

A neutral terminology to define 'invasive' species

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ABSTRACT

The use of simple terms to articulate ecological concepts can confuse ideological debates and undermine management efforts. This problem is particularly acute in studies of nonindigenous species, which alternatively have been called 'exotic', 'introduced', 'invasive' and 'naturalised', among others. Attempts to redefine commonly used terminology have proven difficult because authors are often partial to particular definitions. In an attempt to form a consensus on invasion terminology, we synthesize an invasional framework based on current models that break the invasion process into a series of consecutive, obligatory stages. Unlike previous efforts, we propose a neutral terminology based on this framework. This 'stage-based' terminology can be used to supplement terms with ambiguous meanings (e.g. invasive, introduced, naturalized, weedy, etc.), and thereby improve clarity of future studies. This approach is based on the concept of 'propagule pressure' and has the additional benefit of identifying factors affecting the success of species at each stage. Under this framework, invasions can be more objectively understood as biogeographical, rather than taxonomic, phenomena; and author preferences in the use of existing terminology can be addressed. An example of this recommended protocol might be: 'We examined distribution data to contrast the characteristics of invasive species (stages IVa and V) and noninvasive species (stages III and IVb)'.

Keywords

Biological invasions, definitions, establishment, exotic, introduction, invasion stages, naturalized, NIS, nonindigenous species, terminology.

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INTRODUCTION

Terms and concepts crucial to understanding ecology have often been criticized for their tautological, ambiguous or nonoperational nature (McIntosh, 1985; Peters, 1991). Classic examples of problematic ecological terminology include concepts like ecosystem, diversity-stability, and the ecological niche (see McIntosh, 1985; Peters, 1991; Grimm & Wissel, 1997). While the widespread use of ordinary words in the English ecological literature has allowed rapid dissemination of novel ideas, it also has impeded progress of objective scientific theory (Peters, 1991). Invasion ecology has enjoyed a rapid ascension in the public domain, owing in part to the extensive use of adjectives like 'invasive', 'alien', 'noxious' and 'exotic' (Binggeli, 1994; Chew & Laubichler, 2003). However, subconscious associations with preconceived terms, particularly emotive ones, can also lead to divergent interpretations and a confusion of concepts and theory (see Richardson *et al.*, 2000a; Simberloff, 2003). These differences can become problematic if they cloud conceptualization of the processes they are meant to describe (see McIntosh, 1985; Peters, 1991; Pyšek, 1995; Richardson *et al.*, 2000a; Shrader-

Frechette, 2001). This problem is perhaps best highlighted by the recent publication of widely divergent perceptions of the criteria for 'invasive' species (Davis & Thompson, 2001; Rejmánek *et al.*, 2002; Chew & Laubichler, 2003).

Lack of consensus

Many important terms relevant to invasion ecology theory, like 'invasive', 'weed', or 'transient', include qualities that are open to subjective interpretation. For example, it is generally accepted that the adjectives 'noxious' and 'nuisance' are used to imply adverse effects on humans, either directly (e.g. species that produce toxins that are harmful to humans) or indirectly (e.g. species that infest nature reserves). However, this reliance on human interaction has three important analytical consequences. First, definitions may vary dramatically, describing both species with aesthetically displeasing effects (e.g. Civeyrel & Simberloff, 1996), and those that are vectors for serious human diseases (e.g. Lounibos, 2002). Second, species may be considered a nuisance (or weedy, invasive, etc.) in areas where they have little or no impact simply because they were identified as a nuisance elsewhere (e.g.

Morton, 1996). Thus, the term 'invasive' has been used as a taxonomic description rather than to describe an ecological phenomenon. Finally, a particular species can have both beneficial and detrimental effects. For example, the mosquito fish *Gambusia affinis* has been widely introduced because of its supposed suppression of larval mosquitoes (Fuller *et al.*, 1999), yet it also has negative impacts on native species of insect, fish and amphibian (e.g. Rupp, 1996; Goodsell & Kats, 1999). Given this wide range of subjective criteria, terms like 'nuisance' may have more to do with human perception than with any inherent ecological characteristics. As such, these subjective terms may complicate or confound investigations of invasion patterns and processes.

In addition to a lack of unambiguous, ecologically based criteria, other terms also lack consensus on a more basic level. Ironically, the greatest confusion surrounds the common term 'invasive' and its various derivatives (Richardson *et al.*, 2000a). Explicit or implicit definitions for 'invasive' include: (1) a synonym for 'nonindigenous' (e.g. Goodwin *et al.*, 1999; Radford & Cousens, 2000); (2) an adjective for native or nonindigenous species (NIS) that have colonized natural areas (e.g. Burke & Grime, 1996); (3) discrimination of NIS established in cultivated habitats (as 'noninvasive') from those established in natural habitats (e.g. Reichard & Hamilton, 1997); (4) NIS that are widespread (e.g. van Clef & Stiles, 2001); or (5) widespread NIS that have adverse effects on the invaded habitat (e.g. Davis & Thompson, 2000; Mack *et al.*, 2000). The latter definition has gained popularity with some international conservation organizations (e.g. IUCN, 1999; McNeely *et al.*, 2001), but has been criticized by others (Rejmánek *et al.*, 2002). Richardson *et al.* (2000a) similarly noted that the term 'naturalised' is equally confused, including uses as a synonym for 'alien', 'invasive', 'established', or specifically for NIS able to establish in undisturbed habitats. To reduce confusion, Richardson *et al.* (2000a) called for a biogeographical approach to defining 'established', 'naturalised', and 'invasive' species.

The problem with definitions is not limited to these terms. Table 1 is a nonexhaustive list of adjectives commonly used in the English literature on invasive species. Many of these terms have been used interchangeably to describe the same concept (e.g. nonindigenous, exotic, alien). Other terms have been used inconsistently, to describe dissimilar phenomena (e.g. invasive, naturalized, imported). Although this criticism may at first seem semantic, varied definitions can cloud theoretical issues. This leads to the lumping together of different phenomena, and the splitting of similar ones, which in turn makes generalization difficult or impossible. For example, a particular species may have a widespread region of introduction in which it is only found at low abundance. Such is the case for the common goldfish (*Carassius auratus*), which is found throughout the United States, but rarely achieves high densities (Fuller *et al.*, 1999). Alternatively, the Sambar deer (*Cervus unicolor unicolor*) in New Zealand is constrained geographically, but has reached high densities (King, 1990). The term 'invasive' has been used in both types of cases, but the underlying processes accounting for these two patterns may be quite different; human-mediated transport is likely more important in determining ranges, whereas biological

Table 1 List of some common terms in the English literature on invasion ecology, and their corresponding 'stages'

Term	Stage
Adventive	Stage I–V
Alien	Stage I–V
Casual	Stage II
Colonizing	Stage IVa
Cryptogenic	May be modelled as Stage III–V
Escaped	Stage II–V
Endemic	Not defined by the model
Established	Stage III–V
Exotic	Stage I–V
Foreign	Stage I–V
Immigrant	Stage I–V
Imported	Stage I–V
Introduced	Stage I–V
Invasive	Stage IVa, IVb or V
Native	Not defined by the model
Naturalized	Stage III–V
Nonindigenous	Stage I–V
Noxious	Not defined by the model
Nuisance	Not defined by the model
Pest	Not defined by the model
Spreading	Stage IVa
Temporary	Stage II
Tramp	Not defined by the model
Transferred	Stage I–V
Transformer	Not defined by the model
Transient	Stage II
Translocated	Stage I–V
Transplanted	Stage I–V
Transported	Stage I–V
Travelling	Stage I
Waif	Stage II
Weedy	Not defined by the model

processes (e.g. competitive ability, lack of natural enemies) may be more important for densities of NIS (see Richardson *et al.*, 2000a). Indeed the very terms used to describe NIS are misnomers in that nonindigenous species are actually nonindigenous populations of species. In other words, the same 'species' that are nonindigenous, naturalized, or invasive in one area are native somewhere else. A focus on invasions at a population level has important implications for both invasion ecology and ecological theory.

Problems with invasion terminology reflect a more general dilemma in ecology: the 'nonoperational' or casual use of important terms and concepts (McIntosh, 1985; Peters, 1991). Furthermore, recent attempts to redefine 'invasion' and its derivatives have only reinforced division among invasion ecologists (Davis & Thompson, 2000; Richardson *et al.*, 2000a; Daehler, 2001; Davis & Thompson, 2001, 2002; Rejmánek *et al.*, 2002). A complete restructuring of invasion terminology is beyond the scope of this essay. However, we maintain that failure to operationalize definitions is sufficiently harmful that a consensus on definitions

should be achieved in order to reduce confusion and allow for unambiguous generalizations and predictions. Such a consensus would greatly reduce confusion among researchers, and would facilitate a more directed approach to finding generalizations and better understanding of phenomena associated with biological invasions. Moreover, considering the conservation implications of biological invasions, it is imperative that workers in the field provide clear, objective definitions and models to managers and other officials charged with protection of native biodiversity.

A supplementary lexicon

Davis & Thompson (2000) classified colonizing species into eight categories based on dispersal distance, novelty, and impact. As such, their 'colonizer' model assumes that NIS are simply colonizing species, moved over long distances (usually by humans). The use of generic categories to define NIS may be crucial to uniting invasion paradigms, as explicit, novel definitions with no *a priori* interpretation help eliminate inferential 'baggage' associated with common words and the subtle, subconscious definitions that often vary among authors. However, we disagree with the parameters of the 'colonizer' model, as have other workers (Daehler, 2001; Rejmánek *et al.*, 2002). Contrary to the colonizer model, we argue that the process of becoming nonindigenous is inherently different from the local spread characterized by native colonizers. This difference owes primarily to separate evolutionary histories of NIS and the communities to which they are introduced, as well as, in many cases, the propensity of NIS to interact with humans (Crosby, 1993). Furthermore, the process of becoming 'invasive' (i.e. both widespread and locally dominant), even if it includes negative impacts, is always the climax of a process that includes establishment and local spread, followed by an increase in abundance (see also Richardson *et al.*, 2000a; Kolar & Lodge, 2001). Once established, however, processes that determine species distribution and abundance are conceptually similar for both native and nonindigenous species (Davis *et al.*, 2001).

In a seminal contribution, Richardson *et al.* (2000a) proposed a comprehensive model that described invasions as a process in which NIS progress through a series of invasion stages. Their model was specific to plants, but is conceptually similar to other, more general models (i.e. Carlton, 1985; Williamson & Fitter, 1996; Kolar & Lodge, 2001). However, these studies attempted to clarify terms already common to the invasion literature. Such an approach may be futile, as previous efforts to redefine invasion terminology have been largely unsuccessful (e.g. Shafland & Lewis, 1984; Binggeli, 1994). We maintain that proposals for universal definitions are unlikely to succeed unless authors forego their individual preferences. Consequently, we suggest that a useful invasion framework should (i) be process-based and (ii) include operational terms with no *a priori* meaning (i.e. as 'stages').

We developed a conceptual framework synthesized from Carlton's (1985) ballast water transport model, Williamson & Fitter's (1996) 'tens rule', Richardson *et al.*'s (2000a) barriers to invasion, and Kolar & Lodge's (2001) 'transitions' model (Fig. 1).

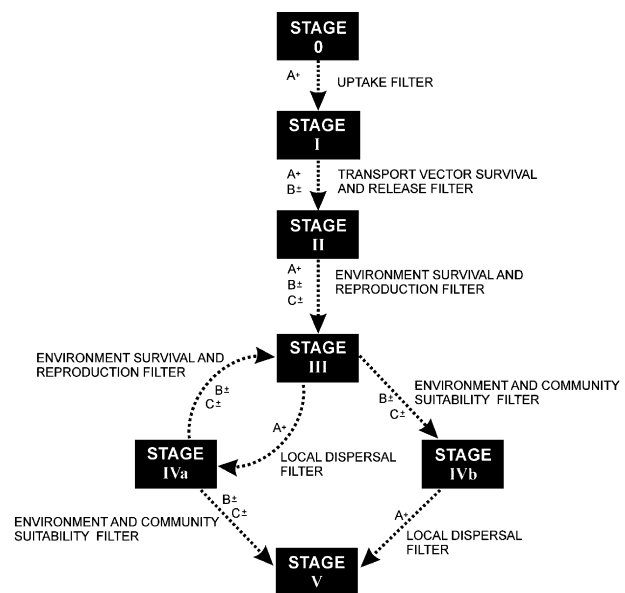


Figure 1 Suggested framework for defining operationally important terms in invasion studies. Potential invaders begin as propagules residing in a donor region (stage 0), and pass through a series of filters that may preclude transition to subsequent stages. Note that stages III through V are divided based on NIS abundance and distribution. Under this framework, a nonindigenous species may be localized and numerically rare (stage III), widespread but rare (stage IVa), localized but dominant (stage IVb) or widespread and dominant (stage V). Adjectives are intended only to aid in conceptualizing each stage, but should not be used to refer to the stage of interest (e.g. 'stage IVb'; not 'dominant'). Three classes of determinants affect the probability that a potential invader will pass through each filter: (A) propagule pressure; (B) physico-chemical requirements of the potential invader; and (C) community interactions. Determinants may positively (+) or negatively (−) affect the number of propagules that successfully pass through each filter.

These models are heavily based on the 'propagule pressure' concept, which focuses on the number of invading 'propagules' for a given introduction, and the frequency with which they are introduced (Williamson & Fitter, 1996). Under this paradigm, potential invaders pass through a series of filters that may preclude transition to subsequent stages. Invading propagules begin as residents in a potential donor region (stage 0), some of which are taken into the transport vector (stage I), usually by humans. If these propagules survive transport and release to become introduced (stage II), they have the potential to establish (stage III) in a novel environment.

Propagule pressure is also likely important for the postestablishment success of NIS (Kolar & Lodge, 2001; Duncan *et al.*, 2003; Rouget & Richardson, 2003). As shown in Fig. 1, a separation of propagule pressure from other factors (i.e. species interactions, resource availability, etc.) implicates four categories of established species, based on two filters — 'local dispersal' and 'environment and community suitability'. Local or regional dispersal of individuals (i.e. propagule pressure) determine which stage III (established) species reach stage IVa (widespread), or

which stage IVb species (dominant) reach stage V (widespread and dominant). Environmental and community-related factors determine which stage III (established) species reach stage IVb (dominant) or which stage IVa (widespread) species reach stage V (widespread and dominant). Under this framework, a nonindigenous species may be localized and numerically rare (stage III), widespread but rare (stage IVa), localized but dominant (stage IVb) or widespread and dominant (stage V).

We suggest that future studies explicitly refer to the invasion stages of interest (Fig. 1). Such an approach utilizes novel terms with no *a priori* definitions and builds upon existing invasion models (Carlton, 1985; Williamson & Fitter, 1996; Richardson *et al.*, 2000a; Kolar & Lodge, 2001). Such a protocol would not replace current terminology, but could greatly reduce confusion by supplementing terms with the invasion stage of interest. An example might be: 'We examined distribution data to identify differences between invasive species (stages IVa, and V) and noninvasive species (stages III and IVb)'. By explicitly stating the stage of interest, it would be clear that the 'invasive' species include those that are widespread, whereas 'noninvasive' species refer to localized populations, regardless of local abundance. Table 1 lists the stage-based analogues for a number of problematic terms.

Besides forming a basis for operationally important terminology, this invasion framework also aids in conceptualizing factors that affect invasion success (i.e. determinants in Fig. 1). For example, the transition of propagules from introduction (stage II) to establishment (stage III) requires survival and reproduction in the recipient region. To predict success at this transition, invasion models have historically focused on biotic resistance of recipient communities, guided largely by the work of Elton (1958). Biotic resistance predicts that interspecific interactions hinder the establishment of NIS due to the negative effects of predation, competition or parasitism (e.g. Moyle & Light, 1996; Mitchell & Power, 2003; Von Holle *et al.*, 2003; but see Levine & D'Antonio, 1999). Thus, the C-class of determinants (Fig. 1) may have a negative value, indicating that biotic resistance can hinder the transition of propagules from introduction to establishment. Alternatively, facilitative interactions can increase the probability of invasion success by creating new trophic or habitat opportunities (e.g. Simberloff & Von Holle, 1999; Richardson *et al.*, 2000b; Bruno *et al.*, 2003). Therefore, the same determinants (C-class) may have a positive value at the same stage. Physicochemical requirements (B-class determinants) of the potential NIS may similarly affect establishment success either positively or negatively, depending on the physicochemical properties of the recipient environment or of the transport vector. For example, lakes with low calcium concentration may be relatively invulnerable to invasion by zebra mussels (*Dreissena polymorpha*), while nutrient-rich grassland habitats may foster establishment of both native and NIS of plant (Ramcharan *et al.*, 1992; Stohlgren *et al.*, 1999). Finally, the probability of establishment success may increase with the introduction of more propagules (A-class), which reduces or eliminates the likelihood of Allee effects and stochastic extinctions (Mack, 1995; Courchamp *et al.*, 1999; Keitt *et al.*, 2001).

Under this framework, a distinction is warranted for 'native' vs. 'stage 0' species. From the perspective of a given community, the designation of 'stage 0' (Fig. 1) should be reserved for species found in the same source region as the NIS of interest (i.e. potential introductions from the same source pool), thus discriminating potential invaders from species native to the recipient community. This distinction is important in better conceptualizing 'propagule biases' (i.e. nonrandom variation in introduction effort) that may confound patterns of invasion (Duncan *et al.*, 2003).

Our stages are deduced logically from the relative importance of propagule pressure and other biotic and abiotic factors, but appear to describe real populations of NIS reasonably well. For example, most of the more notorious invaders (e.g. zebra mussel) form stage V populations because they have been introduced repeatedly to ideal habitats (i.e. 'niche opportunities' *sensu* Shea & Chesson, 2002). Stage V species have therefore passed through both the 'local dispersal' and 'environment survival and reproduction' filters (i.e. highly positive A-, B- and C-class determinants in Fig. 1). Other species, like the goldfish are widespread in the United States owing to repeated introductions through aquarium releases, yet rarely achieve high densities in invaded communities (Fuller, 1999). In this case, goldfish are an example of a stage IVa invader where A-class determinants are strongly positive, while B- and or C-class determinants are weaker — perhaps even negative — as several populations may be sustained only by continuous aquarium releases. Finally, the crested myna (*Acridotheres cristatellus*) invasion of North America may be an example of a stage IVb population. After its introduction in the late 1800 s, the crested myna reached high densities, with ~20,000 birds estimated in a fairly restricted area around Vancouver, British Columbia, Canada (Long, 1981). Interestingly, this population began to decline after 1927, and now may be extirpated from North America (Long, 1981; CWS, 2003). Thus, the invasion 'stage' of a given population is time-dependent, as a population progresses (or regresses) through each stage. Linking ecological processes with nonindigenous populations that transit each stage at different time periods may prove to be a source of fruitful research, particularly where researchers examine nonindigenous populations that are reverting from later stages to earlier ones.

Identifying the stage of a particular nonindigenous population is likewise dependent on spatial scale. A species may be widespread globally or nationally, but restricted at smaller spatial scales. For example, the common goldfish is widespread across the United States, as noted above, but has been found in only a single drainage basin in New Mexico and several other parts of the western United States (Fuller, 1999). We suggest that spatial scale be chosen based on introduction vectors, by separating long-distance transport vectors from those responsible for local spread. Long-distance vectors may be defined as those that are unique to nonindigenous species, while local dispersal vectors may act on both native and nonindigenous species within a given region. For example, invasion of the Laurentian Great Lakes by zebra mussels occurred after long-distance dispersal in the ballast water of transoceanic ships and was subsequently spread to

inland lakes in North America by recreational boating activity (Hebert *et al.*, 1989; Johnson *et al.*, 2001).

INVASIVE VS. NATIVE

A focus on invasion stage has the added benefit of stressing the view that invasions represent biogeographical rather than taxonomic phenomena. As such, invasion stages should refer to individual populations, and not entire species. A similar shift in focus in conservation biology from species to populations has profoundly influenced ecological theory and management practices therein (Hughes *et al.*, 1997; Luck *et al.*, 2003). Such an approach is crucial if invasion ecology is to move beyond the current, widespread practice of contrasting species to identify characteristics of good invaders. Species-level analyses have provided valuable insights because the same species are often invasive in different parts of the world (i.e. invasive populations are a nonrandom sample of the global species pool) (Kolar & Lodge, 2001; Duncan *et al.*, 2003). Nevertheless, a biogeographical focus is imperative because populations of the same species can differ in their population dynamics (Crawley, 1987; Thébaud & Simberloff, 2001; Torchin *et al.*, 2001; Leger & Rice, 2003), and because determinants of invasion success (Fig. 1) act at the level of populations, not species.

Processes that affect local spread and establishment in novel areas may be independent of species origin (i.e. native or non-indigenous; Thompson *et al.*, 1995). As such, stages III to V (Fig. 1) could be used to model the local spread of three types of potential colonizers that might be available from a regional species pool: (i) NIS that have only recently established in the region of interest; (ii) NIS that have been resident for a long period of time; and (iii) native species. Community-level processes like competition, facilitation, disturbance, and local dispersal may therefore prove most useful in modelling the latter stages (III to V) of the invasion process where similar mechanisms operate on populations, independent of their origin or residence time. Alternatively, processes that are unique to the ecology of invasions by populations of nonindigenous species (e.g. human import preferences, survival of harsh transport vectors) would act mostly at the early stages of the invasion process (i.e. stages 0, I and II in Fig. 1).

The approach to defining NIS that we describe here still requires explicit criteria for 'nonindigenous' status. Such criteria are crucial, but likely will be case-specific initially, and standardized criteria may prove to be a source of continued debate (e.g. Webb, 1985; Shrader-Frechette, 2001). However, this shift of focus to invasion stages renders moot the issue of whether the taxa involved are native regionally or originate from other biogeographical areas. Using this framework, even resident native species and established (stage III) NIS might be modelled by the same or similar factors affecting later stages within a given system. Nevertheless, a consensus on operational terminology is required if invasion ecology is to evolve into a more objective discipline. Science progresses best when hypotheses, theories, and concepts are concisely stated and universally understood. The framework we propose herein could form a basis for universal

understanding of invasion processes, and thus provide a marked reduction in the confusion surrounding invasion terms and concepts.

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