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Non-Indigenous Species and Ecological Explanation

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Abstract. Within the last 20 years, the US has mounted a massive campaign against invasions by non-indigenous species (NIS) such as zebra mussels, kudzu, water hyacinths, and brown tree snakes. NIS have disrupted native ecosystems and caused hundreds of billions of dollars of annual damage. Many in the scientific community say the problem of NIS is primarily political and economic: getting governments to regulate powerful vested interests that introduce species through such vehicles as ships' ballast water. This paper argues that, although politics and economics play a role, the problem is primarily one of scientific method. Even if commercial interests were willing to spend the necessary funds to control NIS, and even if government were willing to regulate them, ecological theory is not adequate to provide clear direction for either effort. The paper argues there is no comprehensive, predictive "theory of invasibility," as part of a larger theory of community structure, that might guide ecological decision making regarding NIS, and for at least three reasons. (1) There is no firm definition of "NIS," "native," "exotic," and so on, and ecologists do not use the terms consistently; as a result, biologists debating various accounts of community structure and ecological explanation often do not even make logical contact with each other. (2) The dominant theory used to understand invasibility, island biogeography, has no precise predictive power and is unable to clarify when NIS might promote biodiversity and when they might hinder it. (3) There are no firm, empirical generalizations that reveal when a colonizer or a NIS might be likely to take over a new environment, and when it might not succeed in doing so. As a result, scientists have only rough "rules of thumb" to shore up their arguments against NIS. Given the incompleteness of current ecological theory, the paper closes with several suggestions for ways that study of NIS might enhance understanding of basic community structures and vice versa.

Key words: biodiversity, colonize, exotic, explanation, invasion, island biogeography, method, native, non-indigenous, species

Introduction: Damage from Non-Indigenous Species (NIS)

When people see the play, *Little Shop of Horrors*, most of them probably view it as a theatrical version of science fiction. After all, they likely have never seen any fast-growing vines that threaten human life in the monstrous

way the comedy portrays. But perhaps the truth about biological invasions is more surprising than the fiction showcased in this play. For example, when the thirsty, fast-growing melaleuca tree (*Melaleuca quinquenervia*) was imported from Australia to drink up the swamps of south Florida, nurserymen of the 1930s could not grow enough to satisfy demand. Foresters seeded the Everglades with melaleuca dumped from airplanes. Less than a century later, however, this NIS has invaded more than 600,000 hectares of Florida wetland, and it threatens to destroy the Everglades. Its impenetrable stands displace virtually all other vegetation, and its dense root mat oozes substances poisonous to other plants. Its airborne secretions are poisonous to humans and cause severe respiratory and skin irritation. Conservationists have tried to burn it out, but it is fire-adapted and spreads by burning. Its inner bark is a wet, insulating sponge, while its outer bark is dry, and its leaves are laced with a flammable oil. Although it sucks up water four times as fast as the native sawgrass, it burns with explosive force. Several days after a devastating fire, the tree sprouts new growth and rains millions of seeds onto burnt land. They germinate in only three days, and seedlings may reach six feet in their first year (Bright 1995: 10–11; see Renaud 1996).

Plants are not the only NIS presenting problems. Rats are the most important introduced predators of island birds, and more than 80 percent of the world's major islands now have introduced rat populations and consequent bird extinctions and increased human disease. In fact, NIS have been responsible for some of the most serious health threats to humans. During the 16th century alone, 10 million native Americans, two-thirds of the hemisphere's population, died from Old World diseases introduced by the colonists (Bright 1995: 11–15).

Of the 24 animals on the US endangered species list that had become extinct by 1994, 10 were driven to extinction, at least in part, by NIS. Of the 1,880 species now listed as imperiled by the national Heritage Network, 49 percent are threatened in part because of NIS. One NIS, the zebra mussel, clogs water intake and distribution pipes. It is expected within 50 years to cause the extinction of about 90 different species of freshwater mussels in the Mississippi Basin alone (Simberloff and Strong 2000: B20). And within 10 years after zebra mussels were introduced into Lake St. Clair, the native unionids declined in abundance by 98 percent (Perry et al. 1997: 120).

Ecological data also show that in the rift lakes of East Africa, introduction of the Nile perch and tilapia have contributed to the extinction of native fishes (Lodge et al. 1998: 53). The invasion of the sea lamprey and the alewife into the Great Lakes contributed to the extinction of two native whitefish populations and caused the extinction of the native lake trout (Lodge 1993b: 378). And the introduction of mysid shrimp into Flathead Lake, Montana,

reduced zooplankton and caused a consequent decline in the salmon, the bear, and the eagle population (Lodge 1993a: 134). The introduction of the rusty crayfish northward into the Great Lakes and into Ontario has caused losses in the resident crayfish, snail, and other invertebrate populations (Lodge et al. 1998). San Francisco Bay now has 234 documented introduced species, some of which have wrought serious effects on the bay. The Asian clam, for example, not only takes food from other parts of the bay food web, but it poisons the food of other biota, birds and fish, since it concentrates selenium in its tissues. And the brown tree snake, introduced into Guam from New Guinea, has proved a threat to both humans and animals. It has wiped out 17 species of Guam's vertebrates and 9 of its 18 native bird species. Because the 3-meter snake climbs utility poles, it causes 100 to 200 power outages a year on the island; entering homes, the mildly venomous snake bites children as they sleep (McDonald 1999: A16; Bright 1995: 14–16). Perhaps *Little Shop of Horrors* should have showcased brown tree snakes instead of fast-growing vines.

Response to NIS threats

Cornell University researchers estimated that NIS – like the zebra mussel in the Great Lakes, hydrilla in Florida, and feral pigs in California and Hawaii – annually cost the nation more than \$122 billion annually in environmental damage. Yet according to Interior Secretary Bruce Babbitt, not one marine introduced species, after it has taken hold, has ever been eliminated or effectively contained. E.O. Wilson says such introduced species is one of the most serious threats to biodiversity (McDonald 1999: A15).

In response to the threat from introduced species, biologists are issuing dire warnings. E.O. Wilson speaks of introduced species as “the stealth destroyers of the American environment” (McDonald 1999: A15). Another ecologist worries that invasive species “are likely to rise progressively to the most widespread and dominant proportion of terrestrial biota” (Di Castri 1991: 448). Many other biologists speak of exotic species, introduced by humans, as “biological pollution” (McKnight 1993).

US officials have said they would act to stop the import of potentially damaging species. In 1999, US President Clinton signed an Executive Order that establishes an “invasive species Council” and provides \$29 million per year, in new funds, to help federal agencies coordinate efforts to prevent introduction of new species into the US (McDonald 1999: A15). Conservation groups are urging the US to adopt a variety of regulations, such as requiring permits of ships that discharge their ballast water (containing exotic organisms) at port, and in January 2000, California began requiring all ships

entering the ports of Los Angeles, Long Beach, and Oakland to perform a mid-ocean ballast-water exchange (Zera 2000: 15–16).

The basic mind-set of many of those attempting to cope with NIS is that they represent a political and economic problem, not one of scientific method. As M. B. Usher (1989: 484) put it: “invasive vertebrate species control or eradication has usually proved possible. Scientists have developed the methods; what is needed is the political will to use them.” People need to be willing to use economic resources to solve the NIS problem, says another author (Zera 2000: 18). And additional regulations are the key to this political-economic impasse, says yet another biologist Kaiser (1997: 915).

Ecological underpinnings for action regarding Non-Indigenous Species (NIS)

But are the difficulties with NIS ones that political and economic solutions are sufficient to address? Many scientists appear to believe so, if the claims in the previous paragraph are representative, and they tend to assume that ecological methods are ready for the task of NIS remediation. To address the variety of problems wrought by NIS, ecologists tend to assume that they can appeal to the structure of ecological communities in order to determine what species are normal or native parts of such communities and their included food webs. As one ecologist, writing on “biotic invasives,” put it, although “normal ecosystems are, of course, no longer regarded as strictly fixed categories . . . there is a reality to community structure and there is a dynamic stability that pervades the forms of vegetation in North America and in the world . . . There is a highly significant underlying element of organization and constancy, and this has existed with overall and local changes here and there, and now and then, over hundreds of thousands of millions of years” (Wagner 1993: 2). The challenge, according to this point of view, is to use economic and political resources to help contemporary ecosystems, afflicted with NIS, to return to their “underlying element of organization and constancy.”

Even though the damage wrought by many introduced or non-indigenous species is severe, this paper argues that it is questionable whether human understanding of the structure of ecological communities is adequate to provide guidelines for action regarding NIS. It offers some epistemological and conceptual reasons for arguing that there is no comprehensive, predictive “theory of invasibility,” as part of a larger theory of community structure, that might guide ecological decisionmaking regarding NIS, and for at least three reasons. (1) There is no firm definition of “NIS,” “native,” “exotic,” and so on, and biologists do not use the terms consistently; as a result, biologists debating various accounts of community structure and ecological explanation

often do not even make logical contact with each other. (2) The dominant theory governing invasibility, island biogeography, has no predictive power and is unable to clarify when NIS might promote biodiversity and when they might hinder it. (3) There are no firm, empirical generalizations that reveal when a colonizer or a NIS might be likely to take over a new environment, and when it might not succeed in doing so. Let us consider these points in order.

Lack of conceptual clarity

The most obvious scientific or methodological problem facing the attempt to devise a policy regarding NIS is the absence of clear definitions of various NIS-related terms. On the one hand, insofar as there is a sort of consensus about such terms, this consensus appears to rely on a definition that is both arbitrary and stipulative. On the other hand, insofar as there is no consensus, some definitions appear less arbitrary and less stipulative, but there is no consensus about them.

With respect to the first horn of the dilemma (there is consensus on the definition), one might refer to the classic study by Webb (1985), who examined the way the term ‘native’ was defined in the context of ecology in the UK and Ireland and proposed a consensus definition for the term. He concluded that a native species was one that arrived either before neolithic times, or after neolithic times but without human agency. (Neolithic times ended between 5,000 and 10,000 years ago.) If this is in fact the consensus definition of “native” or “indigenous” species, then it is stipulative and therefore arbitrary in at least four senses. *First*, although the definition refers to biota present before neolithic times, there is evidence that biologists do not classify as native biota that were wiped out by the ice age, even if they were present before the ice age. Hence a species, like *Rhododendron ponticum*, is now classed as an alien weed in the UK, even though it likely was present before neolithic times and was wiped out in the last ice age (Kendle and Rose 2000: 20). *Second*, the consensus definition cited by Webb appears arbitrary in the sense that the neolithic age need not be the cut-off point for what is native or not. Why could not the cut-off be paleolithic times, for example? Or the period at which humans appeared in a particular region? Or some other period? After all, virtually all of the old-field plant species in central and eastern America are European in origin, and yet they would not be classed as “native” even though they are some of the most successful on the continent. The difficulty of choosing any particular time-period, in terms of which to specify what is native, is illustrated by the Roman proverb: “*Tandem aliquando invasores fiunt vernaculi*”: “In time invaders become the natives.”

In other words, Webb's consensus definition of "native" appears arbitrary in that it presupposes a particular time scale, according to which something is native. *Third*, the consensus definition appears arbitrary in that it defines something as native if it arrived without human agency. However, various seeds, for example, could just as well have arrived in a new region in the hair of a human as in the hair of an animal. And if so, then the "human agency" distinction is arbitrary insofar as the same invasive colonization could have occurred either with or without human agency. For example, take the case of the sycamore tree, *Acer pseudoplatanus*. There is evidence that this species from continental Europe was coming closer to the UK by responding to environmental change. But suppose someone stepped in, just as it was about to cross the English Channel, brought it to the UK after the Pleistocene, and thus preempted its chance to be an English native (Kendle and Rose 2000: 21). One could hardly say that this label of 'native' was nonarbitrary in such a case. *Fourth*, the consensus definition of "native" is arbitrary in the sense that it commits biologists to supporting a particular list of biota that reflects a particular environmental and climatic state that has not continued, and cannot continue, forever. The rigid boundaries of so-called native flora are something for which there is no long-term rationale. In other words, the evolutionary foundations of ecological theory undercut any consensus definition of 'native' and, if so, there is no hope of Webb's consensus definition of 'native' being non arbitrary and epistemologically defensible. Thus, the first horn of the dilemma presents obstacles for any resolution of the first problem besetting invasion theory, namely, the problem of conceptual clarity.

With respect to the second horn of the dilemma (there is no consensus on the definition), problems are just as serious. One difficulty is that even articles in reputable journals by top researchers rarely define what they mean by 'native' or 'exotic' species, or else they define the terms in arbitrary ways, or they define them in unclear ways, so that it is difficult to understand the degree to which their claims make logical contact with those of other authors. Consider one recent article in the journal *Science*. The authors, all noted ecologists, spoke of "biotic introductions" to discuss NIS. Yet when they defined "biotic introductions," they simply said "successful establishment of exotic species," and they did not define what they meant by "exotic" (Sala et al. 2000: 1771). Thus their definition fails in at least three respects. First, it is circular in defining biotic introductions in terms of exotic species. Second, it does not define "exotic species." Third, it failed to specify either a temporal, spatial, or theoretical rationale for how to circumscribe what might be "introduced," and it failed to specify whether it counted both human and outside-human-agency introductions as introductions. Noted ecologist David Lodge, a member of the National Invasive Species Council, does a better job

of definition than the *Science* authors, but even his account is epistemologically flawed. In one of his articles Lodge (1993b: 368) says that he uses “the term ‘colonist’ to describe a species that has arrived (with or without human assistance) at a site outside its previous range. ‘Invader’ means an established colonist.” This definition, while an improvement on the previous one, does not specify the relevant spatial “range.” Nor does it specify the relevant temporal scale of “outside its previous range.” Hence, it is impossible to know, precisely, the colonists to which Lodge is referring.

A second difficulty with respect to the second horn of the dilemma is that the absence of consensus points to the impossibility of alternative scientific theories of invasion ever agreeing, much less even making logical contact with each other, because the basic terms, the state variables, they employ are not consistent. Authors use different terms, inconsistent terms, to refer to some of the same species in the same situations. For example, various authors refer to colonizing species as ‘alien’ (Crawley et al. 1996), as ‘exotic’ (Green 1997), as ‘invasive’ (Daehler 1998), as ‘imported’ (Williamson and Fiter 1996), as ‘weedy’ (Fox 1990), as ‘introduced’ (Lonsdale 1994), as ‘non-native’ (Davis et al. 2000), as ‘immigrant’ (Bazzaz 1986), as ‘colonizer’ (Williamson 1996), or as ‘naturalized’ (Hussey et al. 1992). Yet in most cases, as suggested by the earlier discussion of Sala et al. (2000) and Lodge (1993b), the authors do not precisely define the terms at all. If they are defined, they are not defined consistently. As a result, there is no common vocabulary in terms of which to affirm or deny particular claims about invasions or exotic species.

The absence of a common and consistent vocabulary is a problem, As Davis and Thompson (2000: 227–228) point out, because the various terms, used to stand for colonizers, really have a number of disparate characteristics. Using the Davis and Thompson insight, one might divide species into those that have a short (S) or long (L) dispersal distance, are novel (N) or common (C) to the region being colonized, and have a minimal (M) or great (G) impact on the new environment. These eight ways to be a colonizer might be typed as SNM, SNG, SCM, SCG, LNM, LNG, LCM, or LCG. On this scheme, only the SNG type and the LNG colonizers really present a problem, in terms of being dangerous invasives. Hence, one possibility for increasing the conceptual clarity and consistency of studies in invasion ecology would be to use something like this classification scheme, so that the same properties are not attributed to all colonizers, even allegedly non-native colonizers. If one meant species with characteristic SNG, then one should say this or name this in a particular way, so that one did not simply use the term “NIS” and then leave the reader to wonder whether one meant LNG or LNM or some other species set. In this way, ecologists might avoid some of

the problems that have plagued similar terms (such as 'natural') in ecology (see Shrader-Frechette and McCoy 1993: 8, 102–104). Until something like a new conceptual scheme is employed, the ecologists seem to face one or both horns of the dilemma regarding defining terms like "native" or "exotic." And if they face these definitional difficulties, it is not clear how they can develop either the requisite scientific theory, or the later policy, to deal with problems of NIS, in part because, even if there were consensus definitions of 'native' and 'exotic', the problem of time frames might still remain, and ecologists might still be confronted with the horns of a dilemma.

Island biogeography as an inadequate guide to promoting biodiversity

These difficulties with defining terms such as 'native' or 'exotic' are, of course, nothing new for ecology. Ecological theory, in general, has been on rocky ground because of using definitions that often are alleged to be tautological or trivial (see Peters 1991). Ecological theory, in particular with respect to definitions of "community" and "equilibrium" or "stability" (see Shrader-Frechette and McCoy 1993), has been in trouble because of inconsistent uses for key terms and imprecision in the definition of these key terms. Because of these general difficulties with general theory in community ecology, there are also problems with invasion theory.

Even if one could employ consistent and conceptually clear terms for NIS, there would still be a problem with invasion theory, owing to the difficulties associated with using the theory of island biogeography for understanding, and therefore promoting, biodiversity. Although there is no need to explain in detail the problems with island biogeography because it has already been accomplished elsewhere (see Shrader-Frechette and McCoy 1993: 68 ff.), it might be useful merely to review these difficulties in order to see how they impact invasion theory.

Developed by MacArthur and Wilson (1967) to explain how the number of species on an island could remain fairly constant while the taxonomic composition changed, island biogeography supported the observation, among others, that some species on an island were going extinct while other were colonizing it. According to the theory, colonization would occur at a rate dependent largely on the distance between the island and a source pool of colonists, and extinction was more likely on a smaller island because of the larger pool of species it was able to support.

To understand the epistemological and methodological difficulties with the theory of island biogeography, it is important to point out the prerequisites for testing the theory. To test the theory of island biogeography one would have to be able to determine (a) a constant number of taxa, (b) a change in

taxonomic composition, (c) a colonization rate related to the distance between the source pool of colonists and the island, and (d) an extinction rate related to the size of the island. Because (a) through (d) are difficult to determine, the theory has been tested only in a handful of cases. Even so, most alleged tests have relied on various “short cuts,” such as using artificial substrates to represent the islands, using non-empty islands to track colonization, using the questionable species-area relationship (rather than actual observation to determine species numbers), or assuming that undetected colonizations (because of the periodic nature of the sampling) were consistent with the theory of island biogeography (see Simberloff and Wilson 1969; Simberloff 1976).

Because of the largely hypothetical character of the theory of island biogeography, owing in part to the use of short-cut methods to validate it, it enjoys a descriptive consensus among ecologists, in the sense that they use it more than any other theory, but not a normative justification, in the sense that they believe it is as well supported as it ought to be. As a result, the theory is not able to provide much information about the factors that are able to predict greater or lesser species numbers, as a result of invasion by NIS, and hence it offers very little foundation for ecologists’ advice regarding NIS and their effects. Despite its heuristic value in modelling species invasions (see DiCastrì 1991), island biogeography is not able to provide the precise predictive power that policymakers typically need if they are to advise officials on how to deal with NIS.

The absence of empirical generalizations to guide NIS responses

Despite the ambiguous NIS concepts and the absence of a predictive theory of island biogeography to undergird invasion theory, the ecology for understanding NIS does receive some theoretical help from a number of rough rules of thumb. These include, for example,

- (A) IS tend to grow better or are hardier than NIS, as evidenced by the facts that they are established in a region and that they have coevolved with other species in the region (see, for example, Williamson and Fitter 1996; Williamson 1996).
- (B) NIS are likely to become invasive and outcompete natives, as evidenced by the degree to which NIS are implicated as a major cause of extinctions (see Lonsdate 1994; Renaud 1996).

Yet if one examines these rules of thumb, (A) and (B), the problems with predictive power, and lack of classification of various types of NIS, become apparent. According to (A), NISs are supposedly less well adapted to the environment into which they are introduced, yet according to (B), they are

also expected to grow better and to become invasive weeds. Hence, although ecologists subscribe to both rules of thumb, (A) and (B), their predictive uselessness is evident from the incoherence just mentioned. IS obviously cannot be both hardier than NIS yet also victims of competition from NIS. So long as invasion theory is neither coherent nor predictive, and so long as it relies on merely rules of thumb, like (A) and (B), it will not be robust enough, in particular cases, to be very useful in the political and economic battles over NIS.

Or consider the generalization (C) “the longer a plant has been established within a region’s flora, the greater the number of associated species that have adapted to feed on it” (Kendle and Rose 2000: 24–25). Given (C), it is less likely that an established species will become an invasive. And if so, then NIS are more likely than established species to become invasives. Hence, to promote biodiversity and the welfare of associated species, it makes sense to limit NIS. But even (C) is only a rule of thumb, a rough rule that fails to hold in a number of cases, such as when a NIS provides food at a time that native plants do not. *Buddleja davidii*, for example, supports large butterfly populations, even though it is an invader of natural habitats. Or a NIS may support invertebrates feeding on it, better even than natives do, because the NIS may not have some of the defenses against feeders that some coadapted native plants have (Kendle and Rose 2000: 25). Generalization (C) also may fail in the cases in which climate effects, for example, have caused a native species to go extinct and a NIS species can offer some food resources to other biota. In an imperfect world, where species go extinct and environments change, it may even be necessary to restore some genetic stock or to prevent inbreeding depression, with a NIS, rather than have the genetic stock disappear altogether. In this case, although (C) may be a rule of thumb, it is not a rule of thumb whose implementation, in all situations, is likely to promote biodiversity.

Invasion theory is full of rules of thumb that do not have precise predictive power, rules such as (A), (B), and (C), or rules such as, “all things being equal, NIS will be successful colonizers if they have high dispersal rates, or large native ranges, or a broad diet.” Because these rules of thumb do not have precise predictive power, it is impossible to use them to guide reliable public policy. Moreover, the apparent incoherence in (A) and (B) apparently arises because they are too general. Very different predicates (those in (A) and (B)) are affirmed or denied, generally, of NIS and IS. In general, IS tend to grow better than NIS, for example, and in general, NIS are likely to outcompete natives. These two claims, as just formulated, lead to consequences that are not consistent with each other, as already argued earlier in section 6. However, the two claims immediately become consistent if one understands the term

“NIS” in (A) as referring, for example, to species having characteristics SNM, for example, as discussed earlier in section 4, while one understands the term “NIS” in (B) as referring, for example, to species having characteristics LNG, for example, as also discussed earlier in section 4.

In other words, one of the problems with rules of thumb is that they are rough, and they thus refer to the whole group of NIS when they need to refer to particular subsets of NIS having specific characteristics, like those discussed earlier in section 4. Thus, the rules of thumb (A) and (B) run into difficulties, in part, because they fall victim to a fallacy of composition: assuming that what can be predicated of the parts or subsets of NIS can be predicated of the whole group of NIS. The solution to the prediction problem, therefore, is not only the conceptual clarification suggested earlier in section 4 but also the use of natural history and case studies in order to discover empirical generalizations about various types of NIS.

Practical and precise knowledge of particular taxa, coupled with low-level theories – rather than general ecological theory (like island biogeography) – may be the keys to the ecological insights necessary to provide predictive power for solving problems of species invasions. This practical and precise knowledge of natural history, coupled with conceptual and methodological analysis, is a critical departure from the general mathematical models and the untestable principles of past ecological theorizing. This natural-history knowledge, joined to very low-level theories and to conceptual analysis in the method of case studies, is also more capable of being used in practical applications of ecology than is the formulation of null models. While an excellent, classical ideal for ecological method, null models fail to address the uniqueness, particularity, and historicity of many ecological phenomena. Hence, in addition to a top-down account of ecological explanation, we also need to emphasize a bottom-up approach, like that employed in the method of case studies (Shrader-Frechette and McCoy 1993, 1994).

Conclusion: Strategies for NIS

As with earlier ecological examples of using island biogeography to design nature reserves or to promote ecological stability, similar problems beset using invasion theory to guide policy regarding NIS. In both cases, the public-policy needs facing community ecology outreach its grasp. In both cases, the development of ecological theory exceeds its epistemological reliability, its factual confirmation (see Shrader-Frechette and McCoy 1993). And if so, the case of NIS suggests the need for a bottom-up approach to ecology, for detailed natural history information, and for a return to the precise and clear empirical generalizations that characterized both the beginning of the

discipline of ecology and the ways in which it can be most useful to public policy.

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