

In search of a real definition of the biological invasion phenomenon itself

Loïc Valéry · Hervé Fritz · Jean-Claude Lefeuvre · Daniel Simberloff

Received: 26 July 2007 / Accepted: 26 December 2007 / Published online: 1 February 2008
© Springer Science+Business Media B.V. 2008

Abstract The many qualifying terms attributed to invasive species reveal the lack of precision surrounding the notion of biological invasion itself. In spite of several proposed definitions, some basic disagreements persist concerning characterization of the phenomenon. These primarily arise from the lack of pertinence of both of the main current criteria—the geographic (or biogeographic) criterion and the impact criterion—to what is really intended by “invasion.” Faced with this situation, it seems preferable to adopt an ontological approach allowing a return to the basic principles of the elaboration

of a definition. Starting with the nature of the phenomenon itself (i.e., its essence), we try to elucidate the notion of biological invasion and we suggest a general definition compatible with most of the ideas already expressed.

Keywords Biological invasion · Definition · Geographic criterion · Impact criterion · Interspecific competition · Ontological approach

L. Valéry (✉) · J.-C. Lefeuvre
Département d’Ecologie et de Gestion de la Biodiversité,
Muséum National d’Histoire Naturelle, Université de
Rennes 1, Bât 25–Avenue du Général Leclerc,
35042 Rennes cedex, France
e-mail: lvalery@mnhn.fr

J.-C. Lefeuvre
e-mail: jean-claude.lefeuvre@univ-rennes1.fr

H. Fritz
Laboratoire de Biométrie et Biologie Evolutive,
Université de Lyon, Université Lyon 1, CNRS,
UMR 5558, 43 boulevard du 11 Novembre 1918,
Villeurbanne 69622, France
e-mail: fritz@biomserv.univ-lyon1.fr

D. Simberloff
Department of Ecology and Evolutionary Biology,
University of Tennessee, 569 Dabney Hall, Knoxville,
TN 37996-1610, USA
e-mail: dsimberloff@utk.edu

Introduction

ALIEN (Crawley et al. 1996), EXOTIC (Green 1997), NON-INDIGENOUS (Mack et al. 2000; Pimentel et al. 2000; Kolar and Lodge 2001), IMPORTED (Williamson and Fitter 1996), INTRODUCED (Lonsdale 1994), NON-NATIVE (Davis et al. 2000), IMMIGRANT (Bazzaz 1986), COLONIZER (Williamson 1996), NATURALIZED (Richardson et al. 2000a) are among the qualifying terms attributed to invasive species in the field of invasion ecology (Davis and Thompson 2000; see Colautti and MacIsaac 2004 for an exhaustive review of terms). Beyond the simple semantic aspect, this profusion of terms clearly reveals the inaccuracy surrounding the notion of biological invasion itself.

This confusion appeared at the birth of invasion ecology: indeed, in its founding book, *The Ecology of Invasions by Animals and Plants*, Charles Elton (1958) does not propose a definition of the

phenomenon, as Richardson et al. (2000a) and Rejmánek et al. (2002) have noted. Of course, several definitions of biological invasion have been proposed since then (Richardson et al. 2000a; Davis and Thompson 2000; Colautti and MacIsaac 2004; Richardson and Pysek 2004). But, as rigorous and methodical as the approaches of these authors are, their contributions have above all confirmed the existence of persistent basic disagreements about what invasion actually is. These ambiguities probably depend in part on the lack of pertinence of both of the main criteria currently in use: the geographic (or biogeographic) criterion and the impact criterion.

Based on the analysis of both these criteria, we aim to bring new insights to the problem of characterizing biological invasion and to propose a general definition of the phenomenon that does not lead to further confusion and that integrates most ideas already expressed about the subject.

The geographic criterion

Some researchers consider that a species must overcome a major geographical barrier (cf. barrier A in Richardson et al. 2000a or passage from stage 1 to stage 2 in Colautti and MacIsaac 2004) and/or to traverse a great distance (i.e., greater than 100 km according to Richardson et al. 2000a) to be considered invasive (Richardson et al. 2000a; Colautti and MacIsaac 2004; Richardson and Pysek 2004; Pysek and Richardson 2006; Richardson and Pysek 2006). To use the expression of Davis and Thompson (2000), adherents of this view therefore consider that *saltation dispersal* is obligatory. The adoption of that criterion consequently prevents *autochthonous*, *indigenous*, *resident* or *native* species from being invasive even if they begin to dominate communities during local plant succession (Richardson et al. 2000a; Richardson and Pysek 2004; Pysek and Richardson 2006).

However, this stance is not shared by other researchers who believe a species native to a region can also qualify as invasive when it colonizes and dominates a new adjacent or nearby habitat following *diffusion dispersal* (Thompson et al. 1995; Davis and Thompson 2000). This broader notion of biological invasion (i.e., taking into account both dispersal modes) dismisses *ipso facto* the distinction between

native and non-native species. It also helps simplify the notion of invasion, because it frees us from the problem presented by invasive cryptogenic species that are neither clearly native nor clearly alien (Carlton 1996).

More fundamentally, even though they refuse to consider autochthonous species as invasive, some researchers (Richardson et al. 2000a; Pysek and Richardson 2006) recognize that the high functional similarity between native species that suddenly dominate during a local succession and alien species that invade a system (Thompson et al. 1995; Prach and Pysek 1999; Meiners 2007) can reveal the existence of common mechanisms in the two situations. Consequently, a definition that restricts biological invasions to an intrinsically geographical phenomenon (i.e., specific to non-native species) (e.g., Richardson et al. 2000a; Colautti and MacIsaac 2004) rather than to an ecological one does not seem justified at this stage in our opinion, because it departs from husserlian logic and does not allow one to reach the ipseity or essence of the phenomenon—i.e., what makes something itself and not anything else (Husserl 1913). Thus, the biogeographically based definition would lead to the curious situation that a species native to Europe would be invasive if it rapidly colonized an area in North America, but it would not be invasive if it similarly expanded in an area adjacent to its original range—e.g., the European starling *Sturnus vulgaris* L. spreads into Europe (Pascal et al. 2006) but invades North America (Feare 1984). Similarly, Douglas fir (*Pseudotsuga menziesii*) is invasive in New Zealand (Kay 1994) but “encroaches” on grassland habitats in British Columbia (Bai et al. 2004).

A focus on the fundamental ecological criteria inherent in the phenomenon seems to us a more reasonable and general way to define a biological invasion, not necessarily excluding the spatial dimension of the phenomenon.

The impact criterion

The impact criterion also gives rise to a background debate. Indeed, some researchers believe that a species must have a major impact (positive or negative) on the community/ecosystem in which it spreads in order to be considered invasive (Davis and

Thompson 2000; Davis and Thompson 2002; Inderjit 2005). Others works suggest on the contrary that this criterion should not be retained for characterizing the biological invasion phenomenon, on the one hand, because it can prove to be very difficult to assess and, on the other hand, because it gives rise to a margin of interpretation (Richardson et al. 2000a; Daehler 2001; Rejmánek et al. 2002): what is the threshold value from which we can consider that there is an impact? What constitutes a major impact?

Beyond the explanations advanced by Richardson et al. (2000a), Daehler (2001) and Rejmánek et al. (2002), a further fundamental reason leads us to reject this criterion too: at the stage of the definition, the characterization of the phenomenon itself should rest solely on criteria relative to its “substance”, to its “being” (i.e., *ousia* in Greek), and not to its effects or consequences, which are circumstantial and variable. Indeed, from an ontological viewpoint, a definition expresses the nature or the essence of a thing and of that thing only: to use the terms of Aristotle in the book Z of *The Metaphysic* (1991), “*it is from the substance only that there is definition*”. More precisely, this Aristotelian posture assimilates the essence/substance to the quiddity, that is to say the being by itself, that which remains in the modifications of its predicates (i.e., beyond its appearance and its attributes) and thus constitutes the kernel of stability and reality. For this reason, the substance represents, according to Aristotle, the founder gno-seological principle: the substance is identified as the subject par excellence *independently of time and movement*, the prime being (logically and chronologically), the unique and permanent principle around which all the rest revolves.

As an illustration, when an earthquake occurs, seismologists always distinguish the primary phenomenon, characterized by its magnitude on the Richter scale (i.e., instrumental measurement independent of the measure point), from its impact (i.e., nature/type and importance of damages), which may vary considerably depending on fixed factors (e.g., distance from the epicenter, nature and resistance of the subsoil, types of buildings, human population density) or fortuitous (e.g., local time of the earthquake and habits of the population). Consequently, the fact that earthquakes of comparable magnitude should be able to cause very dissimilar losses (i.e., one phenomenon may have different impacts depending

on the context) led scientists to characterize the impact independently of the primary phenomenon itself by means of intensity scales (e.g., Mercalli scale, M.S.K. scale) different from the magnitude scale to avoid confusion (Rothé 1977; Madariaga and Perrier 1991).

Similarly, the effect of a biological invasion—its impact—is circumstantial by nature: it depends on both the identity of the invader (i.e., on its biological traits) and the recipient community/ecosystem (i.e., on the biological traits of resident species). A species that would invade two different ecosystems in the same proportions (e.g., percentage of the occupied area, percentage of the total biomass of the ecosystem)—that is to say, in a way, with the same “magnitude”—need not have the same effect in both these environments.

In this respect, various studies have suggested that the intensity of the impact would be stronger the more marked the differences between the traits of the invasive species and those of the resident species (Grime 1998; Dukes and Mooney 2004; Strauss et al. 2006): more generally, invasion impact would essentially vary according to the probability of addition and/or loss of a functional group within the recipient ecosystem. Indeed, because functional diversity strongly determines the invasibility of a community (Crawley et al. 1999), the loss and/or the addition of some traits would necessarily have considerable consequences for ecosystem functioning (Schulze and Mooney 1993; Chapin et al. 2000). Furthermore, because functional diversity is positively correlated with species richness from a statistical viewpoint (Diaz and Cabido 2001; Hooper et al. 2002), the impact of biological invasions on the functioning of recipient communities/ecosystems will tend on average to be higher when number of native species is lower.

Consequently, impact, which varies greatly depending on multiple factors, is an unsuitable criterion for defining a phenomenon that is stable and constant by nature; in this case, biological invasion. Indeed, the objective is to make what is common and permanent appear, and not what differs in time and space. To use Husserl’s words (1913), it is a matter of extracting from the phenomenon “*its specificity, its permanent network of essential predicates which necessarily occur with it so that others determinations, those one which are secondary and*

relatives, might fall to it"; according to him, the real knowledge is vision of absolute forms.

Such a definition does not negate the importance of research on the impact of biological invasions, especially to implement management and eradication policies (e.g., U.S. Executive Order 13112, article 8(h) of the Convention on Biological Diversity, GISP). It would be particularly useful to determine a scale to measure of "the extent of the impact" (cf. Parker et al. 1999) organized in levels of alert (like the Mercalli scale for the seisms) in order to help managers to define priority actions. The standardization of an operational procedure to quantify impact, allowing classification of invasions in specified categories and organization into a hierarchy could constitute a new area of research.

Towards a mechanistic definition of the biological invasion phenomenon

For the above reasons, the geographic and impact criteria do not seem suitable to us for characterizing biological invasions. In accordance with the previously adopted Aristotelian position, it would be preferable to rely on the phenomenon's quiddity (i.e., substance). Indeed, the permanence/stability that characterizes the latter makes it the founder principle of knowledge, according to Aristotle. From a phenomenological viewpoint, and in husserlian terms, the task thus consists of proceeding to an "*eidetical reduction*", which in others words amounts to going from the phenomenon to the pure essence in order to reach an intuition of the *eidōs* of the thing, that is to say of what it is in its essential and invariable structure once all that is contingent and accidental in it is eliminated (Husserl 1913).

The substance—etymologically viewed as the foundation, "what stands (*-stare*) under (*sub-*)"—thus implies that we should return to the mechanism itself at the origin of the phenomenon. This mechanism common to all biological invasions will constitute the kernel of the definition that we will propose.

In a trivial way, the effort of characterizing the phenomenon thus amounts to identifying the universals/transcendentals (i.e., the general notions resulting through abstraction of the intersection of singular objects) from the search for what is present

in all biological invasions. In this respect, from a theoretical viewpoint, a biological invasion, according to us, always appears in the course of an interspecific competition *sensu lato*—i.e., direct or apparent (i.e., mediated by an interaction of another form like predation or mutualism)—that underscores the superiority of a unique species, qualified as invasive, over the other, functionally similar species that use the same resource in the same way (e.g., nutrient, food, habitat) within an ecosystem. This competitive advantage necessarily occurs after the disappearance of one (or several) barrier(s)/obstacle(s) to the dominance of this species. This lifting of constraint(s), which from a conceptual viewpoint destructures the system and inevitably leads to a redistribution of its elements, can occur in two ways: (i) following the introduction of a non-native species that can benefit from an overwhelming competitive advantage as a result of the lack of common evolutionary history with the recipient community's species belonging to the same guild/functional group—e.g., the "enemy release hypothesis" (Blossey and Nötzold 1995; Keane and Crawley 2002), "novel weapons hypothesis" (Callaway and Ridenour 2004); (ii) following a major exogenous modification of the environment (e.g., eutrophication, loss/addition of top predators, fire/change in fire regime) that changes the competition regime through the redistribution of the selective forces at work (Byers 2002). With this definition, the invasive species can be native or non-native: indeed, a native species can be considered as "novel" towards a changed environment as well (Davis and Thompson 2000; Sax and Brown 2000; Byers 2002).

From an ecological viewpoint, an invasive species is finally always alien to its novel environment as a result of either a change OF the environment (alien species) or a change IN the environment (native species or alien species that spread after a lag time).

In reality, whatever the nature of the change, it is invariably the superiority of the response of a given species over those of functionally similar species that leads to its dominance or to its invasion in the novel environment (Shea and Chesson 2002). That is, the differential response of species associated with a change in and/or of the environment always offers some "niche opportunities"—e.g., through the opening of a novel niche or through the extension of a pre-existing niche—by means of which a species is able

to invade the environment (Shea and Chesson 2002). The stochasticity and brevity of these opportunities have been underlined by Johnstone (1986) and Davis (Pysek et al. 2004) who called it “plant invasion windows” and “transient window opportunity”, respectively.

The idea that interspecific competition *sensu lato* is the unique, indivisible/irreducible and universal mechanism at the origin of the biological invasion phenomenon is moreover reinforced by the theoretical models of Tilman (1999) (i.e., the adaptation of the R^* rule) and Davis et al. (2000) (i.e., the fluctuating resource theory): designed for modeling biological invasions, they are indeed based only on this one interaction. In other respects, Tilman’s model, which was initially developed to explain the course of plant succession and, in particular, the dominance of species (Tilman 1985), establishes the link between alien and native species invasions.

The competitive advantage of an invasive species—i.e., the superiority of its response—following its introduction or the modification of its environment has two origins: (1) in the match between its traits (e.g., behaviour, physiology, anatomy) and those of the other species belonging to the same functional group, and (2) in the new relations (i.e., weakening/strengthening of pre-existing interactions, appearance of new interactions) established between it and all species present in its environment (e.g., predators, mutualists, commensals). In this respect, it seems to us that these new relations like predation (Bruno et al. 2005) or mutualism (Richardson et al. 2000b), when they occur, play only secondary roles in realizing the phenomenon: it is question of contingent, accidental and, by definition, peripheral interactions. Of course, they can influence it (e.g., determine its probability of occurring), but they do not constitute its mainspring mechanism and consequently do not represent its essence. For the same reasons, we believe that however important propagule pressure is in determining whether an invasion occurs, it cannot characterize the phenomenon itself.

Finally, in pursuing the ipseity of the phenomenon, it seems to us that some elaboration is needed concerning two points relative to the spatiotemporal dimension of biological invasions.

First, the use of the term “invasive” to characterize all non-native species present in many places and environments worldwide is not justified: indeed, an

invasive species becomes dominant, in density and/or biomass, in its novel environment, whereas the ubiquitous/cosmopolitan non-native species that have great colonization ability are not always present in sufficient densities and biomasses to become dominant. Even though it is, of course, conceivable that some species can be considered as both invasive and ubiquitous, nothing allows to generalize this linkage.

Secondly, biological invasions have a distinctive temporal element that distinguishes them from the extension of species’ distribution on a geological time scale, which are sometimes termed “invasions”. Indeed, a biological invasion is characterized by its rapidity: the overwhelming competitive advantage of an invasive species always results in an exponential-type increase of the demography and/or of spatial occupation. This criterion differentiates biological invasions from the major (re)colonizations of biota in the course of evolution (e.g., after glaciations), which are very slow processes.

Thus, based on the foregoing considerations, the definition we propose is:

A biological invasion consists of a species’ acquiring a competitive advantage following the disappearance of natural obstacles to its proliferation, which allows it to spread rapidly and to conquer novel areas within recipient ecosystems in which it becomes a dominant population.

This mechanistic definition of the biological invasion phenomenon seems sufficiently general to characterize what is common to all invasions. In return, it deliberately omits some variable aspects (e.g. impact, dispersal means). Nevertheless, these idiosyncrasies peculiar to each invasion still constitute essential subjects of research, both in their own right and in order to facilitate their management.

References

- Aristotle (1991) La métaphysique (Tome 1: Livre A–Z). Librairie philosophique J. Vrin, Paris
- Bai Y, Thompson D, Broersma K (2004) Douglas fir and ponderosa pine seed dormancy as regulated by grassland seedbed conditions. *Rangeland Ecol Manag* 57:661–667
- Bazzaz FA (1986) Life history of colonizing plants: some demographic, genetic and physiological features. In: Mooney HA, Drake JS (eds) *Ecology of biological*

- invasions of North America and Hawaii, Springer-Verlag, New York, pp 96–110
- Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *J Ecol* 83:887–889
- Bruno JF, Fridley JD, Bromberg KD, Bertness MD (2005) Insights into biotic interactions from studies of species invasion. In: Sax DF, Stachowicz JJ, Gaines SD (eds) *Species invasion—Insights into ecology, evolution, and biogeography*, Sinauer Associates, Inc. Publishers, Sunderland, pp 13–40
- Byers JE (2002) Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* 97:449–458
- Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Front Ecol Environ* 2:436–443
- Carlton JT (1996) Biological invasions and cryptogenic species. *Ecology* 77:1653–1655
- Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Sala OE, Hobbie SE, Mack MC, Diaz S (2000) Consequences of changing biodiversity. *Nature* 405:234–242
- Colautti RI, MacIsaac HJ (2004) A neutral terminology to define ‘invasive’ species. *Divers Distrib* 10:135–141
- Crawley MJ, Brown SL, Heard MS, Edwards R (1999) Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecol Lett* 2:140–148
- Crawley MJ, Harvey PH, Purvis A (1996) Comparative ecology of the native and alien floras of the British Isles. *Philos Trans R Soc B Biol Sci* 351:1251–1259
- Daehler CC (2001) Two ways to be an invader, but one is more suitable for ecology. *Bull Ecol Soc Am* 82:101–102
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88:528–534
- Davis MA, Thompson K (2000) Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. *Bull Ecol Soc Am* 81:226–230
- Davis MA, Thompson K (2002) “Newcomers” invade the field of invasion ecology: question the field’s future. *Bull Ecol Soc Am* 83:196–197
- Diaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* 16:646–655
- Dukes JS, Mooney HA (2004) Disruption of ecosystem processes in western North America by invasive species. *Rev Chil Hist Nat* 77:411–437
- Elton CS (1958) *The ecology of invasions by animals and plants*. Chapman and Hall, London
- Feare CJ (1984) *The starling*. Oxford University Press, Oxford
- Green RE (1997) The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *J Anim Ecol* 66:25–35
- Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J Ecol* 86:902–910
- Hooper DU, Solan M, Symstad AJ, Diaz S, Gessner MO, Buchmann N, Degrange V, Grime JP, Hulot FD, Mermillod-Blondin F, Roy J, Spohn EM, Van Peer L (2002) Species diversity, functional diversity, and ecosystem functioning. In: Loreau M, Naeem S, Inchausti P (eds) *Biodiversity and ecosystem functioning—synthesis and perspective*. Oxford University Press, Oxford, pp 195–208
- Husserl E (1913) *Idées directrices pour une phénoménologie*. Gallimard 1950, Paris
- Inderjit S (2005) Plant invasions: habitat invasibility and dominance of invasive plant species. *Plant Soil* 277:1–5
- Johnstone IM (1986) Plant invasion windows: a time-based classification of invasion potential. *Biol Rev* 61:369–394
- Kay M (1994) Biological control for invasive tree species. *N Z Forestry* 39:35–37
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends Ecol Evol* 17:164–170
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends Ecol Evol* 16:199–204
- Lonsdale WM (1994) Inviting trouble: introduced pasture species in Northern Australia. *Aust J Ecol* 19:345–354
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Madariaga R, Perrier G (1991) *Les tremblements de terre*. Presses du CNRS, Paris
- Meiners SJ (2007) Native and exotic plant species exhibit similar population dynamics during succession. *Ecology* 88:1098–1104
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding ecological effects of invaders. *Biol Invasions* 1:3–19
- Pascal M, Lorvelec O, Vigne JD (2006) *Invasions biologiques et extinctions—11000 ans d’histoire des vertébrés en France*. Editions Belin, Paris
- Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50:53–65
- Prach K, Pysek P (1999) How do species dominating in succession differ from others? *J Veg Sci* 10:383–392
- Pysek P, Davis MA, Daehler CC (2004) Plant invasions and vegetation succession: closing the gap. *Bull Ecol Soc Am* 85:105–109
- Pysek P, Richardson DM (2006) The biogeography of naturalization in alien plants. *J Biogeogr* 33:2040–2050
- Rejmánek M, Richardson DM, Barbour G, Crawley MJ, Hrusa GF, Moyle PB, Randall JM, Simberloff D, Williamson M (2002) Biological invasions: politics and the discontinuity of ecological terminology. *Bull Ecol Soc Am* 83:131–133
- Richardson DM, Pysek P, Rejmánek M, Barbour G, Dane Panetta F, West CJ (2000a) Naturalization and invasion of alien plants: concepts and definitions. *Divers Distrib* 6:93–107
- Richardson DM, Allsopp N, D’Antonio CM, Milton SJ, Rejmánek M (2000b) Plant invasions—the role of mutualisms. *Biol Rev* 75:65–93
- Richardson DM, Pysek P (2004) What is an invasive species? Retrieved from <http://www.cabicompendium.org/cpc/library/invasiveplants/> on 02 March 2005
- Richardson DM, Pysek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Prog Phys Geogr* 30:409–431

- Rothé JP (1977) Séismes et volcans. Presses Universitaires de France—Que sais-je? Paris
- Sax DF, Brown JH (2000) The paradox of invasion. *Glob Ecol Biogeogr* 9:363–371
- Schulze ED, Mooney HA (eds) (1993) Biodiversity and ecosystem function. Springer-Verlag, New York
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17:170–176
- Strauss SY, Webb CO, Salamin N (2006) Exotic taxa less related to native species are more invasive. *Proc Natl Acad Sci USA* 103:5841–5845
- Thompson K, Hodgson JG, Rich TCG (1995) Native and alien invasive plants: more of the same? *Ecography* 18:390–402
- Tilman D (1985) The resource-ratio hypothesis of plant succession. *Am Nat* 125:827–852
- Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80:1455–1474
- Williamson M (1996) *Biological Invasions*. Chapman & Hall, London
- Williamson M, Fitter A (1996) The varying success of invaders. *Ecology* 77:1661–1666