Eight Ways to be a Colonizer; Two Ways to be an Invader: A Proposed Nomenclature Scheme for Invasion Ecology

In 1981, Deborah Rabinowitz wrote an article entitled "Seven forms of rarity," in which she presented a simple classification scheme of species rarity based on three dichotomous criteria—species range (large or small); habitat specificity (wide or narrow); and local population size (large or small). The paper, still regularly cited in textbooks and research articles, has become a minor classic, and Rabinowitz clearly succeeded in accomplishing her stated goal, which was to "contribute some clarity" to the investigation of rarity and encourage "new perspectives for people engaged in more practical concerns."

We believe that the investigation of biological invasions could benefit from a similar contribution of clarity and new perspectives. Recent evaluations of the field of invasion ecology (Williamson 1996, 1999,

Lonsdale 1999) have concluded that little progress has been made in the more than 40 years since Charles S. Elton (1958) initiated the modern discipline of invasion ecology with his book, *The Ecology of Invasions by Animals and Plants*. We believe that inconsistent and imprecise use of invasion terminology is one factor that is contributing to the ongoing difficulties of the field. Thus, in a clear, unabashed imitation of Rabinowitz' efforts, we propose a similar classification scheme for invasion nomenclature in an attempt to provide some clarity to the field of invasion ecology and to promote new perspectives.

Depending on the author, a species in the invasion literature might be referred to as *alien* (Crawley et al. 1996), *exotic* (Green 1997), *invasive* (Daehler 1998), *nonindigenous* (Pimentel et al. 2000), *imported* (Williamson and Fitter 1996), *weedy* (Fox 1990), *introduced* (Lonsdale 1994), *non-native* (Davis et al. 2000), *immigrant* (Bazzaz 1986), *colonizer* (Williamson 1996), *native* (Meyer and Florence 1996), *naturalized* (Hussey et al. 1992), *endemic* (Williamson 1996), or *indigenous* (Sauer 1988). In many cases, these terms are not defined, or if they are defined, they are not always defined consistently. Until a commonly accepted vocabulary is adopted by invasion ecologists, we think the field will continue to have difficulty developing reliable generalizations, partly due to misunderstandings and misinterpretations among investigators.

Because species invading a new region and successional species moving into a habitat following a disturbance are both colonizing new sites, the development of a nomenclature scheme based on types of colonizers might clarify communication within the field of invasion ecology. Just as important, we believe such a scheme may help bring to an end the notion that invasions and invading species are unique ecological phenomena, thereby requiring unique explanations.

We acknowledge that not all colonization events are alike. For example, some colonizations occur over a short distance, some over a very long distance; some colonizers are new to the region, some are not; some colonizers have a negligible effect on the new environment, whereas some have very large impact. We think it would be useful to distinguish among different types of colonizers while recognizing the fundamentally similar ecological processes that govern all colonization episodes. To this end, we propose a simple classification scheme for colonization terminology modeled after Rabinowitz's (1981) classification of rarity forms.

The organizing criteria for this classification scheme are based on strictly ecological and geographical concepts. The scheme is organized around three distinctive aspects of the colonizer: dispersal distance (short or long), uniqueness (novel or common to the region colonized), and impact in the new environment (small or great). According to this scheme, there are 2^3 combinations of categories, or "eight ways to be a colonizer" (Fig. 1). The three different criteria will be described in more detail.

Dispersal distance

Whether a dispersal distance is declared to be short or long will largely depend on the system and particular colonizer under scrutiny. Clearly, this category is scale dependent. Nonetheless, short-distance dispersal is considered to be primarily between adjacent, or nearly adjacent, environments. This could be considered *diffusion dispersal*. On the other hand, long-distance dispersal can be viewed as movement typically between widely distant environments, usually separated by a barrier of some sort, a process that could be termed *saltation dispersal* or *punctuated dispersal*. We expect that diffusion dispersal would likely be a much more common event than the latter, which probably occurs only rarely, unless facilitated by humans. Note that an initial colonization episode precipitated by punctuated dispersal may often be followed by subsequent diffusion dispersal originating from within the newly colonized environment. For example, zebra mussels, *Dreissena polymorpha*, were introduced into North America via a saltation dispersal event (Benson and Boydstun 1995). Subsequent spread of this species in North America has been due to both diffusion dispersal (via natural dispersal within and among connected water systems) and saltation dispersal, e.g., mussels transported between water systems on the bottoms of boats (Griffiths et al. 1991).

Origin of colonizer

"Common" or "novel" refers to whether the colonizer is already a resident in the region or a newcomer to the region and therefore expanding its range. This category is also necessarily scale dependent, in space and time. The actual boundaries of "the region" will be largely defined in the context of the system and spe-

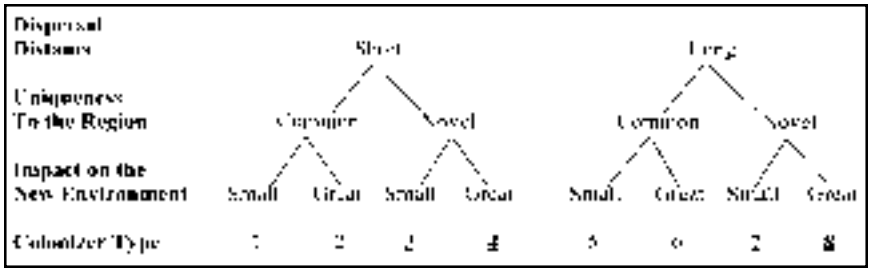

Fig. 1. The eight colonizer types shown as the result of the proposed classification scheme. According to this scheme, Types 1, 2, 5, and 6 can be considered *successional colonizers*; Types 3 and 7 can be considered *novel, noninvasive colonizers*; and Types 4 and 8 can be considered *novel, invasive colonizers*. It is recommended that the word *invader* be used only for colonizer Types 4 and 8.

cies under consideration. In most instances, an expansion of a species' range would involve an extension of the range's latitude, longitude, or altitude. However, range expansion could also include the establishment of the species in a new type of environment, without an extension of the range's latitude, longitude, or altitude. In this special case, it would be appropriate to term the colonizer a "novel" species, even though the species was already present in the region. Whether a species is common or novel to a region is also a function of temporal scale. For example, the old-field plant species of central and eastern North America are largely European in origin. Yet, today, they are some of the most widespread and successful plant species on the continent. Like it or not, these species are here and they are not going back. Continuing to refer to them at this point as alien invaders, or exotics, or even novel plant species, is beginning to make little ecological sense. (As the Romans said, *tandem aliquando invasores fiunt vernaculi* "in time invaders become the natives"). In any case, it will be up to the ecologist to define "novel" and "common" in the context of the system under investigation.

Presence or impact on the new environment

The term "invader" is often used indiscriminately to refer to all alien (novel) species in an environment. Yet, the term "invader" has distinctive connotations. Common synonyms for "invader" are "attacker," "aggressor," "raider," and "assailant." Clearly, an invader is not just any newcomer, but one that has a large impact on the new environment. This impact could involve community, ecosystem, and/or economic effects. Thus, in our classification scheme, newcomers that have a large impact in the new environment are distinguished from newcomers that have a small impact.

As shown in Fig. 1, the classification scheme yields eight different types of colonizers.

Type 1.—These are short-distance (diffusion) colonizers, common to the region (no range expansion), with a negligible impact in the new environment. Examples of such species are the many minor species that colonize, or recolonize, a habitat following a disturbance.

Type 2.—These are short-distance (diffusion) colonizers, common to the region (no range expansion), with a large impact in the new environment. Exemplary species would be any dominant species colonizing, or recolonizing, a habitat following a disturbance, e.g., quaking aspen, *Populus tremuloides*, dominating a postfire habitat, or pocket gophers, *Geomys* spp., that move into an adjacent field once it has been cleared of trees. Any species (common to the region) that plays a keystone role in the new community or ecosystem, e.g., as a predator, herbivore, pollinator, landscape engineer, pathogen, or nitrogen fixer, would be a Type 2 colonizer.

Type 3.—These are short-distance (diffusion) colonizers, novel to the region (range expansion), with a negligible impact in the new environment. Minor species incrementally expanding their ranges, e.g., due to climate or other environmental changes, represent this type of colonizer. Examples are numerous, e.g., the many species of European butterflies that are believed to be gradually expanding their ranges northward in response to the past century's warming trend (Parmesan 1999).

Type 4.—These are short-distance (diffusion) colonizers, novel to the region (range expansion), with a large impact on the new environment. Such colonizers would include dominant or keystone species incrementally expanding their range. In most cases, dispersal by these species is occurring without significant human assistance. Examples are the spread of House Sparrows, *Passer domesticus*, throughout the United States in the 19th and 20th centuries, and the current spread in the United States of buckthorn, *Rhamnus cathartica*.

Type 5.—These are long-distance (saltation) colonizers, common to the region (no range expansion), with a negligible impact in the new environment. This is probably a relatively uncommon type of colonization. One way in which it could occur is during the recolonization of an area that recently experienced a very large disturbance, e.g., the recolonization of the ecosystems on and surrounding Mount St. Helens following its eruption (Turner et al. 1997). In this case, colonizers of species common to the region often had to disperse from great distances (Dale 1991). Another way in which this type of colonization could occur is following the creation of an entirely new habitat in a region, e.g., the creation of a lake or reservoir as part of the construction of a hydroelectric project. Unless other aquatic systems were immediately adjacent to the reservoir, colonists would have to disperse from a long distance. In any case, once established, Type 5 colonizers would have a small impact in the new environment.

Type 6.—These are long-distance (saltation) colonizers, common to the region (no range expansion), with a large impact on the new environment. These colonization events could occur in the same scenarios described for Type 5 colonizers, with the difference that these would be dominant or keystone species. An example is fireweed, *Epilobium angustifolium,* a forb that became very abundant in many areas of Yellowstone National Park shortly after the 1988 fire (Turner et al. 1997).

Type 7.—These are long-distance (saltation) colonizers, novel to the region (range expansion), with a negligible impact on the new environment. This group of colonizers probably represents the largest group of novel species that have colonized environments from a great distance. Despite the impression given by headlines (in both the popular and scientific press), many, if not most, novel species have little impact in their new environment (Williamson 1999).

For example, *Epilobium brunnescens* (native to New Zealand) and *Veronica filiformis* (native to the Caucasus) are both extremely common plants in England, but neither is having any discernible impact on their environments. Given the common connotations of the term "invader," referring to such species as "invaders" makes little ecological sense and can be misleading.

Type 8.—These are long-distance (saltation) colonizers, novel to the region (range expansion), with a large impact on the new environment. This group of colonizers has received the most attention, both in the popular press and the scientific community, since Elton (1958) brought invasion ecology to the public's attention. These are the quintessential invaders, arriving from great distances (often, if not usually, due to human facilitation), and rapidly spreading throughout the new environment, often via both diffusion and saltation dispersal, usually with ecological and economic consequences deemed undesirable by humans. Examples are numerous and well known, e.g., the brown tree snake, *Boiga irregularis*, and purple loosestrife, *Lythrum salicaria*.

An examination of the eight colonizer types reveals that they fall into three main categories. Four of the eight types (1, 2, 5, and 6) are principally colonizers during succession, e.g., colonizing or recolonizing habitats following a disturbance. These are colonization episodes in habitats within the established range of the species. These four types can be referred to as *successional colonizers*. Types 3 and 7 differ from the successional colonizers in that their colonization episodes involve range expansion. However, since these novel colonizers have only a minor impact on the new environment, it does not make sense to call them invaders, under the normal, rather perjorative understanding of the word. Thus, they can be considered *novel, noninvasive colonizers*. Types 4 and 8 are novel and have a large impact, usually undesirable, on the new environment. These colonizers are the *novel, invasive colonizers*, the true invaders.

We are not advocating that ecologists cease using the words "invasion" or "invader." We believe that these terms can be very useful *as long as their usage is restricted to colonizer Types 4 and 8*, and *as long as invasion is viewed as just a specific case of the more general process of colonization*. However, ecologists should think carefully before using words such as "alien" and "exotic." With synonyms such as "strange," "outlandish," "barbarian," and "hostile," usage of these words may serve to perpetuate the recalcitrant conviction that invasions by novel species are governed by different ecological processes than colonizations of habitats by resident species.

The view that invaders and species invasions are unique ecological phenomena requiring unique explanation has been challenged in the past by Johnstone (1986), Huston (1994), and Thompson et al. (1995). However, their calls to bring invasion ecology back into the fold of the rest of ecology have largely been ignored. The recent proposal of a theory of invasibility based on findings and theory from succession ecology (Davis et al. 2000) is evidence that the field of invasion ecology can benefit greatly from existing ecological data and theory obtained and developed outside the field of invasion ecology.

In summary, our eight-celled classification scheme for colonization/invasion nomenclature is intended to promote more consistent use of terminology within the field of invasion ecology, and also to emphasize that species invasions are not ecologically unique events. Thus, it is our hope that the proposed nomenclature scheme will bring some needed clarity to the vocabulary of invasion ecology, while at the same time suggesting some new and productive ways of thinking about species invasions that will accelerate the process of making invasion ecology a quantitative, analytic, and predictive science (Parker and Reichard 1998).

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