Diversity and Distributions, (Diversity Distrib.) (2007) **13**, 527–534

BIODIVERSITY RESEARCH

A century of the ornamental plant trade and its impact on invasion success

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ABSTRACT

We identify a significant relationship between domestic market-based propagule pressure, as measured both in presence in the British horticultural market and in seed prices of ornamental plant species, with success in invasion. We employ a multispecies temporal approach and use a Generalized Estimation Equation model comparing ornamental non-native species introduced into Britain which started to invade with species introduced but not known outside cultivation. Historical nursery catalogues gave information on the availability and prices of seeds of 506 ornamental species in the British horticultural market every 20 years from 1885 to 1985. Higher market frequency and cheap prices of seeds were more significant and had a greater impact on the invading probability 20 years later than at the date of listing in a nursery catalogue. Our results suggest that national economic factors are an important part of the explanation for the invasiveness of ornamental plant species, and hence for the development of potential solutions.

Keywords

Horticultural trade, plant prices, market frequency, propagule pressure, non-native species, biological invasions.

INTRODUCTION

The problem of invasive pests and pathogens has been linked to the growth and development of trade, transport, and travel (McNeely, 2001; Levine & D'Antonio, 2003; Taylor & Irwin, 2004; Perrings *et al*., 2005). The analysis of these pathways has often focused on inadvertent introductions as in ballast water or insects carried by shipping containers (Ruiz & Carlton, 2003a). However, many currently invasive species were deliberately introduced as exotic pets or ornamentals (Cassey *et al*., 2004; Semmens *et al*., 2004; Duggan *et al*., 2006). For plants, the horticultural trade has been identified with the deliberate introduction of species to many areas outside their native range (Mack, 2003). Thuiller *et al.* (2005) consider horticultural exports from South Africa. They use data on living plant material exported from South Africa in a recent 3-year period together with data on the number of tourists to estimate propagule pressure and thereby improve a model based on climate to predict regions at risk of invasion by South African plants.

In fact the majority of species in the alien floras of many areas originate from horticultural introductions (Groves, 1998; Mack & Erneberg, 2002; Pyšek *et al*., 2002). While most attention has been paid to the role of the international trade in species introductions (Jenkins, 1996; Perrings *et al*., 2000; Levine & D'Antonio, 2003; Thuiller *et al*., 2005), equally important factors in the plant invasion process are (1) the repeated local introduction of plants through local market outlets, and (2) the development through plant breeding of traits that increase the likelihood that escaped plants will establish (Mack, 2000; Kowarik, 2003). Both factors are associated with the development of a local horticultural industry. It follows that the risk that an introduced alien plant will escape, establish, and spread depends on the factors that, given incomes, determine gardeners' demand for invasive plants: their preference for 'good garden subjects', the species traits that make plants good garden subjects (ease of propagation, climatic suitability, or resistance to pests and diseases), the relative prices at which exotic plants are sold, and their availability in nurseries. That is, propagule pressure depends on the development of supply of and demand for potentially invasive plants within national markets.

Physically, propagule pressure could be represented by the volume of ornamental plants traded per unit area, but these data do not exist. It therefore is not possible to estimate either demand or supply functions directly. It is, however, possible to identify reasonable proxies. For example, Mulvaney (2001) showed that more frequently planted woody ornamental non-native species in south-eastern Australian cities were more likely to naturalize outside cultivation than less frequently planted species. In this paper we take the frequency with which plants are listed in nursery catalogues to be a proxy for propagule

DOI: 10.1111/j.1472-4642.2007.00359.x
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pressure. These data, along with data on the relative price of exotic species in the national horticultural trade, data on species characteristics and socioeconomic variables, are used to estimate the likelihood that a given traded species would become invasive. 'Good garden subjects' that were supplied by a high proportion of nurseries at a low relative price would be expected to be in high demand. Although it is not possible to estimate either supply or demand, we can observe the correlation between exotic species that establish in the wild and these various proxies.

In this study, we are interested in two problems. The first is, the link between market presence, market price, and the invasion success of deliberately introduced species. It has been shown for deliberately introduced parrots, aquarium fish, and ornamental plants that market availability and frequency are significant determinants of invasion success (Cassey *et al*., 2004; Semmens *et al*., 2004; Lockwood *et al*., 2005; Dehnen-Schmutz *et al*. 2007). We expect that market prices will similarly correlate with invasion success. We have elsewhere observed that the invasive species *Rhododendron ponticum* in Britain was most extensively planted when its price relative to other species was low (Dehnen-Schmutz & Williamson, 2006). Since prices are also of interest as an economic mechanism for regulating the demand for invasive species — and hence as part of a prevention policy — it is interesting to know how they relate to invasion success (Perrings *et al*., 2005).

Second, we are interested in the relationship between the length of time a species has been marketed and the invasion probability of that species. It is well known that the longer a species is present in a new area, the more likely it will start an invasion process (Pyšek & Jarošík, 2005; Rejmánek *et al*., 2005). Time lags from the introduction of a species to the first record of escape or from that first record to the starting point of an increased rate of spread have been observed for many species (Kowarik, 1995; Williamson *et al*., 2005). Among the reasons assumed to explain those lags are species intrinsic life-history traits, climatic change, and changes in the invasibility of suitable habitats (Kowarik, 1995). Recently, changes in vector activity caused by the dynamics of trade have been recognized as a factor in the time to establishment, although there have been no studies analysing this relationship quantitatively (Ruiz & Carlton, 2003b; Crooks, 2005).

Here, we employ a multispecies temporal approach comparing species introduced into Britain which started to invade with species introduced but not known outside cultivation. For a sample of 506 ornamental plant species we used longitudinal data on the invasion process, on market availability, and on seed prices. This analysis therefore combines information on how the market presence and prices of all the species vary at one date (between-variation) and how they vary for each individual plant species over several dates (within-variation). Historical nursery catalogues gave information on the availability and prices of seeds of ornamental species in the British horticultural market from 1885 to 1985. The listing of a species in a nursery catalogue indicates availability at the date of listing. Time as a variable was added to account for time-dependent effects not captured by the socioeconomic variables. In addition we included a set of biological and environmental variables, including propagation methods, to capture the importance of species traits both in terms of the demand for garden plants and the likelihood of establishment following escape.

METHODS

Data

The database contains invading and non-invading plant species used as ornamentals and not native to Britain. The invading group included all those species in the catalogues of alien plants of the British Isles (Clement & Foster, 1994; Ryves *et al*., 1996) listed as garden escapes and as having at least 15 recorded localities, giving a total of 402 species. We use the term 'invading' to indicate that our sample has species from all those stages of the invasion process called by Richardson *et al*. (2000) and Pyšek *et al*. (2004) casual, naturalized, or invasive. Table 1 shows how these terms relate to those used by Clement & Foster (1994) and to our usage here. Note that 'invading' is a much wider term than 'invasive'.

The non-invading group was a sample of 600 species randomly drawn from a list of 5701 species marketed in eight nursery catalogues printed between 1854 and 1867 that we have described before (Dehnen-Schmutz *et al*., 2007). Native species, species found outside cultivation anywhere in the British Isles, and species appearing twice in the list as synonyms were excluded, resulting in a set of 392 non-invading species.

Market information on these species was sampled in nursery catalogues covering 100 years starting from 1885. To keep the sample to a reasonable size and, given the speed of the invasion process (Williamson *et al*., 2005), we sampled at 20 years steps over 100 years and chose five catalogues for each of the six dates (Table 2).

For each date we noted in the catalogues sampled (1) the availability of the species, (2) prices of seed packages, and (3) whether the plants were sold as seeds or otherwise.

The catalogues were selected from the collection of the Royal Horticultural Society's Lindley Library in London, housing the largest collection in the UK of horticultural trade catalogues, dating primarily from 1860 and continuing to the present. The Lindley Library collection represents the best available information on and the most representative data set of the horticultural trade in the UK. Within this collection we focused on catalogues from companies offering a wide range of species, general assortments. Nurseries specializing in particular plant groups (e.g. roses, rhododendrons, bulbs) were excluded.

There is no catalogue of the Lindley Library nursery catalogues. Catalogues are sorted by company name and are only accessible through a librarian. We therefore adopted a random sampling approach without replacement where we asked the librarian for companies known to her to offer a general assortment of species. Once a firm had been selected we took all its available catalogues for the dates studied, provided they remained general. We proceeded in this way until we had five catalogues per date. Changes in the companies used for each date

Table 1 Terminology used in this paper compared with that used by Clement & Foster (1994) for alien species in the British Isles and by Richardson *et al.* (2000) and Pyšek *et al.* (2004).

This paper	Clement & Foster (1994)		Richardson *et al.* (2000) Pyšek *et al.* (2004)	
Non-invading	Not included	Species cultivated in gardens	Cultivated alien but not in any of the categories below	Plant (or its propagule) that has overcome, through human agency, a major geographical barrier
	Introduced	Deliberately planted or sown in the wild		
Invading	Casual	Not persisting in a locality for more than 2 years without re-introduction	Casual	Alien plants that may flourish and even reproduce occasionally in an area, but which do not form self-replacing populations, and which rely on repeated introductions for their persistence
	Persistent	Remaining longer than 2 years without re-introduction, not reproducing by seed or vigorously spreading vegetatively		
	Established	Likely to remain permanently; at least one colony either reproducing by seed or vigorously spreading vegetatively	Naturalized	Alien plants that reproduce consistently and sustain populations over many life cycles without direct intervention by humans
			Invasive	Naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distance from parent plants

Table 2 Nursery catalogues used to assess the market frequency and seed prices of 506 non-native invading and non-invading ornamental plants in Britain from 1885 to 1985. The date of the catalogues varied up to 5 years from the given year if no other catalogue was available. Some companies printed separate seed and plant catalogues, sometimes in different years.

	Dates analysed						
Company	1885	1905	1925	1945	1965	1985	Printing date of the catalogues
J. Backhouse & Son	x	x	x	x			1883, 1905, 1906, 1925, 1941
Barr & Son (Barr & Sugden, Wallace & Barr)	x	x	x			x	1883, 1905, 1925, 1986
Bressingham Gardens						x	1985
J. Dickson & Son	x						1881
E.G.Henderson & Son	x						1881
G. Jackman & Son	x		x	x			1887, 1925, 1946
J. Jefferies & Son		x					1905
Knight's Nurseries Ltd					x		1965
M. Prichard		x	x	x	x		1905, 1925, 1947, 1950, 1964
Notcutt				x		x	1944, 1985
St. Bridget Nurseries					x		1965
Suttons & Son		x			x	x	1905, 1965, 1985
Thompson & Morgan			x	x	x	x	1926, 1927, 1944, 1946, 1968, 1985

are inevitable because the characteristics of the market change with time. Companies run out of business (e.g. Backhouse & Son, Prichard); new companies come into the market like St. Bridget Nurseries and Bressingham Gardens founded 1925 and 1946, respectively; or companies choose to publish only specialized catalogues in certain years (e.g. Barr & Son in 1945 and 1965). Furthermore, even in a large collection like the one in the Lindley Library, it is not always possible to find a suitable catalogue for a specific year. We therefore allowed a range of up to 5 years if five catalogues were not available for a particular year. Prices of plants not sold as seeds were not considered in this study as they refer to less comparable units than seed packages, and may relate to different sizes of plants. Note that we used prices of seeds although the catalogues did not give any information on the number of seeds per package. However, customers using these catalogues would not have had this information either when deciding which species to buy. All seed prices were converted to 2002 prices (McCusker, 2003). If seed prices for a species were

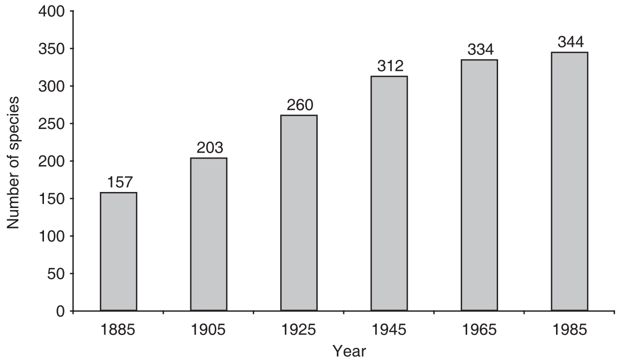

Figure 1 Number of species invading out of a sample of 506 ornamental species at each date analysed. Two hundred and eighty-four of the species invading in 1985 are considered established in Britain, 28 are classified as casuals, and 32 as persistent (Clement & Foster, 1994).

available from more than one catalogue at one date an average price was calculated.

Nursery catalogues, particular early catalogues, have always been a valuable source of information for botanists to get information on the history of introduction of ornamental plants (Harvey, 1972; Campbell-Culver, 2001). They are also an important data source for the analysis of plant invasions (e.g. Mack, 1991; Mulvaney, 2001). The novel approach in our study is to use nursery catalogues to take repeated observations of a sample of non-native species over 100 years. The advantages are those related to the use of longitudinal analysis because the combination of time series with cross-sections enhances the quality and quantity of data (Gujarati, 2003).

Plant traits recorded were life form (annual, perennial, tree, shrub, climber, evergreen, woody); 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. Data on plant traits came primarily from Klotz *et al.* (2002), Preston *et al.* (2002), Brickell (1996), and Lord (2003). We included a time variable that increases by one for every 20-year period the species was present in Britain. For the invading species we used the date they were first recorded outside cultivation (Preston *et al.*, 2002) to determine the invading status of the species at the end of each period. Species for which key biological data were missing were excluded from the analysis. All such species were non-invading species. The final sample size of both invading and non-invading plants was 506. Of these, 157 species were first recorded in the wild before 1885, and 187 escaped from cultivation over the next 100 years (Fig. 1).

STATISTICAL ANALYSIS

We use a longitudinal logistic regression analysis to describe the relationship between the dichotomous outcome variable, success (1), or failure (0) of invasion, and the economic and biological covariates,

$$\ln(\Pr(y_{it} = 1)/1 - \Pr(y_{it} = 1)) = \alpha + \beta x_{it} + \delta z_i + e_{it}\ (i = 1, \dots, n; t = 1, \dots T)$$

where y_{it} is the outcome variable for species i in year t. It is related to a vector of time-variant covariates x_{it}, and time-independent covariates, z_i. The regression coefficient β combines the within-subject and between-subject relationships. The data structure allows testing for causality by using time-lagged covariates where the measure of the time-variant covariate is taken one time point earlier. Since there are repeated observations within one unit (i.e. each ornamental species), the data are temporally correlated, and observations cannot be treated as independent units. In order to assess the effect of the covariates on the risk of invasion, a Generalized Estimation Equation model (GEE) for binary data was used with the xtgee procedure in STATA (StataCorp LP, College Station, TX, USA), specifying a binomial distribution of the outcome variable and a logit link function (Zorn, 2001; Twisk, 2003; Rabe-Hesketh & Everitt, 2004). In that procedure we used robust standard errors clustering for species to account for potential model misspecification or heterostedasticity in the data. The GEE analysis corrects the correlations within subjects by assuming *a priori* a certain correlation structure between subsequent measures of the dependent variable. The correlations are treated as a covariate (i.e. as a nuisance parameter). Given that the dependence within each species is temporal, we assume an autoregressive correlation structure where correlations decrease with the distance between time points. A sensitivity analysis carried out for different correlation structures (exchangeable, unstructured) confirmed that the GEE analysis is robust to this assumption.

RESULTS

The most striking results concern the link between market presence, prices, and invasiveness. Invading species were, on average, sold by more nurseries than non-invading species. The difference is significant from the second date onwards (Mann–Whitney test, Fig. 2a). Similarly, average seed prices of invading species were significantly lower than seed prices of non-invading species at each date except for the years 1925 and 1945 (Mann–Whitney test, Fig. 2b). Note that all the invading points are either above (Fig. 2a) or below (Fig. 2b) the non-invading ones. Those effects have a two-tailed probability of 1in 2^5 (0.03125) for each graph. As the effects are both in the direction of more favourable markets leading to more invasion, they could be combined to give a two-tailed probability of 1 in 2^{11} (0.000488), though all those two-tailed probabilities assume that the data at different times are independent, which cannot be tested.

The probability that a species would escape from cultivation was significantly greater when that species was more frequently available in the market and seeds were sold at lower prices (Table 3). Furthermore, the estimated coefficients of the time-lag variables indicate that species appearing more frequently in the market at one date are more likely to invade at a future date. Species that are frequently sold cheaply at one date have a high probability of invading later. These time-lag variables take into

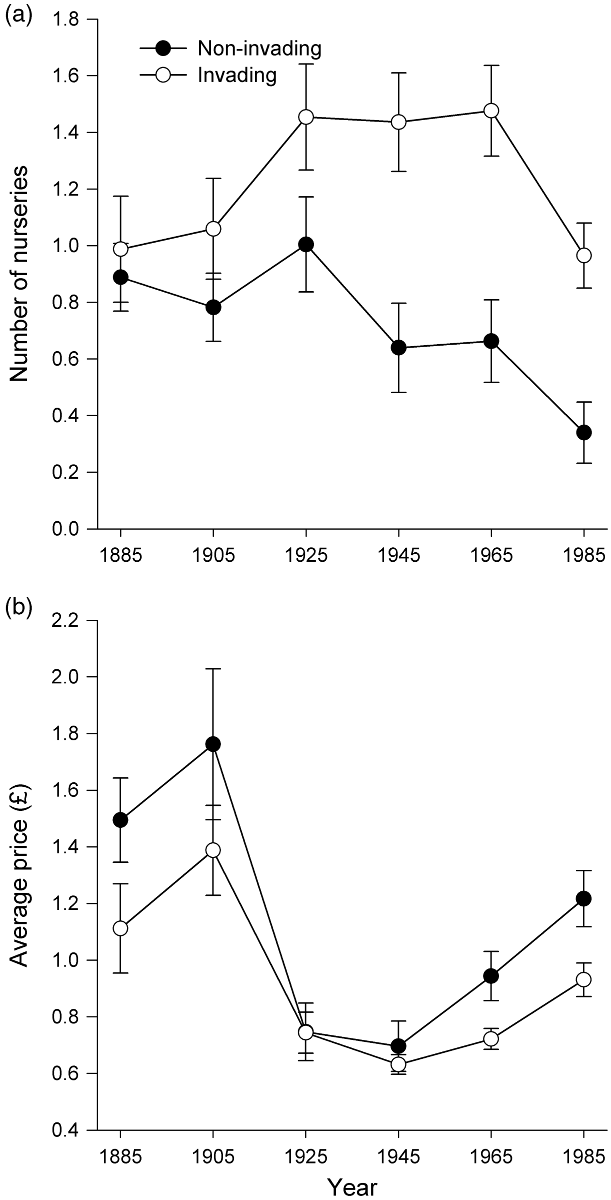

Figure 2 Average number of nurseries selling plants (a) average prices of seeds (b) for non-invading and invading species over the time analysed. Bars give the 95% confidence interval.

account the temporal sequence of a possible cause and effect (Twisk, 2003) and indicate that a causal relationship may exist between species being frequently offered in the market at low prices and escaping later.

The significant time variable indicates that other time effects than those captured in our trade related variables are significant. Particularly, the longer a species is present in Britain the more likely is it to escape from gardens.

Aside from the socio-economic variables, we included a set of biological — ecological variables to control for their possible impacts. This puts our study in line with several studies identifying plant traits that are related to the invasiveness of plant species (Rejmánek & Richardson, 1996; Williamson & Fitter, 1996; Reichard & Hamilton, 1997; Kolar & Lodge, 2001; Frappier & Eckert, 2003; Hamilton *et al.*, 2005). In a review of these types of comparative multispecies studies Pyšek & Richardson (2007) conclude that it is not possible to identify traits that could be generally assigned to invasive species partly due to the variety of research questions analysed and the different data sets used. Similarly, we find that our results sometimes confirm characteristics identified in some studies but sometimes are in contrast to results in other studies. We confirm the importance of the size of a species' native range, here measured as the number of continents in its native range, which is well known to be a good correlate of invasion success (Goodwin *et al.*, 1999; Williamson, 1999). Species originating from Europe were more likely to escape than species from elsewhere and are, in fact, 'overrepresented' in the British alien flora (Crawley *et al.*, 1996). Species of garden origin in our study had a higher probability of invading, confirming the invasive potential of hybrid species (Abbott, 1992; Ellstrand & Schierenbeck, 2000). Species with native congeners had a higher likelihood of escaping, a result previously found for plants introduced to New Zealand (Duncan & Williams, 2002) and Hawaii (Daehler, 2001). Species tolerating lower minimum temperatures had a higher likelihood of escaping from cultivation, whereas a perennial or a woody life-form decreased the probability of escaping. Although Pyšek & Richardson (2007) found that

Table 3 Significant socioeconomic and biological coefficients for the invading probability of 506 ornamental non-native species in Britain from 1885 to 1985*.

Variable	Coefficient	Robust SE	*P*-value
Socioeconomic variables			
Nurseries at current date	0.090	0.035	0.011
Nurseries at previous date	0.146	0.032	< 0.001
Seed prices at current date	–0.288	0.107	0.007
Not sold as seed at current date (d)	–0.324	0.136	0.018
Seed prices at previous date	–0.339	0.087	< 0.001
Not sold as seed at previous date (d)	–0.320	0.120	0.008
Time since introduction	0.329	0.262	< 0.001
Biological variables			
Continents in native range	0.828	0.198	< 0.001
Europe (d)	0.699	0.236	0.003
Garden origin (d)	1.89	0.390	< 0.001
Native genus (d)	0.376	0.180	0.037
Minimum temperature tolerated	–0.027	0.008	< 0.001
Perennial (d)	–0.808	0.278	0.004
Woody (d)	–0.826	0.294	< 0.001
Propagation by layering (d)	–1.510	0.432	< 0.001
Constant	–1.946	0.449	< 0.001

*Dichotomous variables are indicated by (d). Coefficients were estimated in a Generalized Estimation Equation model using an autoregressive correlation structure (n = 2,530 from 506 species at 5 points in time; estimated correlation coefficient 0.8237). The seed price variables take the value zero when the species was not available in the market or was not sold as seed. To correct for this, dummy variables were created that take the value 1 when this occurs ('not sold as seed').

plant height was one of the traits that had strong support from several studies included in their comparison, it was not a significant variable in our species sample. To control for the characteristics of species related to their propagation, we examined the effect of propagation methods recommended in the gardening literature. The only significant variable identified was propagation by layering which was found to have a negative effect on the likelihood of invasion.

DISCUSSION

Our results provide quantitative evidence for the role of the ornamental plant trade as a vector activity (Ruiz & Carlton, 2003b) in plant invasions. We show that the development of the national horticulture industry in Britain to meet demand for exotic plants that are 'good garden subjects' was an important factor in the invasion success of introduced species. We find that the length of time a species with the requisite traits has been present in the market, the number of nurseries selling the species and the price of its seeds all increase the likelihood that it will start to invade. Where the relative price of deliberately introduced species falls, reflecting the relative ease or cost of propagation and care, their subsequent invasion success increases.

We used ecological and biological variables to control for their possible influence on the invading probability of species. None of those results were remarkably different from previous studies analysing the impact of different plant traits on invasion success of plants. What distinguishes our study from other multispecies comparative studies is the inclusion of variables on the relative prices of invading and non-invading species, and the intertemporal approach. We conclude that the development of the national ornamental market provides an important explanation for the invasiveness of ornamental plant species. This has implications both for the way that the problem may be studied and for the development of appropriate policy instruments. Price data provide important early information about local propagule pressure of introduced non-native species, and indicate which species would repay closer scrutiny in the horticultural market. The price mechanism can also be effective in the management of invasions wherever the risks depend on the volume of introductions. McAusland & Costello (2004) and Costello & McAusland (2003) have shown that price-based mechanisms, such as tariffs on plant imports, will always reduce invasion risks by reducing the level of imports. The extent to which they are effective depends on the price elasticity of demand. If the price elasticity of demand is high for any given species and if the probability of escape and establishment increases with the volume traded, then the price mechanism may be used to reduce invasion risks. That is, raising the price of potentially invasive species reduces propagule pressure and hence the likelihood that the species will invade (Perrings *et al*., 2005; Touza *et al*., 2007). If the price elasticity is low or if the risk of invasions is density-independent, then other mechanisms would be preferred.

The role of local markets in the dynamics of invasion success has not been studied previously. The development of new trade routes opens up pathways for the introduction of new species, but escape, establishment, and spread within a country depend on the development of domestic markets. Attention to the threats posed by international trade has missed the critical role of local market development.

ACKNOWLEDGEMENTS

This work was funded by the Leverhulme Trust. We thank E. Gilbert at the Royal Horticultural Society's Lindley Library for her help with the selection of the nursery catalogues and A. Jones for statistical advice.

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