3$, $p = 0.017$).

Only four species in our sample, of which three have escaped, were intensively marketed in both the nineteenth century and now (Tables 3 & 4): *Acanthus mollis* L., *Dicentra spectabilis* (L.) Lem., *Cyclamen hederifolium* Aiton, and *Oenothera macrocarpa* Nutt. *Acanthus mollis* provides an example of a common pattern. The species was introduced in Britain in 1548; was first recorded in the wild, escaping, in 1820; is still spreading, particularly in southwestern England; and was recorded in 111 hec-tads (grid squares of 10×10 km) in the 1988–1995 survey (Preston et al. 2002). It was on sale in four of our eight nineteenth century catalogs and is the commonest species in our sample on sale now (Table 4). Despite continuing changes in the market, it is clear that escaping species have been more widely marketed than nonescaping species.

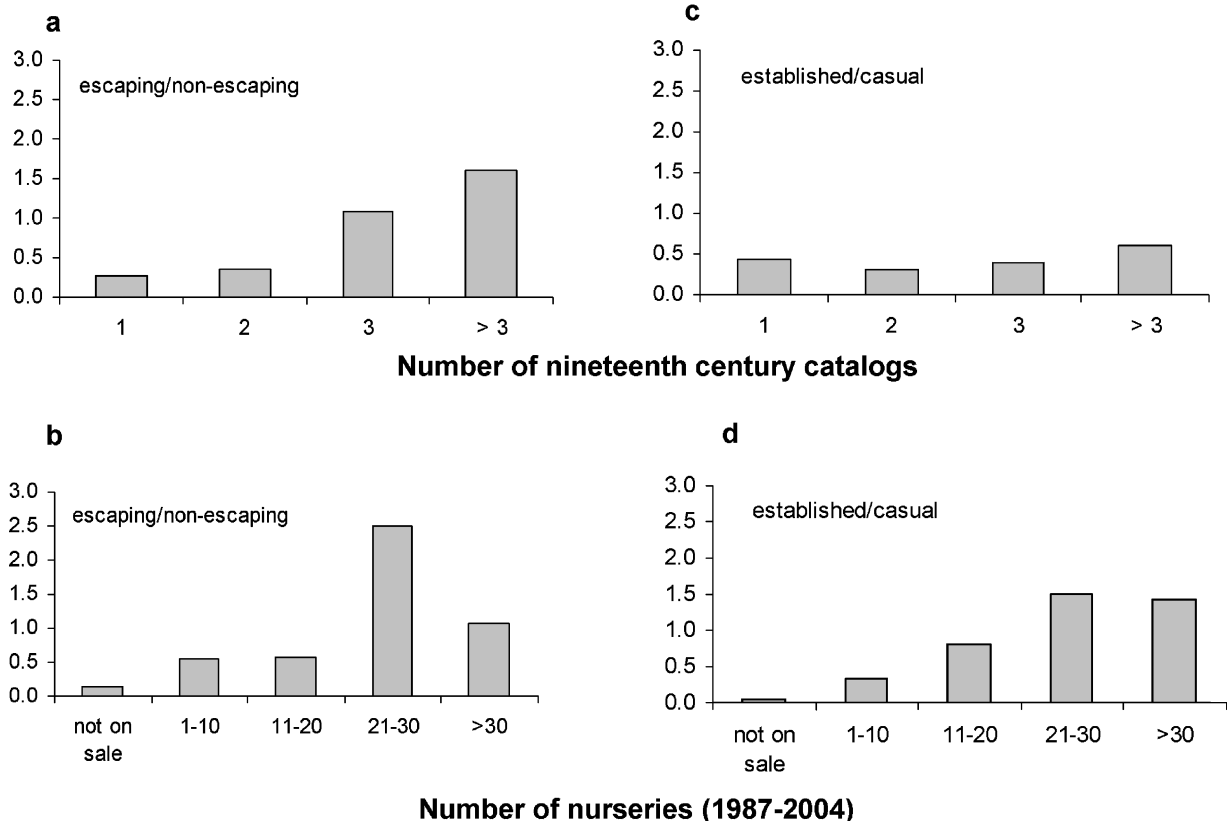


Figure 1. The ratio of (a, b) escaping to nonescaping species and of (c, d) casual to established species for different frequency categories in (a, c) eight nineteenth century catalogs and (b, d) nurseries listed in the *Plant Finder* (editions 1987–2004). The ratios are calculated for samples of 142 escaping and 392 nonescaping species and 42 established and 100 casual species, respectively.

Table 3. The 26 species available from four or more nurseries out of eight in the 1860s and their availability from nurseries today (according to the *Plant Finder* [Lord 1987; Royal Horticultural Society 2004]).

<i>Species</i>	<i>Status</i>	<i>Number of 1860s nursery catalogs that carried the species</i>	<i>Number of nurseries that carried the species from 1987 to 2004</i>
<i>Delphinium grandiflorum</i> L.	not escaping	6	1
<i>Dicentra spectabilis</i> (L.) Lem.	casual	6	73
<i>Oenothera macrocarpa</i> Nutt.	not escaping	6	38
<i>Anomatheca cruenta</i> Lindl.	not escaping	5	31
<i>Aquilegia canadensis</i> L.	not escaping	5	22
<i>Cyclamen hederifolium</i> Aiton	established	5	62
<i>Oenothera acaulis</i> Cav.	not escaping	5	11
<i>Oenothera glazioviana</i> Micheli	established	5	10
<i>Primula auricula</i> L.	established	5	14
<i>Acanthus mollis</i> L.	established	4	80
<i>Amaranthus caudatus</i> L.	casual	4	0
<i>Ammobium alatum</i> R. Br.	casual	4	1
<i>Aquilegia pyrenaica</i> DC.	established	4	2
<i>Browallia americana</i> L.	casual	4	0
<i>Campanula medium</i> L.	established	4	4
<i>Campanula ramosissima</i> Sm.	not escaping	4	1
<i>Crassula dichotoma</i> L.	not escaping	4	0
<i>Cuphea lanceolata</i> W. T. Aiton	not escaping	4	1
<i>Gilia capitata</i> Sims	casual	4	1
<i>Gilia tricolor</i> Benth.	casual	4	1
<i>Helicbrysum bracteatum</i> (Vent.) Andrews	casual	4	0
<i>Ipomoea quamoclit</i> L.	not escaping	4	1
<i>Nemophila menziesii</i> var. <i>Atomaria</i> (Fisch. & C. A. Mey.) Chandler	casual	4	0
<i>Phacelia fimbriata</i> Michx.	not escaping	4	0
<i>Ricinus communis</i> L.	casual	4	2
<i>Solanum melongena</i> L.	casual	4	0

Establishment and Market Presence

Most of the 142 escaping species in our sample were casuals, either recorded recently (86) or not recorded since 1930 (14), 100 in all. Only 42 species have established (Table 2). Although the tests indicated some relationship between market presence and establishment, these were either only slightly significant or not significant. The number of nineteenth century nurseries offering established species (1.93) was higher than those offering casual species (1.88) but not significantly so (Mann-Whitney, $p = 0.91$). By contrast, the number of nurseries currently offering established species (20.48) was significantly higher than the number offering casual species (7.52) (Mann-Whitney, $p < 0.001$). Again, the differences in the frequencies with which casual and established species appeared in catalogs (Fig. 1) were only significant for the modern data (nineteenth century catalogs: $\chi^2 = 0.96$, $df = 3$, $p = 0.81$; current catalogs: $\chi^2 = 23.23$, $df = 4$, $p < 0.001$; or excluding those not on sale, $\chi^2 = 10.77$, $df = 3$, $p = 0.013$).

Factors Associated with Invasion Success

We used a logistic analysis to look more closely at particular factors affecting the two transitions (Table 5). As expected from the analysis above, three socioeconomic

factors were significant for the escaping transition, but none were significant for the establishing transition. The introduction date was significant for establishment, a measure of the long time that species may spend as casuals, but that information was not available for most of the nonescaping species.

Biological variables that positively affected the probability of escaping from gardens were species' height, tolerance of low temperatures, a native range including Europe, and an annual life form. Climbing species were less likely to escape. Being an annual decreased the probability of transition from casual to established status, but belonging to a native genus increased that probability, as did the extent of the native range. None of the propagation variables were significant in either model.

The marginal effects (Table 5) show how the probabilities of escape and of establishment changed with changes in the species' characteristics. For example, a species that was average in all other characteristics, if not sold by any nurseries listed in the *Plant Finder*, had a probability of escaping 0.30 lower than that of a species sold by 1-20 nurseries; if it was sold in more than 20 nurseries, it had a probability of escaping 0.24 higher. The only factor significant in both models—annual life form—had different signs in the two models, with marginal effects of +0.67 and -0.34 for escaping and establishing species,

Table 4. The 26 species most frequently on sale from nurseries from 1987 to 2004, according to the *Plant Finder* (Lord 1987; Royal Horticultural Society 2004), and their availability in eight nursery catalogues in the 1860s.

Species	Status	Nurseries today (1987–2004)	Nursery catalogs in the 1860s
<i>Acanthus mollis</i> L.	established	80	4
<i>Dicentra spectabilis</i> (L.) Lem.	casual	73	6
<i>Eryngium agavifolium</i> Griseb.	not escaping	72	1
<i>Asphodeline lutea</i> (L.) Rchb.	no modern records (old casual)	64	1
<i>Cyclamen hederifolium</i> Aiton	established	62	5
<i>Arbutus unedo</i> L.	established	61	3
<i>Cyclamen coum</i> Mill.	established	56	3
<i>Parthenocissus quinquefolia</i> (L.) Planch.	established	53	1
<i>Lycbnis chalconica</i> L.	casual	52	3
<i>Helleborus niger</i> L.	not escaping	52	3
<i>Baptisia australis</i> (L.) R. Br.	not escaping	52	2
<i>Festuca glauca</i> Vill.	not escaping	51	3
<i>Stachys byzantina</i> K. Koch	established	50	2
<i>Trachelospermum jasminoides</i> (Lindl.) Lem.	not escaping	50	1
<i>Francoa sonchifolia</i> (Willd.) Cav.	not escaping	50	2
<i>Centaurea macrocephala</i> Muss. Puschk. Ex Willd.	casual	46	2
<i>Viburnum tinus</i> L.	established	45	1
<i>Tricyrtis birta</i> (Thunb.) Hook.	not escaping	41	1
<i>Kerria japonica</i> (L.) DC.	casual	41	1
<i>Clematis flammula</i> L.	established	40	3
<i>Oenothera macrocarpa</i> Nutt.	not escaping	38	6
<i>Omphalodes verna</i> Moench	established	37	2
<i>Lobelia cardinalis</i> L.	not escaping	37	2
<i>Buddleja globosa</i> Hope	casual	37	1
<i>Eryngium alpinum</i> L.	not escaping	36	2
<i>Sequoiadendron giganteum</i> (Lindl.)	not escaping	35	1

Table 5. Statistically significant coefficients of the logistic regression analyses for the nonescaping/escaping and casual/established species samples.*

	Nonescaping–escaping (n = 273)				Casual–established (n = 121)			
	estimates	SE	p	marginal effect	estimates	SE	p	marginal effect
Constant	−4.229	0.878	<0.001		6.003	4.691	0.201	
Socioeconomic variables								
species not on sale from 1987 to 2004 (d)	−1.641	0.626	0.009	−0.299				
species sold by >20 nurseries from 1987 to 2004 (d)	0.987	0.398	0.013	0.238				
frequency in nineteenth century catalogues (c)	0.341	0.140	0.015	0.078	0.460	0.243	0.059	0.059
introduction date (c)					−0.006	0.003	0.033	−0.001
Biological variables								
log of species' height (c)	0.359	0.133	0.007	0.082				
european native range (d)	1.502	0.355	<0.001	0.35				
number of continents in the native range (c)					1.171	0.471	0.013	0.151
minimum temperature tolerated (c)	−0.040	0.013	0.002	−0.009				
annual species (d)	3.531	0.637	<0.001	0.671	−3.656	1.022	<0.001	−0.339
climbing plant (d)	−1.672	0.625	0.007	−0.287				
native genus (d)					1.671	0.601	0.005	0.229

*Abbreviations: c, continuous variables; d, dichotomous variables; marginal effect in dichotomous variables is for a discrete change from zero to one. The positive predictive value (Loong 2003) and pseudo R² value were 72% and 0.25, respectively, for the nonescaping/escaping model and 62% and 0.33, respectively, for the casual/established model.

respectively. The RESET test was insignificant for both models, which indicated no problems with the specification of the models. The positive predictive value (Loong 2003) was somewhat higher, 72%, for the escaping model than for the establishing one (62%).

Discussion

The likelihood that introduced ornamental species escaped or established showed that market presence—our indirect proxy of trade volumes and hence propagule pressure—was a strongly significant explanator of escape but only a weak explanator of establishment. Biological variables, on the other hand, were important at both stages although different characters were important at the two stages.

The question arises, then, of whether market presence has a causal effect on the probability of escaping and how this relates to the biological characteristics that make plants good garden subjects. Species escaping by seed flow or that are disposed of in the wild by gardeners are in general vigorous growers and popular with gardeners, and because gardeners' preferences drive demand they are also popular in horticultural trade. Propagule pressure from the horticultural trade is not direct to wild habitats but begins with a propagation stage in gardens. Market presence is a measure of the effectiveness with which the horticultural trade meets gardeners' demand for exotic species with the "right" characteristics. There was a correlation between the length of time that exotic ornamental species with these characteristics have been present in the market, the frequency with which they are marketed, and the likelihood of escape and establishment. Although we have not implemented a test for Granger causality (Gujarati 2003), this correlation indicates a sequential relationship between market-based propagule pressure, escape, and establishment that is consistent with the results of ecological studies on propagule pressure (Lockwood et al. 2005).

We found that of the 27% of ornamental species that had escaped, 30% had since established. Similarly, Kowarik (2005) reports that 25% of the woody non-native species cultivated in the city of Hamburg, Germany, are growing spontaneously. In the German flora 30% of escaped plants are regarded as well established (Kowarik 2005). For edible crop plants in Britain the figures are 95% for escaping and 20% for establishment (Williamson 1996; Williamson & Fitter 1996*a*). The much higher number of escaped species for edible crops supports our contention that propagule pressure is a major factor; the land area under agricultural cultivation is far higher than the land area under cultivation with ornamental plants.

Plant characteristics were important explanators of the probability of escape and establishment. Plant height, annual life form, and hardiness all increased the probability of a species escaping from cultivation. Crawley et

al. (1996) and Williamson and Fitter (1996*b*) found that British non-native plants are generally larger than British native plants. We found that annual species had a higher probability of escaping than nonannual species but were less likely to establish. Ecologically, many annuals are ruderals or competitive ruderals, adapted to colonize new and disturbed habitats (Grime 1979). This may give them an advantage in finding suitable habitats outside cultivation, but it may also explain why they are less likely to establish in the wild than other escaping species.

For establishment the number of continents in the native range was the most significant geographical variable. This variable reflects the size of a species' native range, which is a well-established correlate of invasion success (Williamson 1996; Goodwin et al. 1999). Establishment success was greater if a species belonged to a native genus. This agrees with the results for naturalized plants (which we call established) from Daehler (2001) for Hawaii and Duncan and Williams (2002) for New Zealand. It is yet another rejection of "Darwin's rule" that plant species belonging to a native genus would be less likely to establish due to higher competition with native species of the same genus (Darwin 1859). The effect of the introduction date indicates that the longer a species has been present the more likely it is to establish. The importance of residence time in biological invasions has been shown in several other cases (Pyšek & Jarošík 2005).

The predictive power of our logistic models of escape and establishment, 72% and 62%, respectively, was similar to that of a model for annual weeds in Britain (Perrins et al. 1992) (75%) but much higher than that for aliens of German origin in Argentina (Pyšek et al. 2004) (21%). Higher figures for predictive power in the literature often refer to sensitivity rather than to positive predictive value (Pyšek et al. 2004; Williamson, in press) (e.g., sensitivity in the Argentine study was 81%). Sensitivity is sometimes called accuracy, and positive predictive value has been called reliability. Sensitivity is a measure of explanation, and our study and these others all give useful explanations of invasion success, but none allow reliable predictions.

Our analysis does not test any proposition derived from a model of the economic behavior of actors in the ornamental horticultural industry. Nevertheless, it does provide *prima facie* evidence that supply and demand factors are an important part of the explanation for the invasiveness of ornamental species. The drivers of invasions are both propagule pressure and the properties of introduced species. Because these depend on the structure of the supply of and demand for easily cultivated plants, it should be possible to specify and estimate a model of invasions as a function of the factors that determine supply and demand, including prices, incomes, and other socioeconomic variables. We have shown that the adoption of invasive ornamental plants is correlated with changes in the relative price of those plants (Dehnen-Schmutz & Williamson, 2006). Given this, it should be possible to use price data to provide early warnings about the likely

dispersion of potentially establishing species, or at least to indicate which species would repay closer scrutiny. The science of biological invasions has yet to exploit the rich data available on human behavior. Because most invasions are the product of human behavior, however, this is unduly limiting.

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