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Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies

Peter M. Vitousek

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Biological invasions by exotic species clearly alter the composition and community structure of invaded areas. There is increasing evidence that they can also alter properties of whole ecosystems, including productivity, nutrient cycling, and hydrology. For example, the exotic actinorrhizal nitrogen-fixer *Myrica faya* alters primary successional ecosystems in Hawaii Volcanoes National Park by quadrupling inputs of nitrogen, the nutrient limiting to plant growth. A few other examples of ecosystem-level changes have been documented. Biological invaders change ecosystems by differing from native species in resource acquisition and/or resource use efficiency, by altering the trophic structure of the area invaded, or by altering disturbance frequency and/or intensity. Where exotic species clearly affect ecosystem-level properties, they provide the raw material for integrating the methods and approaches of population and ecosystem ecology.

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Introduction

Much of the recent progress in ecosystem ecology can be traced to studies which have examined the responses of ecosystems to disturbance (Odum 1969). For example, early studies of forest clear-felling (cf. Hesselman 1917, in Stålfelt 1960) demonstrated that soil nutrient availability is usually enhanced in harvested sites. More recently, studies at the Hubbard Brook Experimental Forest (Likens et al. 1970, Bormann and Likens 1979), in Sweden (Tamm et al. 1974, Wiklander 1981), and elsewhere documented that forest cutting alters watershed-level hydrology and nutrient losses; longer-term measurements have documented the reestablishment of biotic regulation of water and nutrient cycling during secondary succession (Bormann and Likens 1979). Studies of a wide range of harvested sites have provided a geographic perspective for patterns in nutrient losses following cutting (Vitousek and Melillo 1979), and detailed experimental studies have evaluated physical and microbial mechanisms controlling variations in loss (Vitousek and Matson 1984, 1985, Matson et al. 1987). The development and testing of theories concerning the regulation of nutrient cycling in forest ecosystems (Vitousek and Reiners 1975, Bormann and Likens 1979, Vitousek and Walker 1987) have been driven in large part by these studies of clearcutting.

Natural disturbances such as fire (Christensen and Muller 1975, Raison 1979) and periodic insect or pathogen outbreaks (Swank et al. 1981, Matson and Boone 1984, Matson and Waring 1984) can affect ecosystems in ways similar to acute anthropogenic disturbance. Viewed on a longer time scale, however, these can also be viewed as cyclic phenomena driven by processes internal to ecosystems (fuel accumulation, nutrient deficiency). Natural disturbance of this sort actually may be integral to the normal functioning of many ecosystems (Holling 1981).

Experimental studies of ecosystem-level responses to disturbance have yielded substantial benefits to applied as well as basic ecology (if indeed the dichotomy has much meaning). For example, studies of lake eutrophication in the Experimental Lakes Area of Ontario are both a convincing analysis of *why* increased phosphorus loading causes eutrophication and a widely comprehensible and politically influential demonstration of how

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the process works (Schindler et al. 1973, Schindler 1989).

Biological invasions by exotic species represent a wholly different kind of disturbance from those described above, but they too could yield both basic and practical results. Population biologists and community ecologists have long used responses to invasion as a means of analyzing population processes (cf. Elton 1958, Moulton and Pimm 1983, Mooney and Drake 1986). If an introduced species can in and of itself alter ecosystem-level processes such as primary or secondary productivity, hydrology, nutrient cycling, soil development, or disturbance frequency, then clearly the properties of individual species can control the functioning of whole ecosystems (Vitousek 1986). Such species then would provide a useful framework for integrating population and physiological processes into ecosystem studies.

Practically, an exotic species which altered ecosystem properties would not merely compete with or consume native species – it would alter the fundamental rules of existence for all organisms in the area. It could have significant social or economic effects if it altered any of the "ecosystem services" (cf. Ehrlich and Mooney 1983) that affect humanity (such as the regulation of water quality). Finally, biological invasions by exotic species may provide a model for evaluating the possible effects of the release of genetically altered organisms (Regal 1986).

Studies of biological invasions are not the only way to examine the ecosystem-level importance of individual species. Many studies have attempted to determine the importance of particular species without actually altering species composition, and a smaller number have experimentally added or removed species and determined ecosystem-level consequences. The latter approach has been very successful with animals; they can often be enclosed or exclosed by the experimenter. However, the same approach is not applicable to abundant perennial plants – for them, removal itself represents a disturbance with ecosystem-level consequences similar to those of clearcutting. On the other hand, studies of ecosystem-level consequences of biological invasions by exotic species can be done with any group of organisms, and the unprecedented mobility of humans and our associated species ensures that there is more than enough material for study.

I will describe an instance in which an exotic plant species clearly alters ecosystem-level characteristics, and then review briefly a number of other invasions which appear to alter ecosystem properties. Finally, I will discuss how the ecosystem-level effects of invading species could be used to provide the raw material for integrated studies of population biology and ecosystem ecology.

Myrica faya in volcanic regions of Hawai'i

Isolated oceanic islands have long been recognized as being unusually susceptible to biological invasion (Wallace 1880, Elton 1958); their biota is highly endemic, usually not very diverse compared with continental areas, disharmonic in species composition (often lacking in major groups such as mammals or ants), and not well adapted to the increased frequency of disturbance which generally accompanies invasion by *Homo sapiens* (Vitousek et al. 1987, Loope and Mueller-Dombois, in press). The Hawaiian Islands are Earth's most isolated archipelago; their native biota are relatively well characterized and quite low in overall species diversity (Carlquist 1980, Mueller-Dombois et al. 1981, Stone and Scott 1985). Biological invasions of Hawai'i are frequent and often highly successful. For example, the native flora consists of about 1100 species – and an additional 4600 exotic plants have been identified there, of which perhaps 800 are invasive and at least 86 represent serious threats to native species or ecosystems (Smith 1985). One species of mammal (a bat) is native; at least 18 more have become established after introduction by humans (Stone 1985).

My colleagues and I have been studying the ecosystem-level consequences of an ongoing biological invasion by *Myrica faya* Ait., an actinorrhizal nitrogen fixer, in a young volcanic region of Hawai'i Volcanoes National Park (HVNP) (Vitousek et al. 1987, Turner and Vitousek 1987). Kilauea Volcano has erupted frequently in historic times, and ^{14}C dating has extended the chronology of lava flows and ash deposits back several thousand years (Lockwood and Lipman 1980, J. P. Lockwood, pers. comm.). Ecosystems developing on recent volcanic substrates in HVNP are relatively low in nitrogen (Vitousek et al. 1983), as is true of primary succession in general (Walker and Syers 1976, Robertson and Vitousek 1981, Vitousek and Walker 1987). Symbiotic nitrogen fixing plants should have a distinct competitive advantage early in primary succession (Walker and Syers 1976, Gorham et al. 1979, Tilman 1982), and indeed they dominate early stages of many primary seres (Stevens and Walker 1970). However, no native symbiotic nitrogen fixers occur early in primary rainforest succession in Hawai'i, despite the occurrence of legumes (particularly *Acacia koa*) later in succession.

Biological invasion by *Myrica faya* adds a symbiotic nitrogen fixer to nitrogen-deficient sites, so it has great potential to alter ecosystem-level properties and processes. *Myrica* was introduced to Hawai'i in the late 1800s, before which the actinorrhizal symbiosis had been absent from the native flora. It was first observed in HVNP in 1961; by 1977 it covered 600 ha despite intensive control efforts (Whiteaker and Gardner 1985). Control was then abandoned, and by 1985 *Myrica* was present in varying densities over 12,200 ha in HVNP and 34,365 ha in the Hawaiian Islands (Whiteaker and Gardner 1985). *Myrica* occurs in sites ranging from

< 15 yr-old volcanic cinder to closed-canopy native rainforest, but its cover is greatest in open-canopied seasonal montane rainforest and in forests thinned but not destroyed by volcanic ashfall. This pattern of dispersal reflects *Myrica's* physiology and mode of seed dispersal (La Rosa et al. 1985, Vitousek et al. 1987). *Myrica* grows very slowly in the shade of a closed forest canopy; it is bird-dispersed, and seed inputs are very highly concentrated under potential perch trees. Consequently, it colonizes most heavily in sites with both perch trees and open canopies.

We predicted that biological invasion by *Myrica faya* would alter primary successional ecosystems in Hawai'i by increasing the amount and biological availability of fixed nitrogen (Vitousek et al. 1987). In order to establish this prediction, three requirements must be met: 1) nitrogen must be limiting to plant and/or microbial activity; 2) nitrogen fixation by *Myrica* must alter ecosystem-level nitrogen budgets substantially; and 3) nitrogen fixed by *Myrica* ultimately must be available to other organisms.

All three requirements are met in open-canopied sites created by volcanic cinder-fall (Vitousek et al. 1987). The first (nitrogen limitation) was determined by fertilizing 26- and 195-yr-old sites with nitrogen, phosphorus, and all other nutrients (including micronutrients but excluding N and P) in factorial combination. Growth of *Metrosideros polymorpha,* the dominant native tree, was doubled by additions of nitrogen; no other nutrient or combination of nutrients had a significant main or interactive effect. Additions of nitrogen (alone) to an open-canopied site yielded an even larger growth increment, while added nitrogen had no effect on growth in an approximately 2000-yr-old site where native nitrogen availability was much greater (Vitousek et al. 1983, 1987). Clearly nitrogen availability does limit primary production in young volcanic sites.

The second requirement (a significant alteration in the system-level nitrogen budget) was evaluated by measuring nitrogen fixation by *Myrica,* fixation by lichens and native non-symbionts, and inputs through rainfall. These measurements were carried out in sites with substantial populations of *Myrica,* in sites with very little *Myrica,* and in one plot where *Myrica* was excluded experimentally. Measurement of fixation by *Myrica* was a 4-step process based on the acetylene reduction assay for nitrogenase (Bergersen 1980). We measured moles of C_2H_2 reduced per mole of $^{15}N_2$ fixed, moles of C_2H_2 reduced per gram of nodule (diurnally and seasonally on three contrasting sites), grams of nodule per individual *Myrica* of several size classes in three sites (Turner and Vitousek 1987), and finally the population and size distribution of *Myrica* in several sites. These calculations yielded an estimated 18 kg ha^{-1} yr^{-1} of nitrogen fixed by *Myrica* in a heavily colonized open-canopied site (Vitousek et al. 1987). Of course, this multiplicative combination of measurements raises the possibility of propagating errors; we are now pursuing alternative estimates based on ^{15}N natural abundance (Shearer and Kohl 1986).

Fixation by *Myrica* is quantitatively more important (in sites where it is abundant) than are other sources of fixed nitrogen. Rainfall added at most 5 kg ha^{-1} yr^{-1} of nitrogen to these sites; native nitrogen fixers (lichens with blue-green algal symbionts like *Stereocaulon volcani, Nostoc* in bryophyte mats, and decomposers of wood and *Metrosideros* leaf litter) added about 0.5 kg ha^{-1} yr^{-1} more (Vitousek et al. 1987). Invasion by *Myrica* can therefore quadruple inputs of fixed nitrogen.

Finally, the availability of *Myrica*-fixed nitrogen was examined by measuring pool sizes of inorganic nitrogen and net nitrogen mineralization in soil under *Myrica,* under *Metrosideros,* and in the open. Soil and forest floor under *Myrica* had significantly higher pool sizes and mineralization of available nitrogen than soil elsewhere; therefore we concluded that biological invasion by *Myrica* alters the availability as well as the quantity of nitrogen in young volcanic sites (Vitousek et al. 1987).

All three requirements were met; consequently biological invasion by *Myrica faya* has been shown to alter ecosystem-level properties of young volcanic sites in HVNP by adding fixed nitrogen. The population-level processes which permit and/or facilitate its invasion, together with the physiological characteristics which cause it to alter nitrogen budgets, therefore have important consequences to local ecosystems. In turn, we should now be able to observe how the altered ecosystem-level properties feed back to affect population and physiological processes of the native biota.

Invasions and ecosystem alterations

How often do biological invasions alter ecosystem-level properties and/or processes? Several recent reviews have addressed this question (Vitousek 1986, Ramakrishnan and Vitousek, in press, MacDonald et al., in press). Much of the available information is anecdotal and unavoidably biased towards successful invasions (cf. Simberloff 1986), in this case those which do alter ecosystems. I believe that the majority of successful invasions do not alter large-scale ecosystem properties and processes in a meaningful way. Nonetheless, some (such as *Myrica faya*) clearly do, and a tentative classification of the ways in which biological invaders can alter ecosystems may be useful. I suggest invaders can change ecosystems where they 1) differ substantially from natives in resource acquisition or utilization; 2) alter the trophic structure of the invaded area; or 3) alter disturbance frequency and/or intensity.

Resource acquisition and utilization

Myrica faya fits into the first category – by fixing atmospheric nitrogen, it expands the resource base for the entire ecosystem, with consequences that could go well beyond its own growth. Another clear example is provided by invasions of salt-cedar (*Tamarix* spp.) in riparian areas of the semi-arid southwestern United States. *Tamarix* is a phreatophyte (rooted into ground water) which does not actively regulate its transpiration; as a consequence it can desiccate watercourses and marshes (Neill 1983). Deeply rooted invading plants can also alter the resource base of an ecosystem by bringing nutrients to the surface where they may be available to a range of organisms (Hodgkin 1984).

Not all changes in resource base increase productivity; in California and Australia, the exotic ice-plant *(Mesembryanthemum crystallinum)* accumulates salt from throughout the rooting zone and thereby reduces soil fertility (Vivrette and Muller 1977, Kloot 1983). It may also increase soil erosion (Halvorson, in press). Plants which produce low-quality acid litter also could reduce overall soil nutrient availability (Pastor et al. 1984). This effect has been documented clearly in tree plantations (cf. Nihlgård 1972, Perala and Alban 1982); whether it occurs as a consequence of natural invasions remains to be documented, but the invasion and rapid growth of *Pinus radiata* in areas of Australian *Eucalyptus* woodland (Chilvers and Burdon 1983) could cause such changes.

Invading species which differ from natives in their efficiency of resource utilization also could alter ecosystem-level processes effectively. One way in which one plant species could be more efficient than another is through differences in life-form; for example, perennials maintain internal storage pools of energy and nutrients which they can utilize in subsequent growing seasons, while annuals have only seed storage and current photosynthesis and nutrient uptake. Adding a perennial to a system dominated by annuals could therefore alter ecosystem properties. The invasion of floating aquatic plants into open-water habitats represents an analogous change. For example, the water-fern *Salvinia molesta* has altered productivity and water chemistry substantially in Africa, India, and Papua New Guinea (Mitchell et al. 1980, Thomas 1981). Invaders which differ from natives in photosynthetic pathway (C_3, C_4, CAM) could also change ecosystems (Ramakrishnan and Vitousek, in press), although I am not aware that any such changes have been documented unequivocally as being due to differing photosynthetic pathways.

Trophic structure

Experimental studies and examinations of biological invasions have demonstrated that manipulating the uppermost level of a trophic pyramid can have ecosystem-level consequences disproportionate to the amounts of energy and/or nutrients involved (Paine 1966, Dayton et al. 1984). This effect may be responsible in part for the observation that it is easier to document ecosystem-level consequences of biological invasions by animals than plants (Vitousek 1986). Animal invasions are particularly disruptive on oceanic islands; these often lacked *any* large generalist herbivore before human settlement. Additions of pigs, goats, and cattle have altered islands dramatically; consequent changes in soil erosion, nutrient cycling, and subsequent invasibility have been identified (Stone 1985, Stone et al., in press, Merlin and Juvik, in press).

The effects of animal invaders on oceanic islands may be so severe because islands often have only two trophic levels, producers and decomposers (excluding specialist herbivores and their carnivores). Adding large generalist herbivores without their predators therefore can depress producer populations and/or standing crop. Subsequent addition of a predator (in Hawai'i, human hunters) often results in greater plant cover (including that of natives) in accessible areas (Jacobi and Scott 1985, Stone et al., in press).

Alterations in trophic structure per se are not the only reason for severe ecosystem-level consequences of animal invasions on oceanic islands. The flora of such islands is often lacking in chemical and mechanical defenses against herbivores (Carlquist 1980); animal invasion can therefore cause more damage than might occur simply by adding another trophic level to a continental area. Invasions by animals can be extremely disruptive in continental regions; European wild boars in the Great Smoky Mountains of the south-eastern United States provide one clear example (Bratton 1975, Singer et al. 1984). In this case, however, the ecosystem-level effect is probably due to physical disturbance (see below), and the invasion may be facilitated by human removal of carnivores (wolves, puma) in the region.

Disturbance frequency and intensity

Biological invaders which alter the disturbance regime of an invaded area can have significant ecosystem-level consequences; natural disturbance regulates both population and ecosystem-level properties in many, perhaps most, ecosystems (Matson and Waring 1984, Pickett and White 1985, Vitousek and Denslow 1986). Invading animals may change ecosystems because they *are* agents of disturbance (in the sense of destruction of biomass – Grime 1979); this effect may be particularly marked on oceanic islands where native plants are poorly protected against grazing. Moreover, the feeding habit of certain animals is particularly destructive – the rooting activity of pigs is most likely responsible for their very striking effects on soils and nutrient cycling (Singer et al. 1984, Vitousek 1986).

Biological invasions also alter ecosystems through their influence on fire regimes. Exotic grasses have invaded semi-arid shrublands and woodlands in many areas; they often produce considerably more aboveground litter than native species. This litter can increase the probability, extent, and severity of fires (Parsons 1972, Smith 1985, Christensen and Burrows 1986, Mack

1986). Moreover, many of these grasses are adapted to rapid seeding or sprouting after fire, while native plants often are not; relative dominance by exotic grasses and the probability of subsequent fires consequently increases after each fire.

This classification of ecosystem-level effects of invading species is tentative, and there may well be examples of ecosystem alteration that are not encompassed within it. Further research on the ways in which invaders can alter ecosystems and the frequency with which they do so would be most useful.

Integrating population and ecosystem ecology

A few biological invaders can be clearly shown to have altered ecosystem-level properties and processes through their own activities. The number of examples is relatively small, but serious attempts to evaluate such effects have been few. Moreover, the lack of detailed background information in most sites and the coarseness of most ecosystem-level measurements make it difficult or impossible to detect small or subtle effects of biological invaders; only major changes can be identified clearly. The fact that there *are* examples in which plant and animal invasions do alter ecosystems is unambiguous evidence that some individual species affect the properties of some ecosystems.

It is perhaps better established that the properties of ecosystems affect population-level processes, including the invasibility of particular communities (Orians 1986). In the case of *Myrica faya* in Hawai'i Volcanoes National Park, nitrogen-limited open-canopied forests represent the primary habitat for colonization. The presence of trees provides perches and perhaps an alternative food source for birds, while substantial light penetration to the soil surface permits rapid growth of *Myrica*. These conditions are realized in seasonal montane forest ecosystems and volcanic-ash damaged rainforest (Vitousek et al. 1987).

More generally, biological invasions by plants are often concentrated in human-disturbed sites (cf. Allan 1936, Egler 1942, Elton 1958), and it appears that many invaders are more successful on more fertile soils (Gerrish and Mueller-Dombois 1980, Bridgewater and Backshall 1981). Invasions of all kinds are more often successful on oceanic islands then continents (Elton 1958), and this is true of invasion into parks and preserves as well as disturbed areas (Loope and Mueller-Dombois, in press).

A demonstration that individual species affect ecosystem-level properties and that ecosystem properties in turn affect species populations does not in and of itself integrate population biology and ecosystem ecology – but it does provide raw material for such an integration. Where individual species invade and alter ecosystems, population-level processes *become* ecosystem-level processes – and where ecosystem properties are changed by invasions, the basic rules of existence for all organisms also change. Native species could be equally important in controlling ecosystems, but their effects are often more difficult to demonstrate. The value in studying invading exotic species is that changes in ecosystems can be observed directly and manipulated experimentally.

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