The importance of biological inertia
in plant community resistance to invasion

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Abstract. Insights into the ecology of historic invasions by introduced species can be gained by studying long-term patterns of invasions by native species. In this paper, we review literature in palaeo-ecology, forest-stand simulation modelling, and historical studies of plant species invasions to illustrate the relevance of biological inertia in plant communities to invasion ecology. Resistance to invasion occurs in part because of environmental, demographic, and biotic factors influencing the arrival and establishment of invading species. We propose that biological inertia within the resident community is a fourth component of resistance to invasion, because of the lag time inherent in eliminating resident species and perhaps their traces after environmental conditions become suitable for invasion by immigrating species. Whether or not an introduced species invades can be conditioned by the presence of the pre-existing community (and/or its legacy) in addition to the other biotic and abiotic factors.

Keywords: Demographic resistance; Ecological resistance; Non-indigenous species; Palaeo-ecology; Range extension.

Introduction

Invasion ecologists generally agree on a need for a unified framework for understanding the ecology of invasive species (Ewel et al. 1999; Parker et al. 1999; Richardson et al. 2000). Most recent work in invasion ecology has stressed three basic elements of the process of biological invasion, all of which emphasize the adaptive strategy of the colonizing species: (1) arrival; (2) establishment; and (3) spread or integration within natural communities (Moyle & Light 1996). With respect to the effects of the existing ecosystem, Lodge (1993a, b) hypothesized that ecological resistance to invading species consists of three elements: environmental resistance (temperature, water flow, chemistry, structure, and abiotic resources), biotic resistance of the invaded community (prey availability, competition, predation, disease, and parasites), and demographic resistance of the invading species (numbers introduced, ability to increase when rare). Environmental conditions during the invasion process act as a major filter that can preclude a species altogether or induce a significant lag time between arrival and spread of an alien invader (Lodge 1993a, b; Kowarik 1995). Biotic resistance consists of negative impacts by the resident community on the invading organism, usually through predation or competition, and is often said to increase with species richness of the recipient community (Simberloff 1986). Demographic factors consist of propagule pressure to the system from an external source, as produced by the reproductive traits of the invader (Lodge 1993a, b).

Even though the environment may appear suitable for a particular introduced species, its invasion may fail not because of its inherent life history traits or competition from similar resident species, but simply because individuals of the resident community are still present. It may also fail because formerly resident species have left chemical traces in the soil that favour themselves and/or are inimical to the invader. Persistence of the resident community (or its legacy) beyond the time when environmental conditions change to favour introduced species invasions is a kind of "biological inertia" to invasion that is a consequence of the life-history characteristics and biology of the resident species rather than a property of the invading species. We propose that biological inertia constitutes a fourth component of ecological resistance to biological invaders that can contribute to lag times for invasion into plant communities, especially forests, by introduced species.

In this paper, we suggest that insights into the ecology of plant invasions can be gained by studying long-term invasion patterns and considering some features of historical invasions. The field of invasion ecology has largely disassociated itself from the field of succession ecology (Davis, M.A. et al. 2001); neither, with few exceptions (e.g. Rejmánek 1999), has it sought insights from the palaeo-ecological literature (Davis et al. 1998). Invasion biologists have emphasized the expansion into native communities by introduced species rather than studying range extensions of native species,

even though invasive characteristics of some native and some introduced invasive plants are similar (Thompson et al. 1995). Here, however, we will treat historical range extensions of native species in the same context as the introduction of species beyond their natural ranges, and we will use case studies on time scales ranging from tens to thousands of years that may offer insight into current and future species range expansions, including introductions of species to areas not contiguous with their original ranges (cf. Lodge 1993b; Vermeij 1996; Davis et al. 1998).

Origins of the concept

Watt (1947, p. 12) first alluded to biological inertia: "The effect on the structure of a community of drought or other efficient cause may persist long after the cause has ceased to operate. In fact, at any given time, there may be no correspondence between structure and the current meteorological factors. The point is best illustrated by reference to communities with long-lived dominants." The term 'biological inertia' was coined by Gorham (1957) to describe the perpetuation of bog plant species long after the environmental conditions suitable for their persistence had disappeared. He used the example of sedges persisting even after habitat conditions were more suitable for *Sphagnum* colonization. They survived in the moss cushions by keeping their roots in the richer peat or in the flowing groundwater beneath the peat (Du Rietz 1949). In a second example, he observed that the reed *Phragmites* persists in a "dwarfed and sterile state" at the edge of pine bogs in Fennoscandia under nutrient and acidic conditions far too severe for its establishment. Gorham thought this population might be a relic of the time when the bogs were shallow ponds and lakes with richer, less acidic edges.

Pearsall (1959) extended the concept of biological inertia by incorporating the time it would take for colonizing species to take advantage of a change in climate or other environmental conditions. He felt that dense vegetation cover prevented invasion and that invaders could enter only where windfalls created openings in which they could establish. He estimated that 500 to 1000 years would be required for an 'appreciable' change in composition of a climax forest in response to climate change in the absence of human disturbance. Such a long period for community change to occur suggests biological inertia of the existing vegetation to invasion by new species, since individuals of a few species live 1000 years and would continue to occupy space for that time period.

Smith (1965) suggested that community inertia is related to the environmental tolerance thresholds, or critical physiological limits, of species. He felt a habitat change that would not kill existing individual plants but would prevent their regeneration is a likely scenario. For example, if a climate change occurred that was just above the critical physiological threshold for existence of an invading species (the non-native could barely tolerate this climate), and if it affected only marginal microhabitats, then regeneration of the existing vegetation with its high production of propagules would be favoured, slowing the rate at which an invading species can spread. If, on the other hand, the environmental change were great enough to disfavour the persistence and especially establishment of new individuals of the native species, the effects of biological inertia would be limited to the life span of the existing individuals. He concluded that, in the long sweep of postglacial history, the immigration and expansion of a species thus depends not only on its competitive abilities and the efficiency of its dispersal mechanisms, but upon the nature and extent of climate change as it relates to the passage of critical tolerance thresholds for persistence and reproduction of native species as well as introduced ones. Note that Smith's conception of inertia is broader than ours and includes aspects of what we would term biotic and environmental resistance. Nevertheless, that part of his definition focusing on the life span of existing individuals falls within our definition.

An expansion of the concept

Thus, early use of 'inertia' was usually to describe the persistence of individuals after the environmental conditions for their establishment had disappeared. The notion evolved towards the usage of inertia as a community property, but it is in fact a property of certain species. In addition to simply the remaining individuals of long-lived species, there may be other inertial components, materials and effects produced by dead and perhaps decayed individuals of resident species that may retard invasion by introduced species. This addition harks back to the classic facilitation, tolerance and inhibition models of succession (Connell & Slatyer 1977), in which the climax community comprises species that create conditions they can tolerate but other species do not (or at least not as well as the members of the climax community). Succession models have traditionally focused on native species, but we suggest that, in principle, these models are applicable to invasion by introduced species as well, and in particular to inertia. That is, species in some communities can create conditions that render the community temporarily uninvasible, inducing a significant time lag for change in community composition. Some such phenomena would be classi-

fied as aspects of biotic and environmental resistance, but others do not fall readily into either category.

Allelopathy – the inhibitory effect of one plant on another through production of chemicals that leach from leaves or roots into the soil (Rice 1984) – is one such phenomenon. Some studies have cast doubt on the general importance of allelopathy, with alternative mechanisms proposed for some specific claimed cases (Williamson 1990; Wardle et al. 1998). Nevertheless, in some instances the evidence for its importance is strong, and there has been a surge in allelopathy studies (Williamson 1990; Wardle et al. 1998). Paradoxically, allelopathy has occasionally been suggested as a possible reason for the invasion success of introduced plants (e.g. Wardle et al. 1998), and a number of trees recognized as invasive have been shown to produce allelopathic effects – e.g. *Ailanthus altissima* (Mergen 1959), *Sorbus aucuparia* (Kuhn et al. 1943), *Pinus radiata* (Lill et al. 1979). Yet allelopathy has not, to our knowledge, been invoked as a factor that might cause a community to resist invasion. If the allelopathic chemical were actively produced by a living plant, it would fall under the rubric of biotic resistance. However, allelopathic chemicals may remain in the soil well after a plant dies (see, e.g. Rice 1984; Grime 2001) and thus could also contribute to inertia. Dead plants have constituents that either directly or by microbial transformation can inhibit plant growth (Grime 2001). These chemicals are not always viewed as allelopathic, but they can have similar effects. For instance, Cole (1985) observed a deep acidic soil produced by thousands of years of decomposition of fir needles in the Grand Canyon and reasoned that such soil could have slowed the replacement by native species of retreating fir and other species in the Southwest in the late Wisconsin and early Holocene. The same sort of phenomenon could retard invasion by an introduced species.

We propose that biological inertia should be considered as a distinctive component of ecological resistance to biological invasion because it differs from the environmental, biotic, and demographic resistances to invasion described by Lodge (1993a, b). Upon arrival, propagules of potentially invading species encounter environmental resistance because of ambient temperature, moisture, and other physical conditions (Fig. 1). This resistance may cause the invasion to fail completely. Or the species may survive, but a long lag time passes before it becomes well established (Kowarik 1995; Crooks & Soulé 1999), and this lag may result partly from inertia. Once well established, the new species may or may not become common or invasive in the resident community, depending on additional biotic and environmental resistances.

Evidence for biological inertia

Holocene invasions

Palaeo-ecological studies yield long-term data sets appropriate for determining rates of spread and lag times for range extensions of species into pre-existing communities of long-lived organisms such as trees (Watts 1973; Davis 1981, 1987; Huntley & Birks 1983; Cole 1985; Cwynar & MacDonald 1987; Delcourt & Delcourt 1987; Birks 1989; MacDonald & Cwynar 1991; Clark 1998; Davis et al. 1998). Watts (1973) described the postglacial range extension of *Pinus strobus* into a forest dominated by *Picea* and *Pinus banksiana/resinosa* in northern Minnesota based on pollen analysis of annually laminated sediments from Lake of the Clouds. Eastern white pine was represented in the pollen record by consistent but low pollen percentages from ca. 9400 to 7350 yr ago. During that time interval,

Fig. 1. A conceptual model of the process of integration of a biological invader into a local area. The elements of ecological resistance are in boxes going from the top to the bottom of the figure and the phases of establishment are in plain text. The different elements of ecological resistance are listed top-down in order of importance. Biological inertia is second in importance to environmental resistance in the establishment of exotic species. The elements of biological inertia, and biotic and demographic resistances, add to time lag effects. Adapted from Moyle & Light (1996).
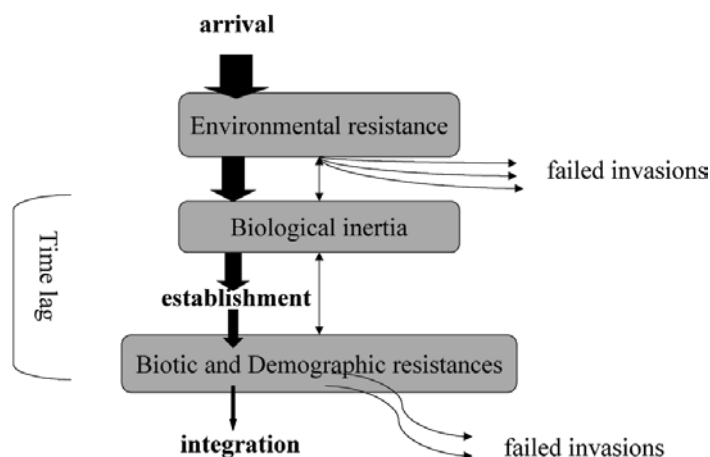
it was spreading northward and westward across the Great Lakes region into Minnesota. Between 7350 and 6400 yr ago, *Pinus strobus* pollen increased to 20% of the pollen assemblage. Watts (1973) interpreted the changes in pollen percentages of *P. strobus* in the Lake of the Clouds as invasion and local population expansion occurring over a time interval of 700 to 1000 yr, a significant time lag between the arrival of *P. strobus* and its incorporation into the forest community. He suggested that disturbances, including fire and windthrows, promoted establishment of seedlings of eastern white pine, by removing long-lived previous occupants. In other words, the disturbances allowed *P. strobus* eventually to overcome the biological inertia of the pre-existing forest community.

Cole (1985) explicitly invoked vegetational inertia to describe a significant time lag observed for species turnover rates in the Grand Canyon after the climate changed from Pleistocene to Holocene conditions, but his definition of inertia only partly matches ours. He found that vascular plant species that dominated in the Pleistocene were eliminated first from marginal habitats, yet they persisted in the most favourable habitats and were replaced slowly during the 1000 to 3000 yr following the initial climate change. He suggested that the slow replacement depended in part on persistent plant communities that created microclimates favourable to their own members (which we would term biotic and environmental resistance). However, an example of biological inertia in the Grand Canyon is greater fir seedling establishment in the shade of mature fir trees and in the deep acidic soil created by thousands of years of decomposition of fir needles. The time lag in change of soil properties might have been responsible for the long persistence of some Pleistocene dominants in the southwestern United States (Cole 1982).

Forest-stand simulation models and lag times for invasion

Forest-stand model simulations of long-term forest dynamics give insights into responses of species, including lags in change of community composition because of biological inertia and because of hysteretic responses. Davis & Botkin (1985) examined the sensitivity of forest vegetation to climate change using the JABOWA model (Botkin et al. 1972) to simulate community response to different magnitudes and durations of temperature cooling. They found that, across the ecotone from northern hardwood to northern conifer forest in New England, climate cooling of 2 °C lasting for several hundred years sufficed to shift dominance from sugar maple to spruce. Maple forest resisted invasion by conifer species because of both the longevity of

maple trees and their influence on seedling establishment as simulated by JABOWA; the first factor is biological inertia. With either a shorter duration or lower magnitude of climate change, effects on community composition were less evident unless the climate change was accompanied by increased levels of ecological disturbance. Davis & Botkin (1985) found both thresholds and lags in response to climate change at the stand level, with the lags exacerbated by inertia.

Shugart et al. (1981) used the FORET stand simulation model to investigate forest dynamics during both climate warming and cooling. For a hypothetical stand composed of *Fagus grandifolia* and *Liriodendron tulipifera*, they performed multiple simulation runs to see how two species with different life-history characteristics would interact in response to a changing climate that slowly and systematically altered relative competitive abilities. The forest was dominated by *Fagus* at cooler temperatures and by *Liriodendron* at higher temperatures. Certain changes in dominance of the species, however, occurred abruptly across temperature thresholds that differed under warming vs. cooling conditions. They attributed this hysteresis to differential lags in response of the two species to climate change. In particular, *Liriodendron* took a long time to replace *Fagus* at warmer temperatures both because of its shade-intolerance that did not permit it to recruit into the understorey of the *Fagus*-dominated forest (biotic and environmental resistance) and because of the long time it takes *Fagus* canopy trees to die (inertia). A quicker transition to *Fagus*-dominated forest under cooling conditions was due to the ability of this species to exist in the subcanopy of *Liriodendron*-dominated forest and quickly recruit into the canopy after the relatively shorter lifespan of *Liriodendron* had ended. Different degrees of inertia of the two species contributed to different lag times in community response to climate change.

Kräuchi (1995) applied FORSUM, a forest successional model that incorporates climate change, to examine vegetation response to climate change at a planted *Picea* site in Switzerland. Without any climate change and a discontinuation of forest management, the forest would be dominated after 300 yr by *Fagus sylvatica* and other tree species. The long time period before significant vegetation changes would occur was attributed to the acidic litter layer that favours *Picea* regeneration and the shading of germinating seedlings by the closed *Picea* canopy. Part of the lag may be attributed to biological inertia: the favourable conditions for spruce regeneration produced by the acidic litter may persist beyond the death of the *Picea* trees themselves.

Biological inertia may be stronger in forests than in grasslands

Most of the field experimental research on biotic resistance has been conducted in open-canopy vegetation, including grasslands (Tilman et al. 1996; Knops et al. 1997; Crawley et al. 1999) and old fields (Palmer & Maurer 1997; Lavorel et al. 1999). Most plants of old fields and grasslands are not as long-lived as those of forests, so one would not have expected at least one prominent component of inertia to be manifested. Certain allelopathic effects, another aspect of inertia, may also not be expected in such systems, because they often have substantial species richness. Wardle et al. (1998) argue that community- and ecosystem-level impacts of allelopathy are far more likely to be found in low-diversity systems such as boreal forests, and that the study most frequently cited as impugning the general importance of allelopathy (Stowe 1979) was conducted in exactly the sort of high-diversity grassland where allelopathy would be expected to be unimportant. Thus, for at least two reasons, one involving direct effects of long-lived individuals and the second related to their indirect effects through modification of soil properties, one might expect biological inertia to be manifested more strongly in forests than in other plant communities.

It is striking that closed forest as a community type is not widely invaded, even by trees generally considered invasive (Simberloff et al. 2002). For example, the pines that have invaded the South African fynbos (Richardson et al. 1994; Richardson & Higgins 1998) are moving into a treeless shrubland. *Pinus contorta* and *Pseudotsuga menziesii* are invasive in New Zealand, but not in closed forest. *P. contorta* invades scrub, tussock grassland, pasture, and open forest (Wardle 1985a, b; Ledgard 2001), while *P. menziesii* is invasive in shrublands, tussock grasslands, and some disturbed native forest (Anon. 1997). It occasionally invades canopy gaps in *Nothofagus* forest but is not viewed as a threat to normal continuous closed forest (Maclaren 1996; Ralston 1997). In Europe, *P. menziesii* has been planted across at least 348000 ha in France, Germany, and Great Britain, but fears that it would become invasive (e.g. Weck 1950) have not been realized. For instance, in Germany it appears in nature only along roads and in oak forests on poor, acidic soil (Knoerzer 1999). In northern Sweden, 565 000 ha of lodgepole pine have been planted (mostly since the 1970s) in areas dominated almost wholly by *Pinus sylvestris* and *Picea abies* (Andersson et al. 1999; Engelmark et al. 2001). Although there has been some dispersal into native forest, most regeneration has been in disturbed areas and there is not yet substantial invasion of closed forest, though there is great concern that such invasion will occur in the future (Andersson et al. 1999; Engelmark et al. 2001). Nilsson & Ericson (1997) noted a general lack of substantial invasion by plants or animals in boreal forest.

On an Argentine island, Simberloff et al. (2002) censused native forest reserves dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis* that surround several abandoned forestry plantations. The plantations include 73 conifer and 62 broad-leaved species (over 100000 individuals of varying ages) planted from 1926-1940. Despite the facts that the introduced trees include many species considered invasive elsewhere and that some thrive in the plantations, only *P. menziesii* and *Juniperus communis* have begun to invade native forest, and even these are found almost exclusively in disturbed areas, and only rarely in natural tree fall gaps. The reasons for the failure of most introduced species to invade the forest reserves here, and for the exceedingly slow rate of invasion by *P. menziesii* and *Juniperus*, have not yet been studied. However, we suggest that because *Nothofagus dombeyi* individuals live to be 600 yr old and *Austrocedrus chilensis* lives to 1000 yr, inertia may play a role. Even if an invasion were underway, it might be decades before this would be evident.

Discussion

We are not claiming that closed forest communities are entirely resistant to the huge suite of non-indigenous species that bombard them today; there are several examples of such invasions (cf. Woods 1993; Nuzzo 1999; Almasi 2000; Webb et al. 2000). However, relative to other plant communities, closed forests seem less afflicted, even on islands (Rejmánek 1996; Simberloff et al. 2002). We are suggesting that inertia may help explain this, as well as the phenomenon of a time lag between establishment and substantial invasion (cf. Kowarik 1995; Crooks & Soulé 1999) may be partially due to inertia.

Many ecological studies are of such short duration that they are unable to detect evidence of biological inertia (cf. Tilman 1988). Extreme environmental changes or dieback of old trees that could break down inertia are less likely to be witnessed in the short time periods characteristic of most ecological studies than are other aspects of plant community resistance to invasion. The extent to which allelochemicals or other chemical traces of past biological communities might aid in conferring inertia is difficult to demonstrate conclusively, as witness the persistent difficulty in producing unequivocal results in experiments on

allelopathy generally (Williamson 1990; Wardle et al. 1998; Grime 2001). Only through long-term ecological studies will the various components of resistance, including climate mismatch, biological interactions, and biological inertia, be documented as important forces in the retarding of biological invasions of resident communities by introduced species.

Natural range extension is a well studied process that can inform our understanding of invasion by non-indigenous species. Biological inertia has been implicated in Palaeo-ecological and simulation studies as a significant factor precluding or retarding establishment of invading plant species. Observed paucity of non-indigenous species in modern, late successional forests is at least consistent with a role for biological inertia, though of course other forms of ecological resistance must play a role. Thus, biological inertia should be considered in future studies of ecological resistance to invasion.

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