FORUM

Plant invasions in undisturbed ecosystems:
The triggering attribute approach

Gurvich, Diego E.[1*]; Tecco, Paula A.[1,2] & Díaz, Sandra[1,3]

Instituto Multidisciplinario de Biología Vegetal (CONICET - UNC) and F.C.E.F. y N., Universidad Nacional de Córdoba,
Casilla de Correo 495, Vélez Sársfield 299, 5000 Córdoba, Argentina;
[2]E-mail ptecco@com.uncor.edu; [3]E-mail sdiaz@com.uncor.edu;
[*]Corresponding author; Fax +54 3514331097; E-mail dgurvich@com.uncor.edu

Abstract

The invasion of a target community by a non-indigenous plant species includes the stages of arrival, establishment and spread, which tend to depend on different characteristics of the invasive species and its context. While the mechanisms behind the invasion of highly disturbed ecosystems are well known, our understanding of the invasion process in undisturbed or weakly disturbed ecosystems is much more limited. Here we propose that, once a non-indigenous species has arrived to a new ecosystem and become established, the likelihood that it spreads, and thus becomes invasive, may depend on just one or very few characteristics, called 'triggering attributes' (TA). We propose that a TA is a vegetative or regenerative attribute discontinuously distributed in comparison to the resident community. This attribute allows the species to benefit from a resource that is permanently or temporarily unused by the resident community. We present an original study case and examples from the literature to illustrate our approach, and we also propose some ways to test it in different ecosystems.

Keywords: Invasion ecology; Niche; *Ligustrum lucidum*; Plant functional trait; *Pyracantha angustifolia*; Spread stage.

Abbreviation: RGR = Relative growth rate; SLA = Specific leaf area; TA = Triggering attribute.

Introduction

A considerable amount of research has been devoted to understanding and predicting plant invasions (e.g. Rejmànek & Richardson 1996; Kolar & Lodge 2001; Shea & Chesson 2002). Several approaches have been developed, including the search for a universal invasive plant syndrome (Rejmànek & Richardson 1996; Kolar & Lodge 2001), the release from natural enemies (Maron & Vilà 2001; Keane & Crawley 2002), and the diversity of the target community (see Levin & D'Antonio 1999; Stohlgren et al. 1999 for discussion). All of them have found only moderate success, particularly in understanding the invasion of undisturbed or weakly disturbed ecosystems (Godfree et al. 2004). In particular, a set of characteristics that consistently distinguish non-indigenous invasive species from indigenous invasive species has not been identified so far (Noble 1989; Thompson et al. 1995; Kolar & Lodge 2001; Hastwell & Panetta 2005). If there is any consensus now, it seems to be that non-indigenous invasive plants do not share a universal suit of traits. In some cases they appear to have some morphological, functional and taxonomic differences with resident species (Rejmànek & Richardson 1996), but they are often similar in many ways (Thompson et al. 1995; Levine & D'Antonio 1999), and invasiveness seems to depend on the composition of the target community, but not necessarily on its diversity (see Shea & Chesson 2002 for a review).

Recently Davis et al. (2000), Davis & Pelsor (2001) and Shea & Chesson (2002) suggested that invasions should be best understood within the framework of community ecology theory, since the same processes that regulate community dynamics in natural ecosystems operate during invasions. Davis et al. (2000) proposed that resource fluctuation is an important factor determining plant invasions, with non-indigenous invaders being

able to spread during windows of opportunity in which competition by indigenous species is low, most notably as a result of disturbances that destroy their biomass. This approach provides a mechanism for invasion, especially in disturbed ecosystems. In such situations, successful colonizers, both non-indigenous and indigenous, should also show 'weedy' attributes, such as high seed output, high growth rate and plasticity, short life span, etc. (Thompson et al. 1995; Rejmànek & Richardson 1996). Shea & Chesson (2002) explained successful invasions using the concept of niche opportunity, i.e. the potential provided by a given community for non-indigenous organisms to have a positive rate of increase from low density. This approach is more general and can be applied to both disturbed and undisturbed ecosystems. However, it does not provide a mechanism for invasion, particularly in undisturbed ecosystems, just a theoretical framework to understand them.

In this paper we propose an approach to understand plant invasions in undisturbed ecosystems. Within the context of our work, we follow the classical definition of Pickett & White (1985), by which a disturbance is "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability or the physical environment". It follows the lines of Shea & Chesson (2002) and complements it by establishing links with plant functional trait theory. It is also in line with Davis et al.'s ideas (2000) in the sense that it requires untapped resources, although not necessarily fluctuating resource levels. Our approach also agrees with the work of Fargione et al. (2003) who found that established species inhibit introduced species from their own functional type, highlighting the importance of functional traits on the invasion process. Our approach is based on the presence of specific plant trait values or states (= attributes *sensu* Lavorel et al. 1997) in the non-indigenous species and in the resident species. In order to take advantage of resources permanently or temporarily unexploited by resident species – niche opportunities –, the phenotype of a non-indigenous invader must differ in some key ways from those of the members of the target community. These differences may be morphological, functional and/or developmental. According to our approach, it is not necessary for a successful invader to be different from resident species in terms of many traits (usually they are not, see Thompson et al. 1995). Strong differences with respect to a single attribute that allows the non-indigenous species to gain access to resources untapped by resident species should be enough to trigger an invasion process. We therefore call such an attribute 'triggering attribute' (TA). As mentioned above, plant invasions in disturbed ecosystems are relatively well understood, and successful invasion mechanisms in such circumstances have been identified (Davis et al. 2000).

Much more difficult to understand, and probably more interesting from the theoretical and practical point of view, is the spread of non-indigenous species into areas with no disturbance or only slight disturbance. It is in these situations where the TA approach offers its highest potential.

Approach rationale: what makes a plant attribute a triggering attribute and how does it work?

The invasion process includes arrival, establishment, spread in the new environment, and impacts on the fitness of resident populations and/or local ecosystem processes (Kolar & Lodge 2001). All of them require specific, and often different, plant attributes. For example, high dispersal capacity may contribute to high arrival rate, but not necessarily be of help in the following steps; nitrogen-fixing capacity may be a key factor in local spread and ecosystem impact, but does not in arrival. Spread and community and ecosystem impacts are the steps in which differences in the attribute distribution of invading and resident species are most relevant. Although in theory our approach could be applied to the understanding of impacts, these have been extensively dealt with in the literature (e.g. Vitousek 1986; D'Antonio & Vitousek 1992; Mack et al. 2000; Levine et al. 2003). In this paper we will only focus on the spread stage.

In order to make use of an untapped resource, or a niche opportunity, a non-indigenous invasive species has to show at least one attribute that is absent in the resident community. By definition, this particular attribute should be discontinuously distributed in comparison to those of the resident species, otherwise the resource in question would already have been used by them. When dealing with trait distributions we do not refer to the nature of the trait (e.g. N-fixing capacity is, naturally, a discontinuous trait, while specific leaf area is a continuous one). Rather, we refer to how the inclusion of a non-indigenous species alters the local distribution of attributes within a trait (Fig. 1). For example, if in a community there is at least one N-fixing species, the inclusion of an N-fixing invader would not alter its distribution. On the other hand, if in a community the relative growth rate ranges from 50 to 150 mg.g^{-1}.d^{-1}, the inclusion of a non-indigenous species with a RGR of 350 mg^{-1}.d^{-1} would make the local RGR distribution discontinuous. This aspect is of great importance in our approach because a distribution analysis of functional traits should give an idea of which attributes could be involved in an invasion and which would be the main mechanism involved. In this sense our approach is analogous to that of Chapin et al. (1996), who proposed that

the importance of any particular species in influencing ecosystem function is related to those attributes that create discontinuities in the trait distribution of the community, because if that species goes extinct its unique function would disappear too. Similarly, Vitousek (1986) argued that when a completely new life form invades an ecosystem, its effect on biodiversity and ecosystem function would be dramatic. For example, replacement of trees by grasses in Hawai'i (D'Antonio & Vitousek 1992) or of grasses by shrubs in the Chihuahuan desert (Jackson et al. 2002) has produced very important changes in those ecosystems.

The TA needs not be a particular or unique attribute *per se*. Rather, it can be a trait state that is absent in the invaded community, which allows the invader to spread by using a resource that is unused or very poorly used by the native community ('niche opportunity'). Obviously, non-indigenous species with a whole constellation of attribute differences with respect to the native community are expected to spread and cause major impact, but the point here is that even a single attribute, if it is sufficiently different to allow the invader to tap unused resources, may be enough to trigger its spread, even if the rest of its attributes are very similar to those of resident species.

We argue that there is no general rule to become a TA. TAs could be attributes of very different nature, linked to reproduction (e.g. fruiting phenology, see below; seed dispersal; Lonsdale 1993), nutrient capture (e.g. N-fixing from the atmosphere; Vitousek & Walker

1989), water capture (e.g. tap-rooted plants; Zavaleta et al. 2001), etc. It all depends on the attributes already represented in the resident community. For example, the possibility of fixing atmospheric nitrogen can be regarded as a TA in Hawai'i but not in Neotropical savanna ecosystems, where N-fixers are common. The tall tussock grass and spiny stem succulent life forms can be considered TAs (or constellations of TAs) in Australia, but not in South America, where they are fairly common in the native floras, and so forth. A TA could be a morphological (e.g. shoot and/or root architecture or size) or ecophysiological characteristic (e.g. photosynthetic pathway, water or nutrient use efficiency, frost resistance). In other words, any attribute that confers the invader an advantage in tapping some resource that is underused by the resident community has the potential to become a TA. Our approach only refers to trait distribution in the target community. A trait that acts as TA in an invaded community may be continuously or discontinuously distributed with respect to other species in the native range of the invading species.

An empirical example

Two non-indigenous invasive woody species have now spread into natural plant communities of central Argentina, even in the absence of major anthropogenic disturbance (Tecco et al. in press). These are *Ligustrum lucidum* W.T. Aiton and *Pyracantha angustifolia* (Franch) C.K. Schneid both native of southeastern Asia. *Ligustrum* and *Pyracantha* were both introduced in central Argentina as ornamental species at the beginning of the 19th century. At present, these species are expanding into the montane woodlands of the region (Delucchi 1991). Although they expand faster in disturbed areas, they also invade in areas with no or little disturbance.

We performed a functional-attribute comparison between these non-indigenous species and 15 of the most abundant indigenous woody species in the woodlands of Córdoba, central Argentina (see Zak & Cabido 2002 for a detailed vegetation description). The plant traits selected for study were specific leaf area (SLA), wood density, plant height, seed mass, fruiting phenology and seed dispersal mode. The importance of these traits for both the established and regeneration phases of the plant life cycle has been widely recognized (Hodgson et al. 1999; Lavorel & Garnier 2002; Díaz et al. 2004). The plant trait information was taken from Díaz et al. (2004).

The addition of non-indigenous species did not cause a discontinuity in the local distribution of most traits (Fig. 2a-d), that is, the non-indigenous species
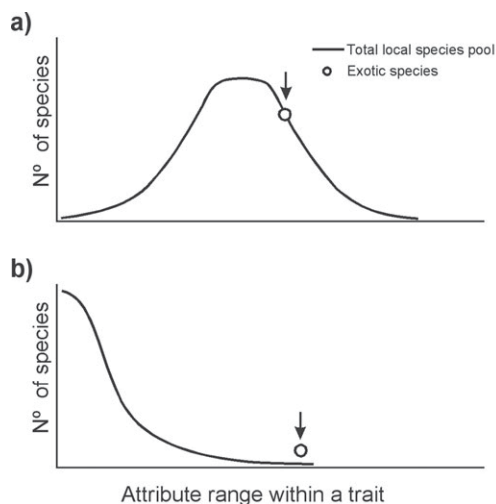
Fig. 1. Hypothetical frequency distribution of attributes, showing examples where a non-indigenous species attribute (indicated by an arrow) falls well inside (**a**), or well beyond (**b**) the attribute range of the indigenous species that form the target community. The species in (**b**) shows a triggering attribute and therefore should be more likely to spread in the target ecosystem than the species in (**a**).
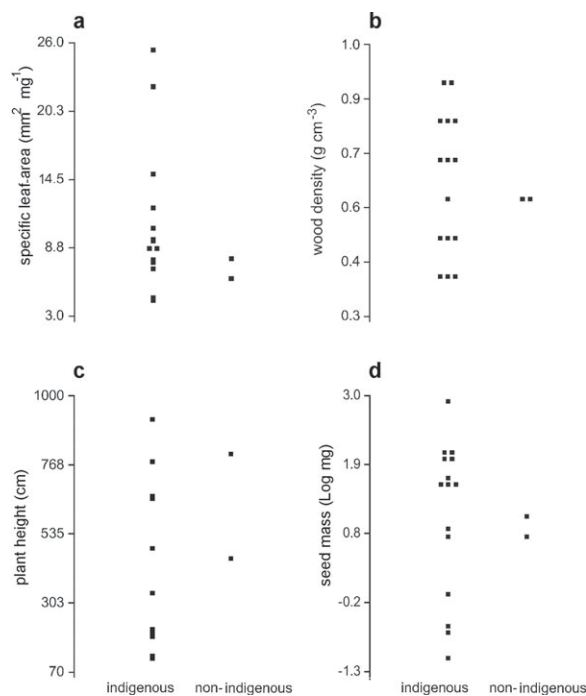
Fig. 2. Comparisons in terms of (**a**) Specific leaf area; (**b**) Wood density; (**c**) Plant height; (**d**) seed mass between the most representative indigenous species of the montane xerophytic woodlands of central Argentina (*N* = 15) and the non-indigenous species *Ligustrum lucidum* and *Pyracantha angustifolia*. Seed mass values are log-scaled to facilitate graphical representation.

showed values well within the resident community's trait distribution. Interestingly, both the relatively low SLA and the relative high wood density suggest that the two non-indigenous species are comparatively slow-growing (Garnier 1992; Castro-Díez et al. 1998). This disagrees with the idea that invasive species are in general faster growing than those of target communities ('weedy syndrome' approach, see above). In contrast to these relatively continuous trait distributions, non-indigenous species differed from the local flora in terms of

reproductive phenology and predominant dispersal mode (Fig. 3). Endozoochorous dispersal of fleshy fruits by birds is common in the resident communities. However, this occurs only during the warm season. Only wind and ungulate dispersal are common in other seasons. In contrast, *Pyracantha* and *Ligustrum* are effectively dispersed by birds in autumn and winter (Tecco et al. in press; Aragón & Groom 2003), when other food sources are scarce and their fruits are avidly consumed.

Our findings illustrate that non-indigenous invasive species can be very similar to indigenous species in terms of many functional characteristics, in accordance to Thompson et al. (1995) and Godfree et al. (2004). However, by offering food supply to birds during the unfavourable season, the non-indigenous species probably achieve more effective dispersal into suitable recruitment sites (Kollmann 1995; Tecco et al. in press). Non-indigenous species are thus benefiting from a resource that is not exploited by the resident species (dispersal by birds during winter), which in turn ensures arrival and seedling establishment opportunities early in the spring. Therefore, in this example, autumn-winter maturation of a fleshy fruit may be considered a TA, since it is an attribute that resident species do not possess, and allows non-indigenous species to take advantage of a resource (bird dispersal) that residents cannot momentarily tap.

Final remarks

The TA approach provides conceptual links between invasibility of a community and invasiveness of particular species and offers predictions that can be empirically tested. Spread of a non-indigenous species requires not only an underused resource (invasibility of resident community), but also an attribute that confers the ability to use it (invasiveness of non-indigenous species). Both concepts strongly depend on functional trait distribution (i.e. differences in key attributes between the invader and the indigenous species) and cannot be assessed in
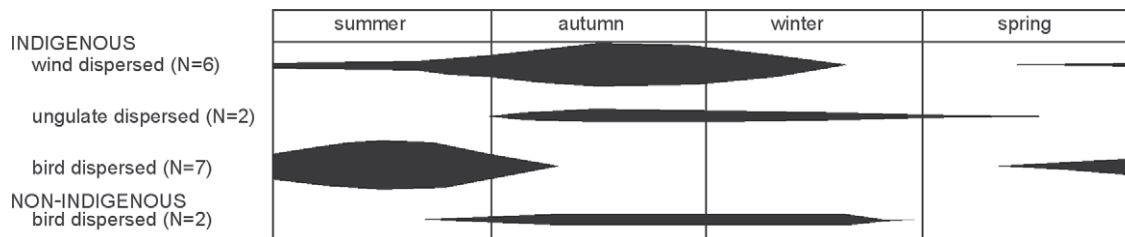
Fig. 3. Fruiting phenology of the non-indigenous species *Ligustrum lucidum* and *Pyracantha angustifolia* and 15 indigenous woody species in the Córdoba mountains, Argentina. The width of the horizontal bars indicates the number of species within each group that are simultaneously dispersing at any given time.

isolation from each other. Therefore, according to our perspective, there is little point in trying to identify a universal 'ideal weed' that could spread into any little-disturbed ecosystem.

We propose that a way to test our approach is to analyse the distribution of functional traits between indigenous and invader species, paying particular attention to attribute discontinuities (Fig. 1a, b). This should be particularly fruitful if accompanied by an analysis of mean environmental conditions, their variability, and their recent changes. Experiments in which a range of plant traits and different levels of resource and disturbance conditions are tested in combination (e.g. Burke & Grime 1996; Davis & Pelsor 2001) are also ideal for this purpose. A complementary approach to the testing of the TA approach is the meta-analysis of case studies of invasion already published in the literature, in combination with information on the traits of the plant species involved, aided by existing plant-trait comparative databases (Díaz et al. 1992; Rusch et al. 2003). Probably the most difficult decision concerns what traits to consider. The main factors limiting productivity and determining disturbance regime of the ecosystem may provide a clue which traits should be given priority. For example, in arid ecosystems, the focus should probably be on traits related to the water economy (e.g. photosynthetic pathway, rooting depth). In nutrient-poor ecosystems, good candidates are attributes directly associated with nutrient capture (e.g. capacity for symbiotic nitrogen fixation). In addition, recent works (e.g. Hodgson et al. 1999; Lavorel & Garnier 2002; Knevel et al. 2003; Díaz et al. 2004) provide lists of key functional traits that are considered of fundamental importance across ecosystems, and thus represent good candidates for a first screening.

References

Aragón, R. & Groom, M. 2003. Invasion by *Ligustrum lucidum* (Oleaceae) in NW Argentina: early stage characteristics in different habitat types. *Rev. Biol. Trop.* 51: 59-70.

Burke, M.J.W. & Grime, J.P. 1996. An experimental study of plant community invasibility. *Ecology* 77: 776-790.

Castro-Díez, P., Puyravaud, J.P., Cornelissen, J.H.C. & Villar-Salvador, P. 1998. Stem anatomy and relative growth rate in seedlings of a wide range of woody plant species and types. *Oecologia* 116: 57-66.

Chapin, F.S., III, Reynolds, H.L., D'Antonio, C.M. & Eckhart, V.M. 1996. The functional role of species in terrestrial ecosystems. In: Walker, B. & Steffen, W. (eds.) *Global change and terrestrial ecosystems*, pp. 403-428. Cambridge University Press, Cambridge, UK.

D'Antonio, C.M. & Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23: 63-87.

Davis, M.A. & Pelsor, M. 2001. Experimental support for a resource-based mechanistic model of invasibility. *Ecol. Lett.* 16: 421-428.

Davis, M.A., Grime, J.P. & Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88: 528-534.

Díaz, S., Acosta, S. & Cabido, M. 1992. Morphological analysis of herbaceous communities under different grazing regimes. *J. Veg. Sci.* 3: 689-696.

Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M. et al. 2004. The plant traits that drive ecosystems: Evidence from three continents. *J. Veg. Sci.* 15: 295-304.

Delucchi, G. 1991. Especies adventicias y naturalizadas nuevas o críticas para Argentina. *Bolet. Soc. Argent. Bot.* 27: 179-181.

Fargione, J., Brown, C.S. & Tilman, D. 2003. Community assembly and invasion: An experimental test of neutral versus niche processes. *Proc. Natl. Acad. Sci. (USA)* 100: 8916-8920.

Garnier, E. 1992. Growth analyses of congeneric annual and perennial grass species. *J. Ecol.* 8: 665-675.

Godfree, R., Lepschi, B. & Mallison, D. 2004. Ecological filtering of exotic plants in an Australian sub-alpine environment. *J. Veg. Sci.* 15: 227-236.

Hastwell, G.T. & Panetta, F.D. 2005. Can differential responses to nutrients explain the success of environmental weeds? *J. Veg. Sci.* 16: 77-84.

Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P. & Thompson, K. 1999. Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* 85: 282-294.

Jackson, R. B., Banner, J.L., Jobbágy, E.G., Pockman, W.T. & Wall, D.H. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* 418: 623-626.

Keane, R.M. & Crawley, M.J. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17: 164-170.

Knevel, I.C., Bekker, R.M., Bakker, J.P. & Kleyer, M. 2003. Life-history traits of the Northwest European flora: The LEDA database. *J. Veg. Sci.* 14: 611-614.

Kolar, C.S. & Lodge, D.M. 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16: 199-204.

Kollmann, J. 1995. Regeneration window for fleshy-fruited plants during scrub development on abandoned grassland. *Ecoscience* 2: 213-222.

Lavorel, S. & Garnier, E. 2002. Predicting changes in composition and ecosystem function from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16: 545-556.

Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T.D.A.

1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends Ecol. Evol.* 12: 474-478.

Levine, J.M. & D'Antonio, C.M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87: 16-26.

Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. Lond. B* 270: 775-781.

Lonsdale, W.M. 1993. Rates of spread of an invading species: *Mimosa pigra* in northern Australia. *J. Ecol.* 81: 513-521.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F. A. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10: 689-710.

Maron, J.L. & Vilà, M. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypothesis. *Oikos* 95: 361- 373.

Noble, I.R. 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. In: Drake, J.A., Mooney, H.A., di Castri, F., et al. (eds.) *Biological invasions: A global perspective (SCOPE)*. John Wiley, New York, NY, US.

Pickett, S.T.A. & White, P.J. 1985. Patch dynamics: a synthesis. In: Pickett, S.T.A. & White, P.J. (eds.) *The ecology of natural disturbance and patch dynamics*. pp. 371-384. Academic Press, New York, NY, US.

Rejmànek, M. & Richardson, D.M. 1996. What make some plant species more invasive? *Ecology* 77: 1655-1661.

Rusch, G.M., Pausas, J. & Lepš, J. 2003. Plant functional types in relation to disturbance and land use: An introduction. *J. Veg. Sci.* 14: 307-310.

Shea, K. & Chesson, P. 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17: 170-176.

Stohlgren, T.J., Binkley, D., Chong, G.W. et al. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.* 69: 25-46.

Tecco, P.A., Gurvich D.E., Díaz, S., Pérez Harguindeguy, N. & Cabido, M. In press. Positive interactions between invasive plants: the influence of *Pyracantha angustifolia* on the recruitment of native and exotic woody species. *Aust. Ecol.*

Thompson, K., Hodgson, J.G. & Rich, T.C.G. 1995. Native and alien invasive plants: more of the same? *Ecography* 18: 390-402.

Vitousek, P. 1986. Biological invasions and ecosystem properties: can species make a difference? In: Mooney, H.A. & Drake, J. (eds.) *Biological invasions of North America and Hawaii*, pp. 163-176. Springer, New York, NY, US.

Vitousek, P. & Walker, L.R. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecol. Monogr.* 59: 247-265.

Zak, M.R. & Cabido, M. 2002. Spatial patterns of the Chaco vegetation of central Argentina: integration of remote sensing and phytosociology. *Appl. Veg. Sci.* 5: 213-226.

Zavaleta, E.S., Hobbs, R.J. & Mooney, H.A. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.* 16: 454-459.