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Naturalization of introduced plants: ecological drivers of biogeographical patterns

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Contents

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Summary

The literature on biological invasions is biased in favour of invasive species – those that spread and often reach high abundance following introduction by humans. It is, however, also important to understand previous stages in the introduction–naturalization–invasion continuum ('the continuum'), especially the factors that mediate naturalization. The emphasis on invasiveness is partly because most invasions are only recognized once species occupy large adventive ranges or start to spread. Also, many studies lump all alien species, and fail to separate introduced, naturalized and invasive populations and species. These biases impede our ability to elucidate the full suite of drivers of invasion and to predict invasion dynamics, because different factors mediate progression along different sections of the continuum. A better understanding of the determinants of naturalization is important because all naturalized species are potential invaders. Processes leading to naturalization act differently in different regions and global biogeographical patterns of plant invasions result from the interaction of population-biological, macroecological and human-induced factors. We explore what is known about how determinants of naturalization in plants interact at various scales, and how their importance varies along the continuum. Research that is explicitly linked to particular stages of the continuum can generate new information that is appropriate for improving the management of biological invasions if, for example, potentially invasive species are identified before they exert an impact.

I. Introduction

Increasing human involvement in the dynamics of biological communities world-wide is reshuffling biotas in many ways – through the exploitation of many species, widespread habitat transformation, and the intentional and accidental movement of species across biogeographical barriers (Mack *et al.*, 2000; Stohlgren *et al.*, 2011). Biological invasions are mediated by many interacting processes that determine the causes and dimensions of the transport of organisms through human activity to areas outside their potential ranges, as defined by natural dispersal mechanisms and biogeographical barriers; and the fate of such organisms in their new ranges, including their ability to survive, establish, reproduce, disperse, spread, proliferate, interact with resident biota, and exert influence in many ways in invaded ecosystems (Richardson, 2011). A huge literature now exists on the ecological aspects and human dimensions of biological invasions (Hobbs & Mooney, 2005; Rejmánek *et al.*, 2005a,b; Pyšek *et al.*, 2006; Richardson & Pyšek, 2008; Pyšek & Richardson, 2010).

Most effort has been directed at invasive species, that is, introduced species that spread from points of initial introduction, often reaching high abundances in invaded ecosystems (Pyšek *et al.*, 2008). Many invasive species have substantial impacts (Levine *et al.*, 2003; van Wilgen *et al.*, 2008; Gaertner *et al.*, 2009; Ehrenfeld, 2010; Vilà *et al.*, 2010, 2011; Pyšek *et al.*, 2012b). The emphasis on such species is understandable as they generate substantial costs to society (Pimentel *et al.*, 2005; Hulme *et al.*, 2009; Kettunen *et al.*, 2009).

The many processes implicated in biological invasions are conveniently conceptualized as occurring along an introduction–naturalization–invasion continuum (hereafter 'the continuum') (Richardson *et al.*, 2000b; Blackburn *et al.*, 2011). It is crucial to understand the ways in which many factors potentially influence the progression of species along the *entire* continuum, thereby structuring the status of different taxa within alien biotas.

Disentangling the roles of numerous factors that determine the outcome of individual invasions is complicated by the fact that many studies that seek to identify sets of factors associated with 'success' of introduced species do not objectively define 'success'. Ultimate 'success' is achieved when a species reaches the end of the continuum – when it is labelled as invasive. Invasive species are categorized based on criteria relating to the ability to sustain self-replacing populations over several life cycles; producing reproductive offspring; and having the potential to spread over long distances. They must thus be introduced, survive, reproduce, disperse and spread (Richardson *et al.*, 2000b, 2011b; Blackburn *et al.*, 2011). Those that only form self-sustaining populations and do not spread substantially are naturalized but not invasive. This distinction is important because the attainment of each stage is mediated by different sets of factors and processes, with some operating across stages (Richardson *et al.*, 2000b; Williamson, 2006; Wilson *et al.*, 2007; Dawson *et al.*, 2009; Pyšek *et al.*, 2009a,b; Jenkins & Keller, 2011). This is not always recognized, and the current knowledge base in invasion ecology is biased in favour of research on the small proportion of introduced species with the greatest impact. We have a better understanding of the determinants of successful invasion than those of naturalization (Pyšek *et al.*, 2008), but naturalization is a critical stage of the invasion process (Richardson *et al.*, 2000b; Blackburn *et al.*, 2011). In this review we are particularly interested in gaining an improved understanding of the mediators of naturalization for introduced plants for the following reasons.

- Naturalization is determined by fewer factors than invasion, as the latter also requires dispersal, which introduces additional complexity. Consequently, predictions of naturalization are potentially more robust than those for invasiveness. Predictors of naturalization are also less likely to be highly site-specific. This is especially so in areas with complex human activities, where transition from naturalized to invasive is mediated by biological factors (e.g. new dispersal opportunities), stochastic factors (roles of initial population sizes, residence times and numbers of introduction attempts) or changed environmental conditions (climate and land use). All of these can be strongly influenced by humans and are highly interactive, and thus very difficult to predict.
- The position of any species on the continuum is dynamic, and all naturalized species are potential future invaders (Kowarik, 1995). Naturalized populations are thus the key component of invasion debt in any region (Essl *et al.*, 2011) and should be given special attention for pro-active management (Wilson *et al.*, 2011).
- Our particular interest is to explore the factors that drive transitions along the continuum. Although our focus here is not on the dynamics of spread and impacts caused by invasive species, we need to examine factors that contribute to the well-known lag phase, locking many species at the naturalization stage, preventing them (at least temporarily) from reaching the final stage of the continuum.

Another issue that has not been given sufficient attention with respect to the movement of species along the continuum is the effect of geographical scale. Abiotic factors and ecological processes operating at fine spatial and temporal scales interact with biogeographical, historical and evolutionary processes to influence the distribution of biodiversity in ways that scale upwards to create patterns that are discernible at different levels of organization, for example, landscape, region, continent and biome (Shea & Chesson, 2002; Rouget & Richardson, 2003; Stohlgren *et al.*, 2006; Chytrý *et al.*, 2008b). This applies both to biotas that have assembled naturally over evolutionary time-scales and to those assembled through, or modified by, human activities relatively recently. However, the literature relating to the large, biogeographical scale of biological invasions shows an uneven distribution of research among the world's regions and biomes, creating a geographical bias (Pyšek *et al.*, 2008). This hampers advances towards a balanced understanding of invasions world-wide. Geography is clearly important in shaping large-scale patterns, and variation among regions in geographical settings of particular invasions creates powerful natural experiments for determining the effects of macroecological, climatic, historical and cultural factors (Sax, 2001; Pyšek & Richardson, 2006; Richardson *et al.*, 2011a; Procheş *et al.*, 2012).

Populations, and not species, invade. Consequently, studies examining invasions into communities at the spatial scale at which interactions between species occur and ecological processes operate should focus at the level of populations. These studies provide information that, if upscaled, can yield insights into the determinants of naturalization at biogeographical scales, where species are the 'currency'. Therefore, the last key issue we explore in this paper is how ecological processes underlying naturalization of alien plants translate into generators of macroecological patterns discernible at large scales, from regional to continental to global.

II. The introduction–naturalization–invasion continuum for conceptualizing biological invasions

Many frameworks have been proposed for elucidating the stages through which a species passes to become an 'invasive alien'

(Williamson, 1996; Richardson *et al.*, 2000b; Heger & Trepl, 2003; Colautti & MacIsaac, 2004; Catford *et al.*, 2009; Blackburn *et al.*, 2011). Most such constructs conceptualize a continuum starting when a species is resident in its natural range, extending until the species is established and spreading following introduction to a new area. Some models focus primarily on the barriers or windows that potentially impede or facilitate progression along the continuum, whereas others address invasion dynamics as a series of stages through which a species must pass to become an invasive alien. Different frameworks have proved useful for different purposes. Two widely used categories of frameworks that fit into the 'barriers' and 'stages' types are one proposed for plants (Richardson *et al.*, 2000b) and another developed using data from both plants and animals, but which has been more widely applied for animals (Williamson, 1996; Williamson & Fitter, 1996). Both frameworks have been applied to invasions in general and across a wide range of taxa (see discussion in Blackburn *et al.*, 2011).

Key differences between the two broad approaches emerge if one considers criteria, mediators and processes required for progression through introduction to having established and reproducing populations (i.e. naturalization, *sensu* Richardson *et al.*, 2000b, 2011b). The Richardson *et al.* (2000b) 'barriers' model recognizes environmental factors that potentially influence growth and survival, and barriers to reproduction. Success at this stage of the continuum, according to the Williamson (1996) model, can also be linked to factors that allow introduced populations to become self-sustaining; these factors are divided into characteristics of the species, those relating to the novel location, and those describing the specific introduction event. The Richardson scheme is individual-based, whereas schemes based on concepts set out by Williamson are implicitly population-based. In the latter, the establishment stage focuses on problems of small population viability. Linking barriers and factors in the two approaches to arrive at a general model is nontrivial. A merger of the two was one of the objectives of a 'unified framework for biological invasions' (Blackburn *et al.*, 2011) which emphasizes that the naturalization (i.e. pre-invasion) segment of the continuum is fundamentally influenced by population and demographic processes.

A steady flow of new frameworks has sought to provide general, widely applicable schemes with heuristic value, but that can also guide management. Most of those that conceptualize biological invasions using stages and barriers give prominence to the naturalization stage. Most are similar to Richardson *et al.*'s (2000b, 2011b) formulation in that survival and self-sustaining reproduction in the recipient region separate casual from naturalized populations (Colautti & MacIsaac, 2004), and that abiotic and biotic conditions may act as constraints, potentially independently of human assistance (Catford *et al.*, 2009). With this emphasis of stage-based schemes on naturalization as a central stage of the invasion process, it is surprising that this stage is seldom studied explicitly and tested using real data to the same degree as the invasion stage (Pyšek *et al.*, 2008). Also surprising is that most factor-based attempts at conceptual syntheses of invasions fail to recognize naturalization as a fundamental distinguishable step (Davis *et al.*, 2000; Blumenthal, 2006; Dietz & Edwards, 2006; Theoharides & Dukes, 2007). For example, Gurevitch *et al.* (2011) suggest that initial colonization and establishment of invading organisms depend on the same kinds of basic processes as other aspects of invasion. However, we argue that the relative importance of these processes and factors differs quantitatively and qualitatively for particular stages along the continuum. This lack of emphasis on naturalization as a key step in invasion is probably because these studies focus on species invasiveness or community invasibility, and because such frameworks are primarily aimed at describing mechanisms contributing to the final outcome of the process of invasion. In the next section, we explore the factors that determine whether a species moves from one stage to the next, and how ecological factors at a community scale translate into biogeographical patterns.

III. The biogeographical background for studying naturalization: variation among populations and regions

There is considerable variation in the number of naturalized species in different regions of the world (Fig. 1), and intriguing biogeographical patterns are emerging (reviewed in Pyšek & Richardson, 2006). Among the most robust of these are that: islands are more invaded than mainlands (Rejmánek, 1996b; Lonsdale, 1999); temperate mainland regions are more invaded than those in the tropics (Rejmánek, 1996b); the number of naturalized species in temperate regions decreases with latitude and their geographical ranges increase with latitude (Sax, 2001); and the number of naturalized species on islands increases with temperature as this factor improves the chance of propagule establishment (Chown *et al.*, 1998).

Different regions currently harbour between 100 and 350 naturalized species from the global pool of 450 species listed by Weber (2003), with Australia, North America and Africa having the highest species richness (Fig. 1). Regions also differ in the proportion of species that have become invasive among all naturalized species introduced – overall and within particular groups (Richardson *et al.*, 2011a). This is partly attributable to inter-regional differences in invasibility (Lonsdale, 1999). Using the same global pool of naturalized species highlights that it is populations, not species, that invade, and that demography is central to the invasion process (Blackburn *et al.*, 2011; Gurevitch *et al.*, 2011). Most of the 50 most widely distributed invasive species globally (as listed by Weber, 2003) have naturalized populations in most of the regions where they occur, but are invasive only in a small subset of regions (Fig. 2). Only three species, *Lantana camara* (invasive in 12 of 20 regions), *Leucaena leucocephala* (11 of 15) and *Carpobrotus edulis* (7 of 12), are more often invasive than naturalized but noninvasive. Biological traits of species are more or less constant in this natural experiment (apart from post-invasive evolution that may occur in one region but not in another depending on biotic and environmental factors in individual regions; Meyerson *et al.*, 2010a,b; Saltonstall *et al.*, 2010). Consequently, differences in the performance of particular species (degree of progression along the continuum) must be explained mainly by the biogeographical setting and human-mediated factors that are highly site-specific (assuming that all

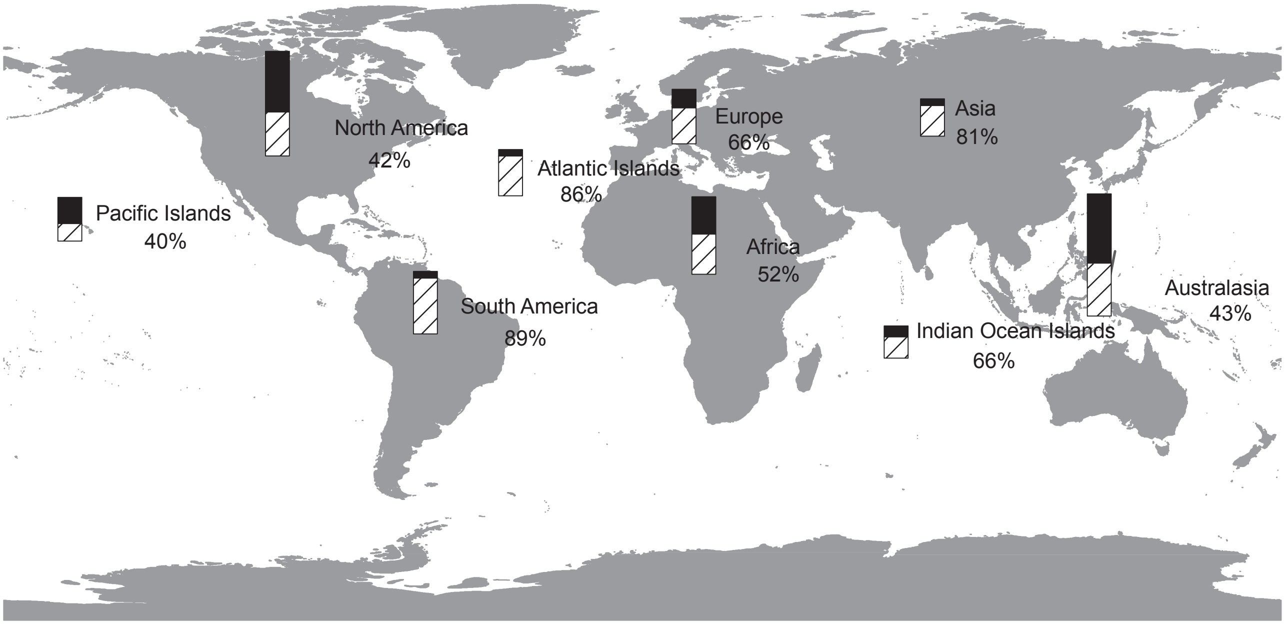

Fig. 1 Numbers of naturalized species in nine regions of the world. Data are from Weber (2003) and are based on global distributions of 450 species that are major invaders in natural and seminatural areas in at least one region (excluding weeds of agricultural and disturbed habitats). The percentages of species from the total pool of naturalized alien species (=total length of the bar) that are recorded as not invading (corresponding to Weber's 'introduced'; Pyšek, 2004) are indicated for each region. Black bars, invasive in natural areas; hatched bars, naturalized but not invasive.

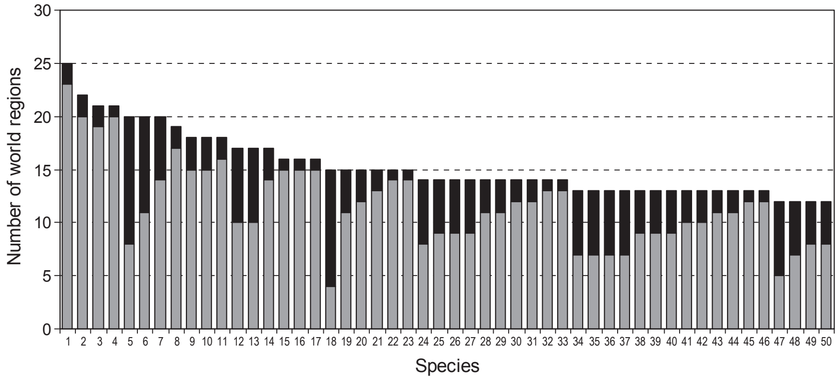

Fig. 2 Variation in population status of the 50 globally most widely distributed species that are major invaders in natural and seminatural areas in at least one region of the world (n = 32). Populations of individual species are therefore invasive in some regions while in others they only reached the naturalization stage. The figure is based on data from Weber (2003). Black bars, invasive in natural areas; grey bars, naturalized but noninvasive. 1, *Datura stramonium*; 2, *Bidens pilosa*; 3, *Xanthium strumarium*; 4, *Chenopodium album*; 5, *Lantana camara*; 6, *Ulex europaeus*; 7, *Ricinus communis*; 8, *Paspalum distichum*; 9, *Elodea canadensis*; 10, *Tagetes minuta*; 11, *Cynodon dactylon*; 12, *Eichhornia crassipes*; 13, *Ailanthus altissima*; 14, *Hydrilla verticillata*; 15, *Sonchus oleraceus*; 16, *Solanum nigrum*; 17, *Oxalis latifolia*; 18, *Leucaena leucocephala*; 19, *Nicotiana glauca*; 20, *Imperata cylindrica*; 21, *Senna obtusifolia*; 22, *Salsola kali*; 23, *Physalis peruviana*; 24, *Arundo donax*; 25, *Phragmites australis*; 26, *Urochloa mutica*; 27, *Pistia stratiotes*; 28, *Cirsium arvense*; 29, *Paspalum dilatatum*; 30, *Xanthium spinosum*; 31, *Rumex acetosella*; 32, *Rumex crispus*; 33, *Plantago lanceolata*; 34, *Pennisetum clandestinum*; 35, *Psidium guajava*; 36, *Lonicera japonica*; 37, *Ageratina adenophora*; 38, *Sporobolus indicus*; 39, *Phalaris arundinacea*; 40, *Opuntia ficus-indica*; 41, *Silybum marianum*; 42, *Egeria densa*; 43, *Melilotus albus*; 44, *Polygonum aviculare*; 45, *Avena fatua*; 46, *Trifolium repens*; 47, *Carpobrotus edulis*; 48, *Schinus terebinthifolius*; 49, *Cirsium vulgare*; 50, *Holcus lanatus*.

species have had enough time to realize their invasion potential). This is further emphasized by the poor support for the role of biotic resistance in structuring geographical patterns of establishment of introduced species; and the good evidence for the dominant role of climate matching (Gaston *et al.*, 2003; see Section IV).

That invasion status (position on the continuum) can be only assigned at the population, not species level is clearly demonstrated by the history of naturalization and invasion of *Ambrosia artemisiifolia* in Central Europe, for example. Depending on local conditions, some populations are still in the casual stage whereas others are naturalized or invasive (Essl *et al.*, 2009). Therefore, the same phenomena also operate at the regional geographical scale.

Accurate inventories of all naturalized species (i.e. not distinguishing invasive species as a subset of naturalized species) are now available for many regions and have been summarized in many studies (Rejmánek & Randall, 1994; Rejmánek, 1996b; Vitousek *et al.*, 1997; Denslow, 2003; Lambdon *et al.*, 2008) and databases (Hulme & Weser, 2011). Importantly, though, checklists that categorize species into objectively defined groups, including casual species, are still rare. Such comprehensive catalogues are extremely valuable as they shed light on inter-regional differences in naturalization rates – the proportion of introduced species from the entire species pool that become naturalized. Data collated in this way can be compared with those from other regions to generate a more meaningful metric of regional invasibility than those based on absolute numbers of species (Pyšek & Richardson, 2006; Catford *et al.*, 2012). Such data have allowed the formulation of quantitative theories such as the tens rule (Williamson, 1996; Williamson & Fitter, 1996) which, despite being strongly influenced by inter-regional differences in the timing of introductions and other key mediators of invasions (Richardson & Pyšek, 2006), show that only a small subset of species progress from one stage to the next along the continuum.

Examples of regions for which complete lists of all alien species are available are summarized in Table 1. Although the list is not exhaustive and notwithstanding obvious differences among regions in sampling intensity and accuracy (particularly for casual species), such data collations offer important insights regarding variations in naturalization rates, which range from 9 to 74%. The effort expended in acquiring complete lists that include casuals partly depends on the size of the region; 18 of the 31 data sets in Table 1 come from islands. Indeed, complete data sets are often available only for small islands where accurate documentation of entire alien floras is potentially possible. The scarcity of analyses that quantify naturalization rates in floras explicitly is therefore, at least partly, attributable to the dearth of comprehensive checklists.

Table 1 Regions of the world for which comprehensive information on alien floras is available

Region	Number of alien species: Total	Naturalized	Casual	Naturalization rate (%)	Source
Scotland	824	77	747	9.3	Welch *et al.* (2001)
Svalbard*	44	6	38	13.6	Lambdon *et al.* (2008)
Henderson Island*	13	2	11	15.4	Waldren *et al.* (1999)[†]
La Possession (Crozet Archipelago)*	58	9	49	15.5	Frenot *et al.* (2001)
Kerguelen*	68	11	57	16.2	Frenot *et al.* (2001)
Hungary	709	145	564	20.5	Lambdon *et al.* (2008)
Czech Republic	1104	257	847	23.3	Pyšek *et al.* (2012a)
Belgium	1969	447	1486	22.7	Lambdon *et al.* (2008)
Sardinia*	518	126	392	24.3	G. Brundu, pers. comm. (2003)
Austria	1086	276	810	25.4	Essl & Rabitsch (2002)
Slovakia	624	167	457	26.8	Medvecká *et al.* (2012)
Romania	384	113	271	29.4	Lambdon *et al.* (2008)
Estonia	412	125	287	30.3	Lambdon *et al.* (2008)
Amsterdam Island*	56	17	39	30.4	Frenot *et al.* (2001)
Great Britain*	1642	558	1084	34.0	Williamson (1993)
Corsica*	472	171	301	36.2	Natali & Jeanmonod (1996)[†]
Poland	810	300	510	37.0	Mirek *et al.* (2002) and B. Tokarska-Guzik, pers. comm.
Var*	448	176	272	39.3	Médail & Orsini (1993)[†]
Wisconsin (USA)	877	353	524	40.3	Wetter *et al.* (2001)[†]
Galapagos*[‡]	600	270	330	45.0	Tye (2001)
Carnac Island*	74	34	40	45.9	Abbott *et al.* (2000)
Queen Charlotte Islands*	111	54	57	48.6	Calder & Taylor (1968)[†]
Lithuania	509	256	253	50.3	Lambdon *et al.* (2008)
Kermadec Island*	173	88	85	50.9	Sykes *et al.* (2000)[†]
Pitcairn*	74	44	30	59.5	Florence *et al.* (1995)[†]
Cyprus*	199	133	50	66.8	Lambdon *et al.* (2008)
Azores*	917	617	300	67.3	Schäfer (2003)[†]
Nauru*[‡]	115	78	37	67.8	Thaman *et al.* (1994)[†]
Hawaiian Islands*[‡]	1160	803	357	69.2	C. Daehler, pers. comm. (2003)
California (USA)	1500	1079	421	71.9	Rejmánek (2000), Rejmánek & Randall (1994) and DiTomaso & Healy (2005)[†]
Taiwan	366	270	96	73.8	Wu *et al.* (2004)

The data sets summarized in the table aimed at collecting information on casual species which makes it possible to calculate naturalization rate, expressed as the percentage of the total number of alien species, including casuals, that have become naturalized. Regions are ranked according to increasing naturalization rate. Species numbers in European countries refer to neophytes, that is, species introduced since the discovery of America (Pyšek *et al.*, 2004).

[*] Island flora.

[†] Original data categorized and adapted in Pyšek & Richardson (2006), to follow terminology relating to the introduction–naturalization–invasion continuum (Richardson *et al.*, 2000a).

[‡] Subtropical zone.

This brief summary of biogeographical-scale patterns of naturalization shows that the numbers of naturalized populations of alien species differ among regions and that variance in these numbers at this broad spatial scale is driven by complex interactions between species traits, site-specific abiotic and biotic conditions, and region-specific environmental and human-mediated factors. Our task is to understand how these factors shape the naturalization stage along the continuum.

IV. Factors determining naturalization in plants

The theoretical framework of factors mediating naturalization is well elaborated, at least to the extent that many key contributing factors are known and aspects of their interactions have been conceptualized (Richardson *et al.*, 2000b; Catford *et al.*, 2009). Some factors are deterministic – for example, ecological factors such as presence of a mating partner, obligatory mutualism, specialized dispersers, as are some plant traits, such as life form. Of the human-related deterministic factors it is mainly the act of introduction – if the species is not introduced it cannot invade – that feeds into determining the multiple roles of residence time. Most factors associated with naturalization are, however, probabilistic, including the effect of propagule pressure (D'Antonio *et al.*, 2001), and their importance varies along the continuum (Fig. 3).

1. Species traits as mediators of plant naturalization

The importance of species traits in invasions is disputed (Thompson *et al.*, 1995; Hulme *et al.*, 2011; van Kleunen *et al.*, 2011; Thompson & Davis, 2011), but there is compelling evidence for a strong link between suites of traits and invasiveness (Rejmánek & Richardson, 1996; Hamilton *et al.*, 2005; Pyšek & Richardson, 2007; Küster *et al.*, 2008; van Kleunen *et al.*, 2010b). Trait–process interactions are strongly context-dependent, position along the continuum being a key part of the context (Williamson, 2006; Dawson *et al.*, 2009; Pyšek *et al.*, 2009a,b; van Kleunen *et al.*, 2010a).

The two issues dealt with in section III (comparisons of the global species pool and those of regional floras) indicate that we need to unravel both the role of different factors in mediating transitions along the continuum and what it is that blocks progress beyond the naturalization stage, preventing many species from becoming invasive. For both questions, but especially the latter, comparisons should ideally be made using species with similar residence times. This is because some naturalized species are not invasive simply because they have had insufficient time to realize their invasion potential (Williamson *et al.*, 2009; de Albuquerque *et al.*, 2011); seeking links between the position of such species on the continuum and their traits is meaningless. Consequently, the most insightful studies have been those that explicitly identified the

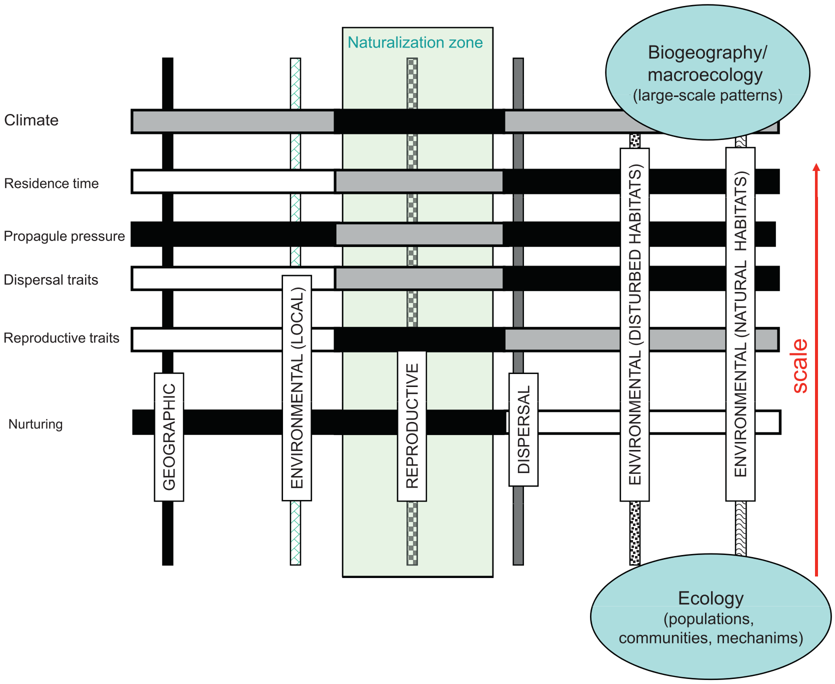

Fig. 3 Variation along the introduction–naturalization–invasion continuum in the importance of factors determining invasion success of introduced species, with focus on the naturalization zone (highlighted area). The importance of the given factor increases with the intensity of shading. While climate and reproductive traits are crucial for the species to become naturalized, dispersal traits mediate invasiveness. The key role of propagule pressure is manifested at the introduction stage, and at the invasion stage when it is created by the invading population itself (Foxcroft *et al.*, 2004). The effect of residence time increases gradually as introduced species have more time to establish and invade. Along the vertical axis factors are arranged according to their importance at different scales: residence time and climate are most important at large scales (determining macroecological and biogeographical patterns of regional invasions and global invasions), nurturing and reproductive traits act mainly at fine scales, and dispersal traits with propagule pressure form the ecological link between the two sides of the spatial continuum.

position of species on the continuum and then sought differences in traits among casual, naturalized but noninvasive, and invasive species (van Kleunen *et al.*, 2010a). The situation is further complicated methodologically because studies that address all naturalized species are to some extent biased because the invasion stage is implicitly included in this category: invasive species are a subset of naturalized species (Richardson *et al.*, 2000b; Blackburn *et al.*, 2011).

Species traits related to propagules are crucial in separating invasive from noninvasive species (Rejmánek & Richardson, 1996; Cadotte & Lovett-Doust, 2001; Lake & Leishman, 2004; Hamilton *et al.*, 2005). Of these traits, prolific seed production regularly emerges as an important determinant of invasiveness (Pyšek & Richardson, 2007 and references therein) but its role in conferring naturalization has been rarely examined. The importance of this factor for the transition from casual to naturalized stage was illustrated by examining introduced Iridaceae taxa; species naturalized outside their native ranges showed a higher capacity for autonomous seed production than species that had failed to naturalize (van Kleunen *et al.*, 2008). In the same family, rapid and profuse seedling emergence separated naturalized from nonnaturalized species (van Kleunen & Johnson, 2007b). Very few studies have, however, looked at the naturalization–invasion transition. A study that measured establishment, reproductive and dispersal traits of 96 neophytes in the Czech flora showed that naturalized but noninvasive species differed significantly from invasive taxa in producing fewer seeds, having heavier and less rounded propagules (presumably less advantageous for human-aided dispersal), and having a lower capacity for dispersal by wind and water (Moravcová *et al.*, 2010).

Many introduced plants rely on mutualisms with local biota in the new range for naturalization and invasion; animal-mediated pollination and seed dispersal, and symbioses between plant roots and microbiota often mediate progress along the continuum (Richardson *et al.*, 2000a; Traveset & Richardson, 2006). Of these mutualisms, symbionts and pollination are most influential at the naturalization stage because they are directly implicated in establishment and reproduction, respectively. The lack of symbionts was a fundamental barrier for establishment and naturalization of ectomycorrhizal plants such as *Pinus* species in parts of the Southern Hemisphere (acting as a deterministic factor). However, most alien plants are well served by generalist pollinators, making pollinator limitation a less potent barrier for naturalization (Richardson *et al.*, 2000a). A deeper insight into how pollination patterns change along the continuum and affect whether species become casual, naturalized but noninvasive, or invasive was recently provided by an analysis of neophytes (species introduced after 1500 AD) in the Czech flora, in a study that explicitly distinguished between the three stages (Pyšek *et al.*, 2011a). Casual and naturalized neophytes were more frequently insect- and less frequently self- and wind-pollinated than were invasive species (cf. van Kleunen & Johnson, 2007a). Casual species also harboured a more diverse suite of insect pollinators from more functional groups than did naturalized neophytes. Overall, the frequency of pollination modes in the neophyte flora gradually changed along the continuum, becoming increasingly similar to that of native species and eventually showing no difference from native species in terms of the frequency of pollination modes (Pyšek *et al.*, 2011a). Pollination mutualisms therefore appear to mediate progression along the continuum probabilistically, with their importance changing with residence time of species in the region. The reason why other studies often do not identify the mode of pollination among traits associated with invasion success (Cadotte & Lovett-Doust, 2001; Sutherland, 2004) is probably because they lump all alien species without consideration of their position on the continuum.

Although most work has focussed on ecological variables, recent research indicates that genetic attributes may be strongly associated with the ability to progress along the continuum (Pandit *et al.*, 2011). Small genome size, important in shaping life-history strategies (Bennett, 1987; Grime *et al.*, 1988), was suggested as a possible 'ultimate' trait associated with invasiveness in disturbed environments (Rejmánek, 1996a, 1999). Its role was neatly illustrated using *Pinus* as a model genus (Grottkop *et al.*, 2004). The stage dependence of genome size as mediator along the continuum is also becoming clearer. Naturalized but noninvasive species in the Czech flora have smaller genomes than their congeners not known to be naturalized or invasive anywhere in the world, but they do not have smaller genome size than invasive species. The implication is that genome size gives alien plants an advantage at the stage of naturalization, but not necessarily further along the continuum (Kubešová *et al.*, 2010).

An evolutionary concept that explicitly addresses the naturalization stage is Darwin's Naturalization Hypothesis which posits that phylogenetic relatedness of introduced species to native elements hampers naturalization through niche overlap with native species (Richardson & Pyšek, 2006; Thuiller *et al.*, 2011). This notion has been widely tested (Daehler, 2001; Lambdon & Hulme, 2006; Strauss *et al.*, 2006; Díez *et al.*, 2008; reviewed in Thuiller *et al.*, 2011). The seemingly contradictory results can be ascribed to differences between regions and species groups tested, and discrepancies in conceptual frameworks and analytical approaches such as different spatial and phylogenetic scales, the use of different metrics, and not considering the role of habitats (Díez *et al.*, 2008; Thuiller *et al.*, 2011). Unless these issues are resolved, the hypothesis sheds little light on the determinants of naturalization (Procheş *et al.*, 2008). Moreover, the studies looking at this hypothesis also do not distinguish, within the tested group of naturalized species, those that invade from those that do not and cannot provide information on the nature of the naturalization–invasion transition.

2. Climate and environmental matching

Close climate matching is fundamental for progression along the continuum in a novel environment. Although it has been shown that some alien species are able to occupy climate niches in the new range that differ substantially from those of the native range, and that novel climatic conditions may not always be a major obstacle for alien species to establish populations outside their native range (Gallagher *et al.*, 2010), there is almost always a high degree of climatic similarity between the native and invaded ranges of major invasive species (Wiens & Graham, 2005). Exceptions can usually be explained by land-use changes in the invaded range. For example, invasion success in climatic zones markedly different from any in the native range can often be explained by anthropogenic amelioration of key climatic constraints, for example through irrigation (Richardson & Thuiller, 2007). Broad-scale climatic matching also fails to define potential invasive ranges for species that are associated with microsites or climates that are not captured by the coarse-scale variables typically utilized in such analyses (e.g. species associated with riparian and other aquatic habitats; Richardson *et al.*, 2007). Notwithstanding these caveats, a close match between broad climatic features of donor and recipient ranges clearly increases the chances of progression along the continuum. Mechanisms and processes driving this relationship and their interactions at different scales and at different positions along the continuum are very seldom considered in predictions. Most screening models, while explicitly acknowledging the pivotal role of climate matching, use very crude metrics for scoring the level of matching between native and novel ranges (discussion in van Wilgen *et al.*, 2009). Many studies lump broad-scale (macro) climatic parameters and diverse other abiotic factors to score the degree of 'environmental matching', again mostly without elaboration of the driving mechanisms and processes (Drake & Lodge, 2006). Individual factors mediate success (survival) differently in different populations of any introduced species, and interact to influence survival, reproduction, or both, in a complex fashion with stochastic factors such as aspects of the introduction history and pathways to mediate progression along the continuum (Wilson *et al.*, 2007).

Environmental matching is important along most of the continuum, as preadaptation to many diverse factors is beneficial at all stages of a plant's life cycle. However, how pivotal a close environmental match is for progression at different sections of the continuum is species- and context-specific. A moderate level of climatic/environmental matching is essential to enable an introduced species to establish, survive and reproduce. This is shown by the broad similarities between naturalized floras in regions with similar climatic regimes such as mediterranean-climate zones. That such regions show marked differences in terms of major invasive species is largely driven by historical factors related to human-mediated biotic exchange (di Castri, 1989), and to factors operating post-naturalization (Kruger *et al.*, 1989). Climate and broad-scale environmental matching as a forcing function for structuring introduced floras seems to act particularly strongly at the beginning of the continuum, influencing processes that mediate naturalization (Fig. 3). The evidence for this can be seen in naturalization rates in regional alien floras rapidly decreasing with latitude; naturalization, expressed as the proportion of species from the entire introduced pool that are able to naturalize, is increasingly difficult as the climate becomes colder at higher latitudes (Pyšek & Richardson, 2006). The interaction of climatic factors is also important in determining the diversity of naturalized species. The number of naturalized neophytes in European countries was shown to depend on the interaction of temperature and precipitation; it increased with increasing precipitation but only in warm and moderately warm climes. This indicates that future effects of climate change on regional diversity of naturalized alien species in Europe will be complex, with drought possibly becoming an important limiting factor in the future (Lambdon *et al.*, 2008).

The importance of climate/environmental matching for progression along the continuum is linked to the role of the size of the native range as a determinant of success at different stages. Many studies have shown that the likelihood of naturalization increases with increasing native range size for plants (Rejmánek, 1996a; Cadotte *et al.*, 2006; Bucharová & van Kleunen, 2009; Pyšek *et al.*, 2009a). Again, most studies fail to link native range size with the degree of success at particular stages of the continuum. An exception is a recent study of the link between native range dimensions (including size) and introduction, naturalization, and invasion (sensu Richardson *et al.*, 2000b) for Australian *Acacia* species (Hui *et al.*, 2011). This study showed that native range size (and other range dimensions) relate to introduction, naturalization, and invasion in different ways. Large range size was strongly correlated with the likelihood of introduction, but more interestingly also with the likelihood of naturalization, but not invasion. There are several potential explanations for the positive association between native range size and the likelihood of naturalization. These include the stronger likelihood that at least some genotypes of introduced species with large ranges will be well adapted to climatic/environmental conditions in any receiving region (Hui *et al.*, 2011). Large native range was the most important predictor in a study that analysed the success of species native to Central Europe as aliens in other parts of the world in two different stages, roughly corresponding to both naturalization and invasion, but there was also an additional effect of climatic matching. The number of climatic zones across which the species occurs in its native range had a significant effect on its success, indicating that tolerance of a wide range of climates, acquired in the native range, was crucial for both naturalization and invasion in the new region (Pyšek *et al.*, 2009a). Another study provided insights into the role of climate in mediating the transition from naturalization to invasion at a global scale; climate-based habitat match was the main filter determining which species from the total pool of naturalized aliens of South African origin become successful invaders of natural habitats in other parts of the world (Thuiller *et al.*, 2005).

3. Propagule pressure, residence time and the importance of nurturing

Generally, identifying individual factors that seem to affect the probability of a species progressing along the continuum sheds little or no light on the mechanisms and processes at play. However, such factors serve as useful 'multipliers' for predictions made using the other approaches (Rejmánek *et al.*, 2005a,b; Richardson, 2006). Residence time and many proxies for 'propagule pressure', encompassing the quantity, quality, composition, rate and other details of the supply of propagules, are widely reported as being positively associated with 'success' of introduced species. As with the factors discussed above, 'success' is unfortunately very seldom tied to a particular position in the continuum, making it difficult to generalize about the role of component factors in mediating progression along the continuum. There are exceptions, however.

For example, the probability of plants becoming naturalized in Florida increased significantly with the number of years the plants were marketed in the state (Pemberton & Liu, 2009). Similarly, residence time for invasive alien species in the Czech Republic is longer than that of naturalized species which is in turn longer than that of casual species (Pyšek *et al.*, 2005). Residence time integrates several components of propagule pressure: the longer a species is present at a site, the greater the size of the propagule bank, the more dispersal opportunities eventuate, and the greater the probability of establishment, and the founding of new populations. Adding more propagules to sites increases the probability of establishment success, but exactly how this probabilistic factor interacts with other factors such as disturbance and resource supply is poorly understood (Hierro *et al.*, 2005).

The issue of propagule pressure is closely linked with pathways of introductions of alien plants to a region (Hulme *et al.*, 2008). It has long been recognized that nurturing fosters naturalization in a new region by buffering small populations from environmental stochasticity and creating propagule pressure (Mack *et al.*, 2000). A consequence of this is that plants introduced for horticulture are more likely to become naturalized than those introduced for many other purposes; they contribute a large proportion to most naturalized floras (Mack & Lonsdale, 2001; Reichard & White, 2001; Pyšek *et al.*, 2002, 2012a; Kowarik, 2005; Pemberton & Liu, 2009). Unfortunately, quantitative data on the number of propagules supplied by individual pathways are rarely available. For species introduced for horticulture, information can be used on the total pool of species imported for cultivation (Kowarik, 2005; Hulme, 2011) and naturalization success is related to proxies of propagule pressure such as planting intensity (Mulvaney, 1991; Křivánek *et al.*, 2006) or nursery sales (Dehnen-Schmutz *et al.*, 2007a,b). In some studies, proxies of planting intensity integrated the effect of residence time: early horticultural or forestry introductions were more likely to naturalize than late introductions in Australia (Mulvaney, 1991) and the Czech Republic (Křivánek *et al.*, 2006) and marketing time was a significant predictor of naturalization in Florida (Pemberton & Liu, 2009).

For species introduced as stowaways or contaminants of commodities, however, the quantitative data on propagule pressure are virtually always missing (Lee & Chown, 2009a,b). Quantitative evidence of how pathways affect progression along the continuum can be inferred by looking at the efficiency of pathways, defined as the 'success' of species they deliver. In Central Europe, introduction pathways for species brought in deliberately as commodities led to easier naturalization than was the case for unintentional introductions; this pattern also held for invasions. In general, the proportion of naturalized and invasive species among all introductions delivered by a particular pathway decreases with a decreasing level of direct assistance from humans associated with that pathway, from release and escape to contaminant and stowaway (Pyšek *et al.*, 2011b).

A study that addressed the combined role of residence time, propagule pressure and species traits in three stages of invasion, conducted on alien woody plants cultivated for forestry purposes in Central Europe (Pyšek *et al.*, 2009b), points to the strong stage dependence of the determinants of invasion. Whereas the probability of escape from cultivation increased with planting intensity and with residence time in the Czech Republic, that of naturalization depended on the residence time in Europe, suggesting that some species were already adapted to local conditions when introduced to the region. High propagule pressure resulting from planting leads to the eventual escape of woody species from cultivation, regardless of their biological traits. Biological traits such as fruit size and ability to tolerate low temperatures do, however, play a role in naturalization and invasion (Pyšek *et al.*, 2009b).

4. The role of habitats and disturbance

Local-scale studies seldom distinguish between the naturalization and invasion stages, as such work usually focuses on identifying mechanisms and factors underlying the performance of a species in a community. At this scale it is less meaningful to categorize species as invasive or naturalized-but-noninvasive (Chytrý *et al.*, 2008a). Criteria relating to the ability to disperse are tenuous at this scale, so measures of 'invasiveness' are generally derived from the abundance of the population in the site, and usually expressed in terms of cover or degree of dominance. The ecological background of naturalization relates to disturbance, availability of resources (nutrients and moisture), and interactions with resident biota (competition, mutualism and herbivory). At this scale, disturbance is the crucial factor affecting establishment (Hobbs & Huenneke, 1992; D'Antonio *et al.*, 1999; Rouget & Richardson, 2003; Leishman & Thomson, 2005), and is thus influential in mediating naturalization, whereas plentiful resources are needed for a species to become abundant, corresponding with invasion (Davis *et al.*, 2000; Davis & Pelsor, 2001). Much work has been done on determining mechanisms of community invasions (Rejmánek *et al.*, 2005a,b for a synthesis); studies at this scale have yielded robust evidence that habitat quality plays a major role in determining the level of invasion; the proportion of alien species in plant communities in Europe depends primarily on the type of habitat, even more than on propagule pressure and climatic conditions (Chytrý *et al.*, 2008a,b). Quantitative evidence for the interaction of environment and propagule pressure at the local scale was provided by a study on *Metrosideros excelsa* in South Africa (Rejmánek *et al.*, 2005a,b).

Habitat type, however, affects the probability of naturalization and/or invasion partly because species arrive in new regions preadapted to certain habitats in their native ranges. Donor habitats in native regions contribute differently to the number of naturalized species they supply to Central Europe, and the pattern also differs for naturalized and invasive species: while woodlands were the main donor of the former, riparian habitats were major donors for the latter (Hejda *et al.*, 2009). This study found another difference between species representative of particular stages. Casual species in Central Europe were recruited from a wider range of habitats in their native range than they occupied in the invaded range; naturalized but not invasive species inhabited a comparable spectrum of habitats in both ranges, and invasive species occupied a wider range of habitats in the invaded than in the native range. This supports the idea that the invasive phase of the process is associated with changes in biological features that allow for extension of the spectrum of habitats invaded.

5. Synthesis: interaction of multiple factors

One of the fundamental questions of plant invasion biology over the past few decades has been whether it is possible to link success of alien plants to their traits. Recent research has clearly shown that many other factors are also important, often more influential than traits, in determining invasive success. This has meant that the key question has transformed into the quest for insights into the relative importance of a broad suite of factors, and the extent to which results from particular case studies can be generalized (Thuiller *et al.*, 2006; Wilson *et al.*, 2007; Catford *et al.*, 2009; Pyšek *et al.*, 2009a,b). Although many studies address these complex issues using real data from different regions of the world (Hamilton *et al.*, 2005; Wilson *et al.*, 2007; Küster *et al.*, 2008), those that distinguish continuum stages and seek to score the importance of factors separately are still rare (Dietz & Edwards, 2006; Dehnen-Schmutz *et al.*, 2007b; van Kleunen *et al.*, 2007; Gravuer *et al.*, 2008; Pyšek *et al.*, 2009a,b). The underlying reason for this is the lack of appreciation of the distinctiveness and importance of the naturalization stage (Pyšek *et al.*, 2008) and, for macroecological analyses, the shortage of comprehensive catalogues of regional alien floras (see section III 'The biogeographical background for studying naturalization: variation among populations and regions').

In the above sections we have reviewed evidence from many sources to show that different determinants affect progression along the continuum in different ways at different stages; the influence of each factor is highly stage- and context-dependent (Williamson, 2006; Dawson *et al.*, 2009; Pyšek *et al.*, 2009a,b; Fig. 3). The summarized evidence suggests, for example, that climate match together with massive reproduction are crucial for naturalization, whereas traits and dispersal-related factors are implicated further along the continuum. The pivotal role of propagule pressure is manifest at the introduction stage, when it is closely linked with nurturing, and increases the probability of a species escaping from cultivation, overcoming local environmental barriers and occurring as a casual. Further along the continuum, once populations have become established and the species is naturalized, propagule pressure again assumes importance, but then is predominantly generated by the invading populations themselves (Foxcroft *et al.*, 2004). Increasing residence time allows species more opportunities to establish, undergo population growth, and spread. The factors examined can also be roughly arranged according to their changing importance along the second axis, representing scale, as depicted in Fig. 3. The major role of reproductive traits, including adaptations acquired via nurturing, at fine scales translates into an increasing role of dispersal traits and propagule pressure at larger spatial scales. These interactions are framed by the major macroecological drivers represented by climate and residence time.

Patterns of naturalization and invasion differ across geographical regions and over scales of space and time; full understanding of the drivers of naturalization can only be realized if we integrate the role of ecological factors operating at smaller scales with that of factors that exert influence at the macro scale. Innovative ways of obtaining such insights are crucial for substantial advances in invasion science. This review has highlighted that studies focusing meticulously on the understanding of individual phases of the continuum are still rather rare. Yet, relating substantial new insights on determinants of invasion that are relevant to management to particular invasion stages would pave the way for better integration of research outputs into risk assessment and prioritization protocols. Understanding why and under which circumstances species become naturalized would provide a more objective basis for proactive management, by allowing managers to target potentially invasive species before they start to exert ecological impacts on ecosystems and economic costs to human society.

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