Spatio-temporal dynamics of plant invasions:
Linking pattern to process[1]

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Abstract: Biological invasions are characterized by remarkable spatio-temporal dynamics, with many species having extended their distribution range from within a single region to much of the globe within the last century. The comparative analysis of the spatio-temporal dynamics of over 100 taxa from studies undertaken worldwide provides the basis of a critical assessment of current knowledge. At the scale of single habitats, simple reaction-diffusion models may be accurate enough to predict the spread of new invaders without recourse to complex life history parameterization. Average rates of local spread reported for invasive species in the literature range from 2 m·y^{-1} to a maximum of 370 m·y^{-1}. Average rates of long-distance dispersal are at least two orders of magnitude greater than estimates of local dispersal, with a maximum of 167 km·y^{-1}. While local-scale studies do pick up dispersal events of several kilometres, study sites are rarely sufficiently large or monitored for long enough to characterize these events accurately. Long-distance dispersal events may occur during periods of negligible population increase and appear to bear little relationship to population size. At regional scales, invasive species rarely move across the landscape as a continuous front and both local and long-distance dispersal determine spatial patterns. At these larger spatial scales, both local and long-distance dispersal require parameterization, and this has been achieved through spatially explicit individual-based simulation models using two or more dispersal functions. It is doubtful whether a single estimate of spread encapsulates the spatio-temporal dynamics of invasive species at this scale. Thus, estimates of spread drawn from successive distribution maps will tend to be biased towards long-distance dispersal events. The frequency and distribution of introduction events play a key role in invasion trajectories, and the stochastic nature of such events may explain why the longer a species has been introduced into a region the greater the likelihood that it becomes invasive. However, cumulative counts of localities or samples only provide one perspective on the invasion process and need to be associated with spatial information to depict spread more realistically. This review highlights that monitoring of invasive species must be approached from a hierarchical perspective with data gathered at more than one spatial scale. Such an approach will improve predictions and integrate landscape attributes into invasion dynamics.
Keywords: alien plants, lag-phase, landscape, plant dispersal, population growth, reaction-diffusion, spatial scale.

Résumé : Les invasions biologiques ont une dyamique spatiotemporelle particulière. L'aire de répartition de plusieurs espèces s'est grandement étendue au cours du dernier siècle; alors qu'elles se limitaient à l'intérieur d'une seule région par le passé, elles occupent maintenant une grande partie du globe. Nous avons procédé à une analyse comparative de la dynamique spatiotemporelle de 100 taxons à partir d'études menées un peu partout dans le monde. Cela nous a permis de faire le point sur les connaissances actuelles en la matière. À l'échelle d'un habitat, les modèles simples de réaction-diffusion peuvent être assez précis pour prédire l'envahissement de nouvelles espèces sans qu'on doive recourir à une étude complexe des paramètres des cycles vitaux. Dans la littérature, les taux moyens de dissémination locale rapportés pour les espèces envahissantes varient de 2 m·an^{-1} à 370 m·an^{-1} au maximum. Les taux moyens de dissémination sur de longues distances sont au moins deux fois supérieurs à ces taux, et atteignent un maximum de 167 km·an^{-1}. Les études menées à une échelle locale peuvent décrire des cas de dissémination s'étendant sur plusieurs kilomètres. Par contre, les études effectuées sur un site en particulier ne couvrent pas une assez grande superficie ou se déroulent sur une période de temps trop courte pour caractériser adéquatement ces cas de dissémination. La dissémination sur de longues distances peut se produire pendant des périodes d'accroissement négligeable des populations et n'a que peu de liens avec la taille de celles-ci. À une échelle régionale, les espèces envahissantes se déplacent rarement sous la forme d'un front continu dans le paysage. Dans les faits, ce sont les processus de dissémination sur de courtes et de longues distances qui façonnent les patrons de répartition. À plus grande échelle spatiale, il est nécessaire de définir les paramètres qui influencent les taux de dissémination sur de courtes et de longues distances, ce qui a été fait à partir de modèles de simulation spatiaux basés sur les individus et utilisant deux ou plusieurs fonctions de dissémination. À cette échelle, il est peu probable qu'un seul estimé d'expansion puisse expliquer la dynamique spatiotemporelle des espèces envahissantes. Par conséquent, les estimés d'expansion faits à partir de cartes de répartition successives ont tendance à être fortement influencés par la dissémination sur de longues distances. La fréquence et la répartition des introductions sont des facteurs-clés dans les trajectoires que prennent les invasions. La nature stochastique de tels événements pourrait expliquer pourquoi les espèces qui ont été introduites depuis longtemps dans une région ont plus de chances de devenir envahissantes. Quoiqu'il en soit, les dénombrements cumulatifs de localités avec espèces envahissantes apportent des précisions sur un aspect bien précis du processus d'invasion. Ils doivent être complétés par des informations de nature spatiale afin de décrire l'expansion de façon plus réaliste. Cette étude illustre à quel point le suivi des espèces envahissantes doit se faire avec une perspective hiérarchique où les données sont recueillies à plus d'une échelle spatiale. Une telle approche permettra d'améliorer les prédictions concernant les invasions et d'incorporer les caractéristiques du paysage dans la dynamique des invasions.
Mots-clés : croissance de la population, décalage, dissémination des plantes, échelle spatiale, paysage, plantes exotiques, réaction-diffusion.

Nomenclature: Weber, 2003 and original sources listed in Tables I and II.

Introduction

Biological invasions are characterized by remarkable spatio-temporal dynamics, with many species having extended their distribution range from within a single region to much of the globe within the last century (Holm *et al.*, 1977; Weber, 2003). Understanding the drivers of range extension and the determinants of both the rate and magnitude of spread is central to the management of biological invasions (Ewel *et al.*, 1999; Sakai *et al.*, 2001; Wittenberg & Cock, 2001). The dramatic spread of non-native species has been facilitated by association with intercontinental commerce and travel (*e.g.*, ballast, seed contaminants, horticultural trade), ability to disperse along regional transport networks (*e.g.*, roadsides, canals, railways), and capacity for local colonization and population increase. Thus, a hierarchy of processes operating at different temporal and spatial scales determines the dynamics of biological invasions. Processes occurring at any one spatial scale may be structured by what happens at smaller or larger spatial scales such that the process of interest is constrained to operate within the bounds set by the system of which it is a part (O'Neill, 1989). An understanding of the interplay between processes operating at different spatial and temporal scales will identify whether "top-down" or "bottom-up" control occurs and emphasize the most appropriate scale on which to predict future changes in invasion trajectories (May, 1989). Such scale dependency is also of practical significance since alien taxa that exhibit high rates of spread are likely to become widely distributed and troublesome (Forcella, 1985). However, to date, invasion studies that integrate across different spatial scales are rare, and a clear disassociation exists between analysis of intercontinental invasion "pathways" and intraregional spread. Current understanding of invasion pathways is rudimentary and largely restricted to catalogues of species origins and transport vectors (Hulme, in press). In contrast, the numerous studies of intraregional spread build on a substantial knowledge based on species dispersal (Bullock, Kenward & Hails, 2002). Given this significant bias, our critical appraisal of the spatio-temporal dynamics of invasions largely focuses on intraregional studies.

The shape of things to come: Patterns in invasion trajectories

Unfortunately, as the crucial aspect of recognizing an invasive species is the invasion itself, plant invasions are in the majority of cases studied post hoc (Fuller & Boorman, 1977; Pyšek, 1991; Perrins, Fitter & Williamson, 1993; Pyšek & Prach, 1993; 1995; Delisle *et al.*, 2003; Frappier *et al.*, 2003) and studies rarely describe the whole process of invasion from its beginning. Where this has been possible, studies have generally found a period of slow initial spread (lag-phase) in which the alien occurs in a few isolated locales, followed by a phase of rapid range expansion (exponential phase) and a third phase of little or no areal extension (Robinson, 1965; Mack, 1981; Usher, 1986; Lonsdale, 1993).

Considerable interest exists in the factors that determine the length of the lag-phase between introduction and exponential increase (Crooks & Soulé, 1999). Lag-phases of up to 180 y have been found for herbaceous species (Pyšek & Prach, 1993) and 150 or more years for woody plants (Kowarik, 1995). If the lag-phase reflects biological attributes, then it may be possible to predict invasion potential before the phase of exponential increase.

The genotypic hypothesis suggests that the lag-phase represents the time required for the development of genotypes with increased dispersal ability (Hobbs & Humphries, 1995). This hypothesis predicts that the length of the lag-phase is proportional to generation time and that long-distance dispersal is an intrinsic attribute of the species concerned. While there is evidence in support of the first prediction (Kowarik, 1995), long-distance dispersal events appear to be largely driven by extrinsic factors (Higgins, Nathan & Cain, 2003).

The demographic hypothesis postulates that soon after introduction, alien populations expand slowly at their margins by short-distance dispersal and that their spread is limited by the local availability of suitable habitat (Cousens & Mortimer, 1995). The rapid spread associated with exponential increase is initiated by long-distance dispersal (mainly human-mediated) that establishes new satellite populations in suitable habitat. The change to rapid spread becomes more likely with an increase in population size as well as with proximity to and frequency of long-distance dispersal vectors.

The extrinsic hypothesis proposes that lag-phases are a result of inclement environmental conditions that give way to exponential population increase as these conditions improve (Sakai *et al.*, 2001). Changes in soil disturbance, nutrient enrichment, climate, dispersal vectors, and intraspecific interactions may result in increased population growth and/or dispersal.

Although all three hypotheses are plausible (and not mutually exclusive), the lag-phase may be no more than an artefact. First, it is notoriously difficult to distinguish statistically between a single exponential phase of increase (constant per unit area rate of increase) and one that has both a lag and exponential phase (Cousens & Mortimer, 1995; Williamson *et al.*, 2005). This statistical shortcoming is compounded by evidence that changes in the intensity and techniques of plant surveys through time can introduce bias into data that could be interpreted as distinct phases of invasion (Cousens & Mortimer, 1995). Second, the lag-phase may depend on the scale of observation. Invasions are discontinuous in time and space and comprise both local population expansion and new introductions. Thus, although population growth rate may occur in a discrete area, this may not correspond to the rate of spread. Hence what appears to be a lag may actually conform to a constant exponential expansion rate when viewed from a coarser spatial scale.

The temporal and spatial patterns of population expansion of three alien riparian weeds in England and Wales provide an opportunity to assess the ecological basis underlying lag-phases (Figure 1a). At a relatively fine spatial resolution of observation (10 × 10 km square) a clear lag-phase can be discerned for all three species. The three species encompass a wide range of herbaceous
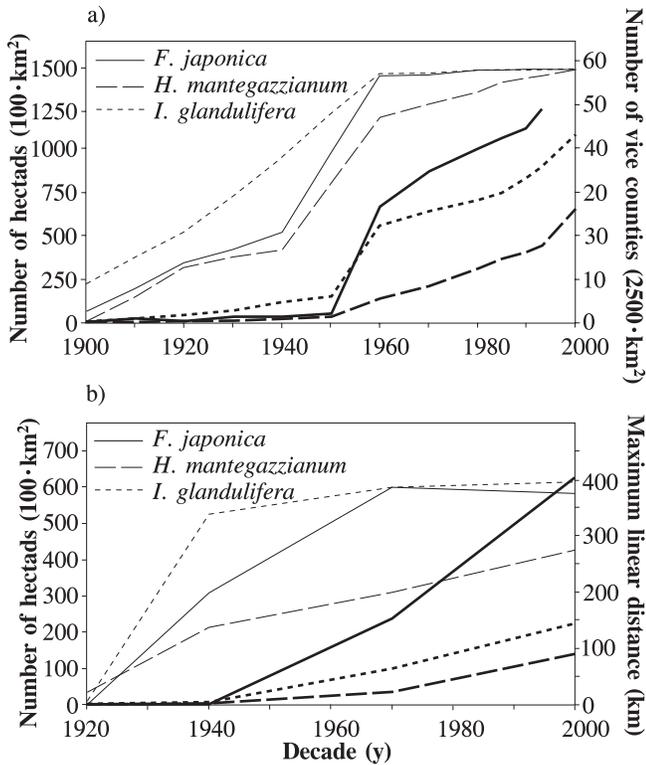
FIGURE 1. a) The rate and extent of spread of *Fallopia japonica*, *Heracleum mantegazzianum*, and *Impatiens glandulifera* in England and Wales observed at two spatial scales: cumulative number of hectads (10-10-km squares, bold lines) and vice-counties (thin lines) occupied since 1900. b) The rate and extent of spread of *F. japonica*, *H. mantegazzianum*, and *I. glandulifera* in Ireland as assessed by cumulative number of hectads (10- 10-km squares, bold lines) and the maximum distance from the original introduction (thin lines) occupied since 1920. Data from the UK Biological Records Centre (unpubl. data).

life histories, including annual (*Impatiens glandulifera*), monocarpic perennial (*Heracleum mantegazzianum*), and clonal perennial (*Fallopia japonica*). The similarity in length of lag-phase (40 y) and synchronous exponential increase suggest that their temporal trajectories are not entirely driven by life history traits. At a coarser spatial resolution (vice county), the lag-phases are far less pronounced, and this may be indicative that the patterns more accurately reflect the frequency of long-distance dispersal events and new introduction rather than local population expansion. This interpretation is further supported by an inverse relationship between apparent lag-phase length and number of introductions (Cousens & Mortimer, 1995). Thus, the frequency and distribution of introduction events play a key role in invasion trajectories, and the stochastic nature of such events may explain why the longer a species has been introduced into a region the greater the likelihood that it becomes invasive (Scott & Panetta, 1993).

These findings further highlight the central role chance events play in determining the characteristics of invasion (Crawley, 1989). At each step of the invasion process, from arrival of the invasive plant through its establishment, spread, and persistence, stochastic events influence the outcome of the interaction between the invader and host community (Mollinson, 1986). Some examples of stochastic events that facilitate invasion

include extreme events (flooding, drought, fire), nutrient enrichment, overgrazing, access to new vectors (cars, ungulates, rivers), and disturbance (Humphries, Groves & Mitchell, 1991). These events, while crucial to the development of the invasion, occur infrequently in both time and space. The temporal and spatial scales of the vast majority of studies on plant invasions (focusing on single habitats over only a few years) are insufficient to document either the nature or frequency of these events, let alone their role in the invasion. Only by examining plant invasions over long temporal periods and across large spatial scales will the properties of these rare events be observed and characterized as probabilities associated with particular plant species and/or habitat traits. Thus, events that are unpredictable at the small scales commonly studied by ecologists may become predictable at larger spatial scales. For these reasons the major developments in the spatial ecology of biological invasions have arisen through modelling initiatives.

Invasion models and plant dispersal: The sting in the tail

Plant dispersal has been addressed using a variety of theoretical approaches, including reaction-diffusion, integrodifference, random-walk, and simulation models, leading to a rich theory for estimating rates of spread (reviewed in Higgins & Richardson, 1996; With, 2002; Higgins *et al.*, 2003). The probability density function describing the spatial redistribution of propagules about a parent plant ("dispersal kernel") has been the subject of intensive mathematical and biological study. Models and detailed biological studies have shown that it is the characteristics of the dispersal kernel that determine the rate at which plants can spread spatially when introduced into new environments.

Most biological invasion models fall into one of two major approaches. The earliest approach, and still the most popular, is the reaction-diffusion model. Reaction-diffusion (RD) models are based on partial differential equations of the form:

$$\frac{\partial N}{\partial t} = rN + D\left[\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2}\right] \qquad [1]$$

where $N(x, y, t)$ is the population density at time t at point x,y on the landscape, r is the per capita population growth rate, and D is the diffusion coefficient. The diffusion coefficient determines the dispersal kernel that is usually approximated by a Gaussian distribution. The models have been developed to include logistic rather than geometric population growth and a range of distribution functions (Hengeveld, 1994). As there is no preferred direction, the population will spread out radially. The rate of advance (z/t) is given by:

$$\frac{z}{t} = \left(4rD\right)^{\frac{1}{2}} = 2r^{\frac{1}{2}}D^{\frac{1}{2}} = 2\sqrt{(rD)} \qquad [2]$$

Thus, the rate of spread is constant and proportional to the square root of the per capita population growth rate and the diffusion coefficient. Furthermore, the square root of area occupied will increase linearly with time.

The underlying assumption that seed dispersal follows a diffusion process led to "Reid's paradox of rapid plant migration" since the rates of spread predicted by RD models were much less than those observed for the post-glacial advance of trees (Clark, 1998; Clark *et al.*, 1998). Attempts to overcome this limitation have included using two or more dispersal kernels to represent local and long-distance dispersal (Allen *et al.*, 1991; Collingham, Huntley & Hulme, 1997; Higgins, Richardson & Cowling, 2001).

Integrodifference equation (IDE) models (Kot, Lewis & van den Driessche, 1996; Clark *et al.*, 1998) differ from RD models in that they do not assume that reproduction and dispersal occur simultaneously but break these down into two separate stages. The model is thus composed of two parts: a difference equation that describes population growth at each point on the landscape and an integral operator that accounts for dispersal.

$$N_{t+1}(x) = \int_{-\infty}^{\infty} k(x, y) f\left[N_t(y)\right] dy \qquad [3]$$

Here, $N_{t+1}(x)$ is the future population density at a point x, which is a function of population growth at each source point $y(f[N_t(y)])$ and the shape of the dispersal function k that determines the movement of individuals from y to x. More complex versions of the model include x in two dimensions and N_t as a vector of interacting species or stages within a population.

The advantage of IDE over RD models is that they can incorporate leptokurtic or "fat-tailed" distributions that more realistically encompass rare long-distance dispersal events and thus overcome the paradox found in RD model predictions. A major limitation of applying IDE models to simulate actual invasion scenarios is uncertainty about the shape of the dispersal kernel, particularly over long distances. Even small changes in the "tails" of the dispersal kernel can result in order-of-magnitude changes in predicted spread rates. Furthermore, even where sufficient data are available, kernels with different shaped "tails" can produce similarly good fits to observations yet produce drastically different estimates of spread (Clark *et al.*, 1998). As a consequence, population spread when dispersal is fat-tailed is inherently unpredictable (Clark *et al.*, 2003).

Both RD and IDE models have been used to explore the role of landscape structure on the rates of spread (With, 2002). Although elegant, such simulations have but largely confirmed the long-held belief that spread through a patchy environment will depend on the degree of habitat heterogeneity, size and distribution of patches, distance between suitable patches, and population characteristics such as growth rate and dispersal ability (Mooney & Drake, 1986). Assessing what represents suitable habitat for an invasive species is not without its own problems, especially where populations are not at equilibrium but still expanding (Collingham *et al.*, 2000; Rouget *et al.*, 2004). Thus, running dispersal models in realistic landscapes carries a significant risk of error propagation arising from uncertainty in both dispersal and habitat suitability parameters.

To what extent do these models map onto reality? At the scale of single habitats, simple reaction-diffusion models may be accurate enough to predict the spread of new invaders without recourse to complex life history parameterization or detailed knowledge of the dispersal kernel (Frappier *et al.*, 2003). Small-scale studies will provide the necessary parameters for deterministic models of invasion that are most likely to yield reliable approximations when the number of arriving individuals is large or during the later stages of successful invasion, when population densities are high. At larger spatial scales, both local and long-distance dispersal require parameterization, and this has been achieved through spatially explicit individual-based simulation models using two or more dispersal functions. Higgins, Richardson, and Cowling (2001) were successful in producing realistic model estimates for both the rate and pattern of *Acacia cyclops* and *Pinus pinaster* invasion into South African fynbos habitats. Collingham, Huntley, and Hulme (1997) had less success in modelling the spread of *Impatiens glandulifera* across England and Wales. Although the model fit was fair, new occurrences of *I. glandulifera* at isolated locations and/or in previously uncolonized river catchments were underrepresented. The differential success of these two examples highlights important constraints on modelling invasions. The fynbos model suffered much less from model uncertainty in that the scale of the long-distance dispersal function was larger than the scale of the study and thus was less sensitive to model specification. Furthermore, the data resolution (aerial photographs *versus* 10-   10-km grid cells) reduced parameter uncertainty in the classification of habitat suitability in fynbos. Finally, the larger scale of the United Kingdom study exposed the model to greater inherent uncertainty in the form of stochastic processes such as flood events that might facilitate spread. Thus, significant challenges remain in forecasting rates of spread in regional models of invasion (Higgins *et al.*, 2003). Perhaps only through a comparative analysis of case studies will generalities emerge regarding the spatio-temporal dynamics of biological invasions.

Rates of spread: Dispersal, diffusion, and data deficiencies

DATA AND ASSUMPTIONS

Although numerous studies report changes in the distribution of alien species between at least two time intervals (Tables I and II), comparative analyses of rates of spread are often fraught with difficulty. Data sources represent a variety of assessments, including number of individuals, number of localities, area invaded, and linear distance between origin and furthest occurrence of the species. Are such estimates comparable? If spread is equivalent to the rate of advance, then the rate of spread is a function of population growth and dispersal, and both need to be assessed to measure rates of spread. The cumulative number of individuals, populations, or localities recorded over a specific time interval is often used to calculate rate of spread (Perrins, Fitter & Williamson, 1993; Williamson *et al.*, 2005; Figure 1). Although an increase in area is implicit in such calculations since more individuals or localities occupy more space, such data primarily represent population growth, not dispersal. Imagine two species with the same population growth rate but a

Table I. Rates of linear spread of alien plants reported in the literature. Measure of linear spread was based on the distance between the source population at the beginning of invasion and the point it reached over the period covered by study. Note that values of the rate of spread are in $m \cdot y^{-1}$ for local dispersal (a) and in $km \cdot y^{-1}$ for long-distance dispersal (b). Family names are abbreviated following the system in Mabberley (1997). Start of invasion is indicated where original data cover the whole period of invasion, length of which is indicated by Duration (? - duration unkown); empty cell indicates that the value was measured in later stages of invasion. Within a and b, species are arranged according to the decreasing rate of spread.

Species	Family	Life form	Region invaded	Habitat	Start	Duration (y)	Rate of spread	Data	Range	Source	Method
a) Local dispersal ($m \cdot y^{-1}$)											
Opuntia stricta	Cac	succ_per	South Africa	savanna	1953	50	370	op	7,000	Foxcroft et al., 2004	pd
Mimosa pigra	Fab	shrub	Australia	riparian		6	87.3	op	2,062	Lonsdale, 1993	a
Centaurea diffusa	Com	ann_herb	British Columbia	grassland		3	40	o		Myers & Berube, 1983	fm
Pinus radiata	Pin	tree	South Africa	shrubland	1947	30	31	o	116.5	Higgins, Richardson & Cowling, 2001	a
Acacia cyclops	Fab	shrub, tree	South Africa	shrubland		61	26.0	os	21.3-30.6	Higgins, Richardson & Cowling, 2001	a, m
Vaccinium corymbosum × angustifolium	Eric	shrub	Germany	bog, forest, wasteland	1967	30	25.3	os	1.7-56.7	Schepker & Kowarik, 1998	ds
Pinus pinaster	Pin	tree	South Africa	shrubland		61	24.1	os	17.5-31.4	Higgins, Richardson & Cowling, 2001	a, m
Prunus serotina	Ros	tree	Germany	forest, arable land		27-45	14.6	os	6.0-22.0	Kowarik, 2003	ds
Ammophila arenaria	Gra	per_grass	California	dunes	1901	87	14.0	o		Buell, Pickart & Stuart, 1995; Higgins, Richardson & Cowling, 2001	a
Pinus halepensis	Pin	tree	South Africa	shrubland	1953	38	12.7	o	96.3	Rouget et al., 2001	a
Heracleum mantegazzianum	Api	mp_herb	Czech Republic	pasture, wasteland	1957	45	10.8	os	3.8-26.7	Müllerová et al., in press	a
Pinus radiata	Pin	tree	South Africa	shrubland	1953	38	8.5	o	40.2	Rouget et al., 2001	a
Spartina anglica	Gra	per_grass	New Zealand	seashore		?	7.2			Lee & Partridge, 1983	
Frangula alnus	Rha	shrub, tree	New Hampshire	forest		36	6.7	op	0.4-7.9	Frappier et al., 2003	ag
Rhododendron ponticum	Eric	shrub	United Kingdom	forest, dune		20	5	o		Fuller & Boorman, 1977	a
Pinus canariensis	Pin	tree	South Africa	shrubland	1945	46	4.0	o	8	Rouget et al., 2001	a
Pinus pinaster	Pin	tree	South Africa	shrubland	1953	38	3.5	o	46.9	Rouget et al., 2001	a
Spartina anglica	Gra	per_grass	New Zealand	seashore		9	2.8	os	0-5.3	Lee & Partridge, 1983	ds
Impatiens glandulifera	Bal	ann_herb	United Kingdom	various			2	o		Perrins, Fitter & Williamson, 1993	fm
b) Long-distance dispersal ($km \cdot y^{-1}$)											
Wedelia trilobata	Com	per_herb	Queensland	riparian		15	167	o		Batianoff & Franks, 1997	fl
Lycopus europaeus	Lam	per_herb	Québec	riparian		11	45	max		Delisle et al., 2003	fl
Hydrocharis morsus-ranae	Hyd	per_herb	Québec	riparian		17	15	max		Delisle et al., 2003	fl
Epilobium ciliatum	Ona	per_herb	United Kingdom	various		30	9.1	o		Williamson, Preston & Telfer, 2003	gm
Heterotheca latifolia	Com	per_herb	Georgia, South Carolina	various		7	8.9	os	4.8-12.1	Plummer & Keever, 1963	a, fm
Eschscholtzia californica	Pap	per_herb	Chile	wasteland	1892	45	8.4	op	5.3-11.6	Arroyo et al., 2000	fl
Veronica filiformis	Scro	per_herb	United Kingdom	various		30	4.7	o		Williamson, Preston & Telfer, 2003	gm
Fallopia japonica	Pol	per_herb	United Kingdom	various		30	4.3	o		Williamson, Preston & Telfer, 2003	gm
Impatiens glandulifera	Bal	ann_herb	United Kingdom	various		30	3.9	o		Williamson, Preston & Telfer, 2003	gm
Impatiens glandulifera	Bal	ann_herb	Czech Republic	various	1896	99	3.7	o		Williamson et al., 2005	fl
Impatiens glandulifera	Bal	ann_herb	United Kingdom	various	1839	154	2.6	ini	38.0	Perrins, Fitter & Williamson, 1993	gm, m
Hypericum perforatum	Hyp	per_herb	Victoria	arable land, pasture	1880	25	2.0	o		Harris & Gill, 1997	ds
Fallopia sachalinensis	Pol	per_herb	United Kingdom	various		30	2.0	o		Williamson, Preston & Telfer, 2003	gm
Impatiens glandulifera	Bal	ann_herb	United Kingdom	various		20	1.9	os	5.0	Usher, 1986	gm

TABLE I. Concluded.

Species	Family	Life form	Region invaded	Habitat	Start	Duration (y)	Rate of spread	Data	Range	Source	Method
Impatiens parviflora	Bal	ann_herb	Czech Republic	various	1816	179	1.8	o		Williamson *et al.*, 2005	fl
Impatiens parviflora	Bal	ann_herb	United Kingdom	various	1848	148	1.6	ini	24.0	Perrins, Fitter & Williamson, 1993	gm, m
Solidago gigantea	Ast	per_herb	Czech Republic	various	1851	144	1.4	o		Williamson *et al.*, 2005	fl
Impatiens capensis	Bal	ann_herb	United Kingdom	various	1841	152	1.4	ini	13.0	Perrins, Fitter & Williamson, 1993	gm, m
Senecio squalidus	Com	per_herb	United Kingdom	various		30	1.4	o		Williamson, Preston & Telfer, 2003	gm

Life form: ann – annual, per – perennial, mp – monocarpic perennial, succ – succulent.

Data: o – overall rate of spread measured as a distance between the point where the species was first reported and the most distant point reached over the study period (Duration), or calculated from the model of spread over the whole period. If the value is available for different periods of invasions (op) or different sites or directions of spread (os), the maximum (a single value) or range of values is shown in the next column (Range); ini – initial rate of spread calculated from logistic regression; max – maximum value is shown where overall rate is not available.

Method of collating the data and calculating the rate of spread: pd – population density, ag – age structure, a – aerial photographs, fm – field measurements, m – calculated from statistical model, fl – floristic records, including herbaria, gm – repeated grid mapping, ds – distance from the source population.

two-fold difference in dispersal ability. Estimates of the rate of spread derived from plots of the cumulative number of individuals would be similar in both cases even though a four-fold difference might exist in the maximum species range. An alternate measure of spread can be derived from the progressive increase in area a species occupies (Mack, 1989). This approach has been widely applied to isochrone (pollen) maps to assess the spread of tree species from their position at the glacial maximum to their present distribution. For much of this period, the square root of the area plotted against time gives a straight line, and combined with published estimates of *r*, rates of diffusion were calculated to be between 1.7 and 9.1 $km^2 \cdot y^{-1}$ (Birks, 1989). Although consistent with predictions from RD models, observed rates of spread were too high to have arisen through random diffusion (Clark, 1998; Clark *et al.*, 1998). This reflects that RD models work best at local scales but do not encompass regional events such as long-distance dispersal. At regional scales, invasive species rarely move across the landscape as a continuous front, and both local and long-distance dispersal determine spatial patterns. It is doubtful whether a single estimate of spread encapsulates the spatio-temporal dynamics of invasive species at this scale. Estimates of spread drawn from successive distribution maps will tend to be biased towards long-distance dispersal events. This can be illustrated through comparison of maximum distances from origin and the number of localities occupied by three riparian weeds in Ireland. Such analyses indicate that long-distance dispersal events do not represent invasion trajectories particularly well (Figure 1b). Long-distance dispersal events may occur during periods of negligible population increase and appear to bear little relationship to population size.

CONSTRAINTS TO ASSESSMENT OF THE RATE OF SPREAD

The rate of spread is often quantified by reconstructing the history of invasion from literature data and/or herbarium records plotted over time (Weber, 1998; Petřík, 2003; Mandák, Pyšek & Bímová, 2004). However,

such data need to be weighted to control for the increasing intensity of floristic research over time; this was done by comparing trends between native and alien species (Stadler, Mungai & Brandl, 1998; Delisle *et al.*, 2003) or by taking into account the number of herbarium specimens in the country (Mihulka & Pyšek, 2001). Where data have been collected on a fixed sampling grid, the number of occupied cells over time can be used to calculate the intrinsic rate of increase and infer the spatial dimension of spread (Perrins, Fitter & Williamson, 1993). However, the rates of spread calculated from such data are strongly determined by the cell size, and they assume dispersal equates to random diffusion. The former will tend to overestimate areal coverage and spread, while the assumption of random diffusion will underestimate long-distance dispersal. Do these biases balance out to give realistic rates of spread? The limited evidence suggests not. Data from sampling grids and floristic records provide estimates of spread for *Impatiens glandulifera* of around 3 $km \cdot y^{-1}$, yet spatial simulation models require higher rates of spread to accurately simulate the spread of this species in England and Wales (Collingham, Huntley & Hulme, 1997). The foregoing highlights that no single method currently used to assess rates of spread is an adequate measure of the spatio-temporal dynamics of invasive species. Several measures are required: the population growth rate and values for both the frequency and distance of local and long-distance dispersal events. Unfortunately, adequate data for all these parameters are not available for invasive species. Yet, even where suitable data for some of the measures exist, the nature of the data can often hinder comparisons. For example, invasion trajectories are rarely linear; thus, interspecific differences in rates of spread may be detected if comparisons are made at different phases of invasion even where the overall trajectory is similar (Figure 1a). Ideally, comparisons should be made at similar phases of the invasion trajectory, preferably the exponential phase to provide maximal estimates of spread (Williamson *et al.*, 2005).

TABLE II. Rates of areal spread of alien plants reported in the literature. Measure of areal spread was based on the area covered by invading populations. Note that the values of the rate of spread are in $m^2 \cdot y^{-1}$ for local dispersal (a) and in $km^2 \cdot y^{-1}$ for long-distance dispersal (b) and those of invaded area are in m^2 and km^2, respectively. Family names (Taxon) are abbreviated for vascular plants following the system in Mabberley (1997); Chlo - Chlorophyta. Date of the beginning of invasion and the period over which it is followed (Duration) is indicated where available; empty cell indicates that the value was measured in later stages of invasion. Within a and b, species are arranged according to the decreasing rate of spread.

Species	Taxon	Life form	Region invaded	Habitat	Start	Duration (y)	Rate of spread	Data	Range	Invaded area	Source	Method
a) LOCAL DISPERSAL ($m^2 \cdot y^{-1}$)												
Caulerpa taxifolia	Chlo	alga	France	sea bottom	1984	5	2,000	o		10,000	Meyer, Meinesz & de Vaugelas, 1998	fm
Heracleum mantegazzianum	Api	mp_herb	Czech Republic	pasture, wasteland	1957	45	1,261	os	139-3,275	41,900	Müllerová et al., in press	e, a
Rhododendron ponticum	Eri	shrub	United Kingdom	forest, dune		20	1,100	o		28,000	Fuller & Boorman, 1977	e, a
Spartina anglica	Gra	per_grass	New Zealand	seashore		9	21.9	o			Lee & Partridge, 1983	pp
Spartina anglica	Gra	per_grass	New Zealand	seashore		4	12.8	o			Lee & Partridge, 1983	
Spartina anglica	Gra	per_grass	New Zealand	seashore		41	1.2	o			Lee & Partridge, 1983	
b) LONG-DISTANCE DISPERSAL ($km^2 \cdot y^{-1}$)												
Bromus tectorum	Gra	ann_grass	Great Basin	grassland	1889	40	4,878	o		200,000	Mack, 1981; 1989	e
Opuntia stricta	Cac	suc_per	Australia	scrub, riparian, wasteland	1839	81	2,963	op	656-10,000	240,000	Harper, 1977	e
Cryptostegia grandiflora	Asc	climb_w	Victoria	forest, arable land	1865	134	2,612	o		350,000	Baskin, 2002	e
Parthenium hysterophorus	Com	ann_herb	India	pasture	1951	45	449	op	415-800	20,200	Shiva, 1996; Evans, 1997	e
Centaurea solstitialis	Com	ann_herb	California	grassland	1869	130	350.3	o		40,000	Mack, 2000	e
Solanum viarum	Sol	per_herb	Florida	pasture	1980	15	333	op	10-1,690	5,000	Cuda et al., 2002	e
Chromolaena odorata	Com	climb_w	South Africa	forest, grassland, savanna	1943	39	205.1	o		8,000	Henderson & Wells, 1986	e
Hypericum perforatum	Hyp	per_herb	USA: W coast	arable land, pasture, wasteland	1900	44	181.8	o		8,000	Harper, 1977	e
Acacia mearnsii	Fab	tree	South Africa	various	1858	140	178.6	o		25,000	Versfeld, Le Maitre & Chapman, 1998	e
Lantana camara	Ver	shrub	South Africa	forest, riparian, savanna	1858	140	157.1	o		22,000	Versfeld, Le Maitre & Chapman, 1998	e
Melia azedarach	Meli	tree	South Africa	savanna, riparian, wasteland	1800	198	151.1	o		30,000	Versfeld, Le Maitre & Chapman, 1998	e
Opuntia aurantiaca	Cac	suc_per	South Africa	karoo	1858	134	121	o		15,000	Henderson & Wells, 1986	e
Opuntia ficus-indica	Cac	suc_per	South Africa	karoo	1780	162	55.6	o		9,000	Richardson et al., 2000	e
Schinus terebinthifolius	Ana	tree	Florida	riparian, mangroves, grassland, wasteland	1926	71	39.4	o		2,800	Jones & Doren, 1997 Schmitz et al., 1997	e
Tamarix ramosissima[1]	Tam	shrub	USA: NW states	riparian, wetland	1877	121	38.7	op	1.9-89.7	4,684	Robinson, 1965; Zavaleta, 2000	e, a
Hakea sericea	Pro	shrub, tree	South Africa	shrubland: fynbos	1830	118	31.2	o		4,800	Macdonald & Richardson, 1986	e
Melaleuca quinquenervia	Myrt	tree	Florida	riparian, forest	1906	75	24.8	o		1,860	La Rosa, Doren & Gunderson, 1992	e
Eragrostis lehmanniana	Gra	per_grass	Arizona	grassland	1932	59	24.6	o		1,450	Anable, McClaran & Ruyle, 1992	e
Hypericum perforatum	Hyp	per_herb	New South Wales	arable land, pasture, wasteland	1890	96	20.8	o		2,000	Harris & Gill, 1997	e
Hypericum perforatum	Hyp	per_herb	Victoria	arable land, pasture, wasteland	1880	36	20.7	o		745	Harper, 1977; Harris & Gill, 1997	e
Clidemia hirta	Mela	shrub	Hawaii	forest	1941	51	19.6	op	0.1-36.2	1,000	Smith, 1992	e

TABLE II. Concluded.

Species	Taxon	Life form	Region invaded	Habitat	Start	Duration (y)	Rate of spread	Data	Range	Invaded area	Source	Method
Opuntia stricta	Cac	suc_per	South Africa	savanna	1953	50	13.2	o		660	Foxcroft *et al.*, 2004	e
Lygodium microphyllum	Schi	climb_f	Florida	wetland	1966	33	13.1	op	4.1-72.2	433	Volin *et al.*, 2004	
Miconia calvescens	Mela	shrub, tree	Tahiti	forest	1937	59	11.9	o		700	Meyer, 1996	e
Ageratina riparia	Com	per_herb	Hawaii	wasteland	1926	46	11.3	o		520	Davis, Yoshioka & Kageler, 1992	e
Myrica faya	Myri	shrub, tree	Hawaiian Islands	forest	1925	57	5.1	op	1.1-12.8	343.6	Whiteaker & Gardner, 1992	e
Tamarix ramosissima[1]	Tam	shrub	USA: Rio Grande Basin	riparian	1926	21	5.1	o	2.2-7.6	106.3	Robinson, 1965	e
Tamarix ramosissima[1]	Tam	shrub	USA: Pecos River	riparian	1912	48	4.8	op	0.8-5.2	230.3	Robinson, 1965	e
Clidemia hirta	Mela	shrub	Molokai	forest	1973	19	3.3	op	0.1-5.0	63	Smith, 1992	e
Mimosa pigra	Fab	shrub	Northern Territory	riparian	1890	94	3.2	o		300	Lonsdale, 1993	e
Eichhornia crassipes	Pon	aq_per	Lake Victoria	water bodies	1989	5	3.1	o		15.45	Mack, 2000	e
Caulerpa taxifolia	Chlo	alga	Mediterranean sea	sea bottom	1984	12	2.6	o		30.9	Meyer, Meinesz & de Vaugelas, 1998	e
Passiflora mollissima	Pas	climb_w	Hawaii	forest	1928	43	1.7	o		71.6	La Rosa, 1992	e
Vaccinium corymbosum × angustifolium	Eri	shrub	Germany	bog, forest, wasteland	1967	30	1.7	o		50.0	Schepker & Kowarik, 1998	e
Passiflora mollissima	Pas	climb_w	Hawaii	forest	1958	23	1.1	op	0.1-2.6	25.7	La Rosa, 1992	e
Passiflora mollissima	Pas	climb_w	Hawaii	forest	1921	57	1.1	op	0.8-8.9	62.6	La Rosa, 1992	e
Passiflora mollissima	Pas	climb_w	Hawaiian Islands	forest	1923	38	0.8	o		49.0	La Rosa, 1992	e
Schinus terebinthifolius	Ana	tree	Florida	riparian, mangroves, grassland, wasteland	1970	27	0.74	o		20.0	Jones & Doren, 1997; Schmitz *et al.*, 1997	e
Spartina townsendii	Gra	per_grass	France	seashore	1906	17	0.6	o		10	Oliver, 1925	e
Pinus halepensis	Pin	tree	South Africa	shrubland	1953	38	0.25	o		9.5	Rouget *et al.*, 2001	e, a
Pinus radiata	Pin	tree	South Africa	shrubland: fynbos	1947	30	0.078	o		2.36	Richardson & Brown, 1986	e, a
Solanum tampicense	Sol	per_herb	Florida	riparian	1983	13	0.05	o		0.6	Cuda *et al.*, 2002	e
Ammophila arenaria	Gra	per_grass	California	sand dune	1901	87	0.023	op	0.014-0.052	1.96	Buell, Pickart & Stuart, 1995	e, a
Solanum torvum	Sol	per_herb	Florida	pasture, wasteland	1899	102	0.02	o		2.5	Cuda *et al.*, 2002	e
Robinia pseudoacacia	Fab	tree	Italy	forest, arable land	1954	43	0.017	o		0.75	Bertacchi, Lombardi & Onnis, 2001	e, a
Fallopia japonica	Pol	per_herb	United Kindom	urban	1902	96	0.006	op	0.005-0.022	0.6	Meyer, Meinesz & de Vaugelas, 1998	fm

Life form: ann – annual, aq – aquatic, bi – biennial, clim_w – woody climber, clim_f – climbing fern, per – perennial, mp – monocarpic perennial, par – parasitic, succ – succulent.

Data: o – overall rate of spread, measured as an increase in invaded area over time or calculated from a model of spread over the whole period. If the value is available for different periods of invasions (op) or different site replicates (os), the range of recorded values is shown (Range).

Method of collating the data and calculating rate of spread: e – estimate of invaded area, a – aerial photographs, fm – field mapping, pp – permanent plots.

[1]*Tamarix* species invading in SW United States are a taxonomically complicated group that includes more species, of which *T. ramossissima* and *T. chinensis* are most common (Zavaletta, 2000).

Sampling non-linear invasion trajectories at different time intervals can lead to quite dissimilar estimates for rates of spread. For example, for *Fallopia japonica* decadal surveys give a mean annual rate of increase of 15%, surveys every 50 y raise this estimate to 36%, and if only the start and end dates are compared then the average is 295%. This problem will always arise where the different phases of the invasion trajectory do not span an equivalent time period (see reported values in Tables I and II where range is available). The most parsimonious option is to estimate the geometric mean rate of spread derived from the difference in population size between the first and last census.

Estimates of the timing and duration of the different phases of population growth (lag, exponential, and asymptote) depend on the spatial scale at which these phenomena are observed. The consequence is that at coarse resolutions the temporal trajectories of invasions tend to

overestimate both the area occupied and rate of spread (Figure 1a). Data resolution often becomes coarser as the spatial scale of the study increases. Thus, apparent increases in rate of spread from local (within a habitat) to regional (across many habitats) or even continental (across many regions) scales (Figure 2) may be artifacts if data resolution is not similar.

The above caveats constrain comparisons across study species and sites. In Tables I and II, data available in the literature are summarized. They indicate that the reported rates of spread are collected on various spatial and temporal scales and by using a variety of methods. The majority of primary data are not detailed enough (longitudinal data are especially rare) to allow for proper statistical analysis and calculation of the rates of spread on a solid basis (but see Lonsdale, 1993; Perrins, Fitter & Williamson, 1993; Williamson *et al.*, 2005). Per-year estimates of the rate of spread based on the area invaded over the given period of time are not a valid measure of the rate of spread (see above) and preclude statistical analysis. Nevertheless, compilation of datasets relating to local and long-distance spread, using linear (Table I) or areal measure (Table II), may provide insights into general patterns as well as limitations of these assessments.

RATES OF LOCAL SPREAD

Average rates of local spread reported for invasive species in the literature range from 2 $m \cdot y^{-1}$ to a maximum of 370 $m \cdot y^{-1}$ (Table Ia). The considerable interspecific variation highlights that a variety of dispersal mechanisms may facilitate rapid local spread, *e.g.*, animals (*Opuntia stricta*, *Acacia cyclops*, *Vaccinium corymbosum* × *angustifolium*), water (*Mimosa pigra*), wind (*Pinus* sp. div.). This is consistent with studies that have found associations between dispersal traits and invasiveness (Richardson *et al.*, 2000; Lloret *et al.*, 2004). However, intraspecific variation is at least as great as that between species. For example, the mean rate of spread of *M. pigra* over a 6-y period was 87.3 $m \cdot y^{-1}$, but the highest value recorded in a single year was more than 20 times as high (Lonsdale, 1993). Similarly, the maximum values recorded for *Pinus radiata* (Richardson & Brown, 1986), *P. halepensis*, and *P. pinaster* (Rouget *et al.*, 2001) are many times higher than the mean (Table Ia). Such studies provide an insight into the frequency of long-distance dispersal events. Over a period of 50 y, one population of *Opuntia stricta* spread up to 18.5 km from its origin, an average rate of 370 $m \cdot y^{-1}$ (Foxcroft *et al.*, 2004). However, in the first 2 y, outlying populations were established up to 14 km away. This suggests that relatively long-distance hops occurred early in the invasion, when the population was relatively small. This trend is also evident for riparian weeds in Ireland (Figure 1b). Estimates of the area occupied through local spread have sometimes been drawn from aerial photographs, and maximum recorded values range between 1,100 and 2,000 $m^2 \cdot y^{-1}$ (Table IIa). The rate of spread is usually presented as a linear or area measure. If a reaction-diffusion process adequately represents spread, then these two measures can be directly compared since the former is proportional to the square root of the latter. This is most likely to be true for local rather than long-

distance spread. These studies examine field sites that only extend over a few hectares and thus rarely pick up long-distance dispersal events (Fuller & Boorman, 1977). Without the influence of long-distance dispersal, these estimates are probably a fair reflection of local spread. At least on land, clonal species have lower rates of spread than those that reproduce by seeds. The influence of habitat suitability on rates of local spread is highlighted by the order of magnitude variation in the clonal spread of *Spartina anglica* in different New Zealand coastal sites (Lee & Partridge, 1983).

RATES OF LONG-DISTANCE SPREAD

Long-distance dispersal can occur on a remarkable scale, as is illustrated by *Wedelia trilobata*, which spread from a single focal area and covered 2,500 km of the Queensland coastline in 15 y, averaging thus some 167 $km \cdot y^{-1}$ (Batianoff & Franks, 1997; Table Ib). While local-scale studies do pick up dispersal events of several kilometres (Foxcroft *et al.*, 2004), study sites are rarely sufficiently large or monitored for long enough to characterize these events accurately. Nevertheless, a few studies, such as that on *Heterotheca latifolia* in Georgia, have painstakingly recorded distances of new populations from the known source (Plummer & Keever, 1963). This study reveals average long-distance dispersal of 8.9 $km \cdot y^{-1}$, at least two orders of magnitude greater than estimates of local dispersal. If the species were diffusing across the landscape, such linear rates of spread would give rise to areal occupancy of no more than 200 $km^2 \cdot y^{-1}$, yet published data produce estimates exceeding 2,000 $km^2 \cdot y^{-1}$ (Plummer & Keever, 1963). This is probably because areal estimates reflect the maximum rather than mean linear estimates of spread. Although most studies describe long-distance spread of between 3 and 500 $km^2 \cdot y^{-1}$ (Table IIb), indirect estimates of spread drawn from distribution maps can give much higher values, up to 5,000 $km^2 \cdot y^{-1}$ for *Bromus tectorum* (Mack, 1989). Larger-scale studies may suffer from biases as a result of data resolution such that the relationship between the rate of invasion and scale of the study is highly significant, explaining 70% of variation in the data (Figure 2). While areal estimates of spread may be impressive, their ecological value is questionable since they are not qualified by density estimates that might indicate a realistic scale of the invasion (Hulme, 2003).

Comparison of spread at different spatial scales

There are a limited number of data sets that provide an indication of how the rate of invasion differs across various spatial scales. A valid measure for comparison is doubling time, *i.e.*, the period needed to double the distribution or number of an invading species. Lonsdale (1993) compared the rate of increase in *M. pigra* on a local scale, measured by invaded area, with the rate computed for the study region as a whole, expressed by the number of infestations. On the local scale (Adelaide River, Australia), the average doubling time over the 6-y period of study was 1.2 y. Across the whole region (Northern Territory), the doubling time was much higher, 6.7 y, the
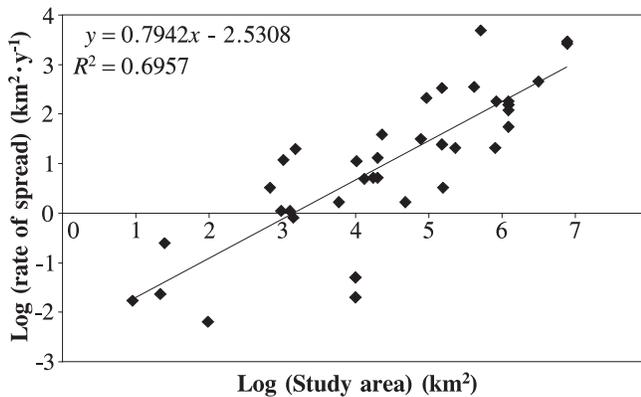
FIGURE 2. Scale dependence of published data on the rate of areal spread. Rate of spread of invasive species (km$^2 \cdot$y^{-1}, see Table II) is plotted against the total area at which the data was collected (km^2, estimated from primary sources). Note the log scale. $F = 84.60$, df = 1, 37, $P < 0.0001$.

rate of spread being lower because of the separation of suitable wetland habitats by eucalypt savannas that *M. pigra* can colonize less readily.

A similar comparison can be made for *Heracleum mantegazzianum*, another species for which there is detailed information on the course of invasion at local and national scales, in this case in the Czech Republic. Using the most recent national data (P. Pyäek & K. Prach, unpubl. data) and plotting cumulative number of records against time yields the doubling time 13.2 y for localities (Ln [localities] = –0.51 + 0.052 y) and 14.3 for mapping squares (Ln [squares] = –0.51 + 0.048 y; $F_{2, 164} = 1,481.0$; $P < 0.001$; $R^2 = 94.8\%$). These estimates do not significantly differ (deletion test: $F_{1, 202} = 2.14$; ns) from the doubling time of 13.9 y calculated at the local scale in the Czech Republic from changes in area occupied (Müllerová *et al.*, in press). That this species spread at a similar rate at both national and local scales suggests that the constraints to its spread imposed by landscape features and availability of suitable habitats were similar at both scales.

WHAT DO WE KNOW ABOUT THE FACTORS AFFECTING THE RATE OF SPREAD?

Given the limitations of the data analyzed above, their interpretation can hardly go much beyond statements on the range of values found at particular scales and measures of invasion. Only data on long-distance dispersal assessed as areal spread allow some conclusions to be drawn, as they are recorded in a similar way by different authors. These data are also most frequently reported as they are related to control efforts (in order to estimate the initial situation before the control measures are applied), of interest to landscape managers and the public (as part of the argument for raising awareness of invasive species problems), and, recently, easier to obtain, using modern technologies such as remote sensing and GIS.

However, given the variety of invading species, the range of life forms and species traits, and the variety of habitats and regions invaded, the available data are too scarce to allow rigorous analysis (the data in Tables I and II are by no means exhaustive, but we believe they repre-

sent a reasonable sample of what is available). More detailed insight into the factors affecting the rate of spread can only be obtained from studies using data collected in a more standard way (based on the same sources) and from the same area, where the scale factor is irrelevant and the same habitats are available for each species. Few studies match these criteria.

The available literature does not provide evidence of a close relationship between the rate of spread and traits of invading species. The data in Tables I and II suggest wind-, water-, or animal-mediated dispersal may be equally efficient mechanisms of local spread. Pyäek (1997) analyzed the initial rates of spread of 40 aliens in the north-west USA that had reached their final distribution in the area (reported by Forcella, 1985). Non-clonal species spread 34% faster than clonal species, but the relationship was only marginally significant ($P = 0.08$). Williamson *et al.* (2005) used information on taxonomy, life form and strategy, breeding system, and propagule size to explain the variation in the rate of spread of 63 naturalized aliens of the Czech flora, but none of these appeared to affect the rate of spread significantly. In their study of naturalized woody plants in New Zealand, Bellingham *et al.* (2004) did not find the rate of spread to be related to the relative growth rate of seedlings. That species traits are unlikely to provide straightforward explanations of dispersal rates is supported by generally poor correspondence between dispersal-related traits such as morphologically defined dispersal syndrome and long-distance dispersal events (Higgins, Nathan & Cain, 2003). For Mediterranean islands, wind-dispersed species tended to have a wider regional distribution than species dispersed by other means, but this trend was only occasionally found for local abundance on two islands (Lloret *et al.*, 2004). Neither growth form nor stem height explained trends in regional or local distribution. Thus, while species traits may be important in determining species establishment and naturalization rates (Daehler, 2003), the evidence to date suggests that the rate of spread cannot as yet be similarly defined. However, the lack of reported correspondence between the rate of spread and species traits may also be the result of lack of knowledge of crucial traits for any reasonable number of species.

The study of Williamson *et al.* (2005) nevertheless indicated the importance of economic and landscape features for the rate of spread of alien species. There was a significant negative relationship between the logarithm of doubling time and the date of introduction for perennial species in the Czech Republic, indicating that those that were introduced later spread faster. This result suggests that increased population density and economic activity have made the landscape more suitable for this set of alien plants. Further, if rates of spread are compared among countries, the same species spread faster in Britain than in either Ireland or the Czech Republic.

Conclusion

There appears to be a significant mismatch between the theoretical perspectives of dispersal and the availability of appropriate data pertaining to the spread of invasive species. The gathering of spatial data on invasive species

has almost become an end in itself (Hulme, 2003) with only limited attention as to how such data might be applied. The absence of clear standards prevents direct comparisons and thus inhibits the integration of theory and data. Although best practice in biological invasions calls for adequate monitoring (Wittenberg & Cock, 2001), little attention has been given to the key attributes of invasive species distributions that require detailed attention. This review has highlighted that monitoring must be approached from a hierarchical perspective, with data gathered at more than one spatial scale. Although spatial extrapolation and interpolation tools available in GIS (*e.g.*, krigging) can convert distribution data into attractive maps, estimates of area occupied are often misleading (Hulme, 2003). Spatially referenced point data are far more useful for estimating model parameters such as dispersal kernels. Cumulative counts of localities or samples only provide one perspective on the invasion process and need to be associated with spatial information to depict spread more realistically. Setting aside questions of data, a key message is that, throughout the world, non-native species have considerable potential to spread over large areas in a relatively short time; this review illustrates the magnitude of their spread by using values recorded in various parts of the world. This underlines the considerable urgency of integrating an understanding of spatio-temporal dynamics into invasive species management.

Acknowledgements

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