

A conceptual framework for comparing species assemblages in native and exotic habitats

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Exotic (nonnative) species are known to have a wide variety of impacts on native biota. One potential set of impacts that have been poorly studied are the effects of replacing native habitat-providing species with exotic ones, e.g. when native trees that compose a woodland are replaced by an exotic tree plantation. Here we develop a graphical model that can be used to explore how multiple taxonomic components (such as birds, mammals and plants) respond to such changes. We suggest that four categorical responses are possible, with respect to changes in species richness (or other quantitative measures) of taxonomic groups within species assemblages. First, that each taxonomic group compared between habitats will be relatively unchanged, e.g. have equivalent values of species richness. Second, that a decrease (for example in species richness) of one group will be compensated for by an increase (in species richness) of another group. Third, that one or more groups will decrease without any compensated increases in other groups. Fourth, that one or more groups will increase without any compensated decreases in other groups. We provide empirical support for 3 of these 4 responses, with respect to measures of species richness, with much evidence for equivalency between habitats. These types of comparisons should provide a valuable tool for evaluating 1) the efficacy of environmental mitigation efforts that artificially create or restore habitats and 2) the types of changes that have occurred over time or across space as native habitat-producing species are replaced by exotic ones. Finally, this conceptual framework should help to broaden the range of possible changes considered by ecologists who study the impacts of exotic species.

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The impacts of exotic (nonnative) species are variable, often poorly understood, and difficult to predict. On the one hand, some exotic species have been shown to have severe detrimental impacts on native biota, causing declines in abundance, contraction of geographic ranges, and extinction of native species (Elton 1958, Ebenhard 1988, Fritts and Rodda 1998); exotic species have caused changes in community structure and ecosystem functioning (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998); and exotic species have caused tremendous detrimental economic impacts (Pimentel et al. 2000). On the other hand, most exotic species have not been documented to have any detectable effect on native

biota (Simberloff 1981); some exotic species have been shown to provide critically needed habitat or resources to endangered native species (e.g. exotic eucalypt trees provide over-wintering sites for monarch butterflies in California, Lane 1993); and many exotic species provide sources of great economic gain (e.g. European honey bees in North America). The complexity of potential impacts caused by exotic species has hindered the formation of robust generalizations regarding their effects. Indeed the field of invasion biology generally lacks a theoretical framework that spans the range of topics of interest to ecologists, evolutionary biologists and conservationists. Certainly, much progress has been

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made in the past few decades in understanding the factors that influence successful colonization and establishment of exotics (Forcella and Wood 1984, Rejmánek 1996, Rejmánek and Richardson 1996, Duncan et al. 1999, Lockwood 1999, Davis et al. 2000, Sax 2000, Blackburn and Duncan 2001, Kennedy et al. 2002, Mack 2003, Torchin et al. 2003), and in determining patterns of exotic diversity and biotic homogenization (McKinney and Lockwood 1999, Stohlgren et al. 1999, Sax 2001, 2002a, Sax et al. 2002, Davis 2003, Olden and Poff 2003). In spite of this progress, many potential impacts of exotic species remain poorly characterized.

One set of impacts that are poorly understood are those changes that occur when exotic species replace native species that previously provided habitat for an entire species assemblage. Examples of native species that provide habitat include trees that provide habitat for forest species, large brown macroalgae (kelps) that provide habitat for kelp forest species, and host organisms that provide habitat for parasite species. Native species that provide habitat have been replaced by exotic species intentionally, e.g. when a native forest is cut down and replaced by a plantation of exotic trees (Keenan et al. 1997), and unintentionally, e.g. when a native seaweed species is excluded by an invasive exotic species (Viejo 1999). Following such replacements, there are often significant changes in associated species assemblages (Springett 1976, Friend 1982, Mitra and Sheldon 1993, Ellis 1995, Sousa et al. 1997, Pérez-Ponce de León et al. 2000, Sax 2002b). In spite of numerous examples of such changes, however, no conceptual framework to describe the extent and importance of these changes has been developed, and the full range of possible impacts on community structure and function has not been explored.

Here we explore some of the differences that could exist between species assemblages in native and exotic habitats. We do not consider differences in species composition because we believe that existing techniques to determine similarities between species assemblages are largely sufficient. Here, we are particularly concerned with comparing quantitative measures, such as species richness, evenness and diversity, of different taxonomic components of assemblages in native and exotic habitats. By taxonomic components, we mean those taxonomically distinct groups of species that are of interest to ecologists and which together contribute to an entire species assemblage; generally these will include groups such as vascular plants, mammals, birds, insects, et cetera, but the ultimate levels chosen are subjective and will depend upon the comparisons being made. In addition to taxonomic components, trophic or functional groups could also be compared. Regardless, however, of the unit of comparison chosen, in order to best understand the differences between habitats formed by native and exotic species, we believe that it is

important to simultaneously consider how different components of species assemblages may vary, e.g. to simultaneously consider changes in birds, mammals, plants and insects; this perspective contrasts with the manner in which most studies have been conducted to date, where the focus has been solely upon changes observed in a single taxonomic group, such as birds, mammals or mollusks (Friend 1982, Ellis 1995, Tattersfield et al. 2001). Here, we develop a graphical model that illustrates the range of possible differences that can occur among multiple taxonomic components of species assemblages within habitats formed by native and exotic species. We also examine empirical evidence to evaluate the extent to which the range of possible responses occurs in nature.

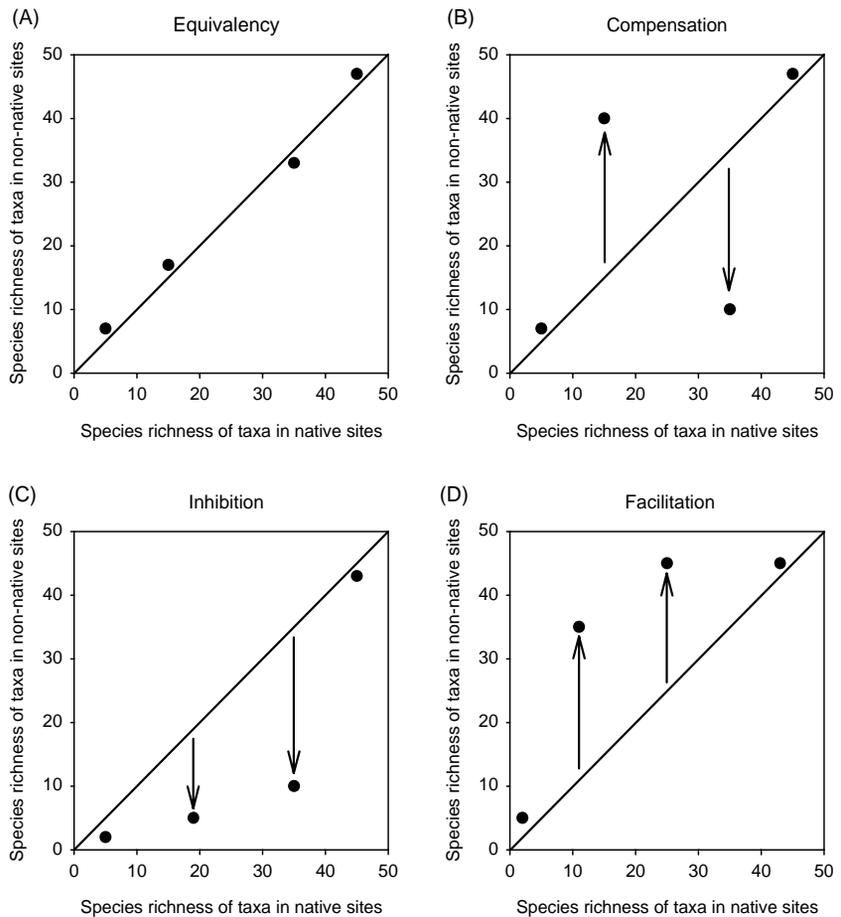
A graphical model

The approach we employ could be used to compare any characteristics of species assemblages that can be quantified, e.g. species richness, abundance, evenness, or diversity. Here we focus on comparisons of species richness. We do this for two reasons; first, because species richness is easy to conceptualize, and second, because much empirical evidence exists for species richness with which to evaluate whether the responses described in our model occur in nature.

To begin, measures (in this case of species richness) must be available for several components of species assemblages found in habitats formed by native and exotic species. Ideally, multiple representatives of each habitat type are available, as this allows within-group means and variances to be calculated (an advantage that we discuss below), but this method can also be used to compare a single pair of native and exotic habitats. As discussed above, we envision that taxonomic components (e.g. birds, mammals, insects, etc.) will generally serve as the units of measure, but trophic or functional components (e.g. detritivores, herbivores, carnivores, etc.) are also conceivable. Sax (2002b) illustrated this method with taxonomic components by comparing the diversity of arthropods, amphibians, mammals, birds and vascular plants in native oak woodlands and exotic eucalypt woodlands in California. He found the mean species richness of most groups to be relatively equal; clearly, however, other outcomes of such comparisons are conceivable.

We envision that any quantitative characteristics of assemblages can vary among taxonomic components and between habitat types in one of four categorical ways (Fig. 1). First, the measured characteristic of each taxonomic component could be relatively similar between habitats, e.g. if the richness of mammals is similar in both habitat types, the richness of birds is similar in both habitat types, the richness of plants is similar in

Fig. 1. Conceptual framework for comparing multiple taxonomic components of species assemblages in different (native and exotic) habitats. Taxonomic components (or taxa), which are represented as points in this figure, could include any natural division of organisms, such as birds, mammals, plants and insects; see text for details. Any quantitative measure of a taxonomic component could be used, but we illustrate this framework with species richness values. (A) Equivalency occurs when the (species richness) value of each taxonomic component that is compared between habitat types is roughly equal. (B) Compensation occurs when a decrease in the value of one component is compensated for by an increase in the value of another. (C) Inhibition occurs when one or more components decrease in value, without compensated increases in other components. (D) Facilitation occurs when one or more components increase in value, without compensated decreases in other components.



both habitat types, etc. (Fig. 1A – equivalency). Second, a decline in one taxonomic component could be compensated for by an increase in another, e.g. a decrease in the richness of mammals could be compensated for by an increase in the richness of birds (Fig. 1B – compensation). Third, a decline in one or more components could occur without compensated increases in other components (Fig. 1C – inhibition). Fourth, an increase in one or more components could occur without compensated decreases in other components (Fig. 1D – facilitation). Many subtle variations on these four categorical responses are possible, e.g. inhibition could occur generally to all components or singularly to one component; we believe, however, that these four categorical responses accurately summarize the range of outcomes likely to occur. It should also be noted that the aggregate (or total) species richness of the entire assemblage found in exotic habitats is unchanged relative to native habitat in cases A and B (equivalency or compensation), lower in case C (inhibition) and greater in case D (facilitation).

Distinguishing among these responses, and evaluating the magnitude of any particular response can be done statistically in a number of ways. First, the number of

points on either side of the line of equality can be compared with an expected ratio of 1:1 using the Pearson statistic or other goodness-of-fit test. Second, the slope from a regression analysis could be compared to a null expectation of a slope of 1. Finally, individual points that deviate from the line of equality could be examined with analysis of variance techniques, e.g. t-tests with appropriate corrections for multiple comparisons, if points were based on mean values. However, as this subject is being introduced for the first time, and as these types of examination are inherently graphical, we rely here upon a visual examination of these responses to distinguish among them.

Empirical evidence

To demonstrate the potential utility of this conceptual framework for describing differences between (native and exotic) habitat types, we searched the literature for comparisons of habitats structured by native and exotic species. We identified numerous studies with relevant data for species richness; here, we present six

comparisons from five separate studies. Before presenting the results of this effort, we first provide a context for these comparisons by briefly describing pertinent characteristics of the habitats considered and methodologies used in these studies.

Habitat comparisons

Temperate woodlands

Sax (2002b) compared native woodlands comprised principally of *Quercus agrifolia* (coast live oak) and *Umbellularia californica* (California bay tree) with exotic woodlands comprised of *Eucalyptus globulus* (blue gum tree) in the coastal mountains of central California. The eucalypt woodlands are plantations that had been abandoned approximately 80 years prior to the study and had been unmanaged during that time. In each of three 'native' and three 'exotic' woodlands sampling that standardized for effort was conducted for rodents (with live traps), amphibians (with searches of cover items), birds (with timed counts), plants (with transects and quadrats), and leaf litter invertebrates (with core samples and berlese funnels). Data compared here are from samples taken in the spring (during the 'wet season' of California), when the greatest number of species are detectable. The richness values reported are mean values for native and exotic habitats.

Riparian vegetation

Ellis (1995), Ellis et al. (1997) and Ellis et al. (2000) compared native riparian vegetation dominated by *Populus deltoides* (cottonwood trees) with exotic riparian vegetation dominated by *Tamarix ramosissima* (saltcedar) along the Rio Grande River of central New Mexico. Saltcedar has invaded these areas within the last 100 years. In each of two 'native' and two 'exotic' habitats sampling that standardized for effort was conducted for rodents (with live traps), birds (with transects and point counts), and for surface-active arthropods (with pitfall traps). Data compared here are from repeated samples taken in the spring, summer and fall seasons, with comparisons pooled across seasons. The richness values reported are average values for native and exotic habitats.

Saltmarsh and mudflats

Hedge and Kriwoken (2000) compared three habitat types in the Little Swanport Estuary of Tasmania: 1) native saltmarsh vegetation dominated by *Sarcocornia quinqueflora* and *Juncus kraussii*, 2) mudflats free of vegetation, and 3) areas invaded by *Spartina anglica*. This invasive species was introduced into Australia in the 1930s (Kriwoken and Hedge 2000). Ten regions of the estuary were selected and all three habitat types were sampled in each region for macroinvertebrate infaunal

species (using sediment cores and sieves). Data were collected in the winter and may or may not reflect the composition of species expected at different times in the year. The richness values reported are the total number of species sampled in native and exotic habitats.

Intertidal algae

Viejo (1999) compared habitats composed of the native seaweed, *Cystoseira nodicaulis*, with habitats composed of the exotic seaweed, *Sargassum muticum*, in the low intertidal-shallow subtidal zone on the north coast of Spain. *S. muticum* had invaded this area within 10 years prior to the samples taken in this study. Roughly equal sampling effort was made in native and exotic habitat, 42 and 46 samples respectively. Each sample of algae was taken from the substratum, washed to collect all visible animals, and sorted to identify the mobile epifauna. Samples were collected over a 12 month period and comparisons were pooled across dates. The richness values reported are the total number of species sampled in native and exotic habitats.

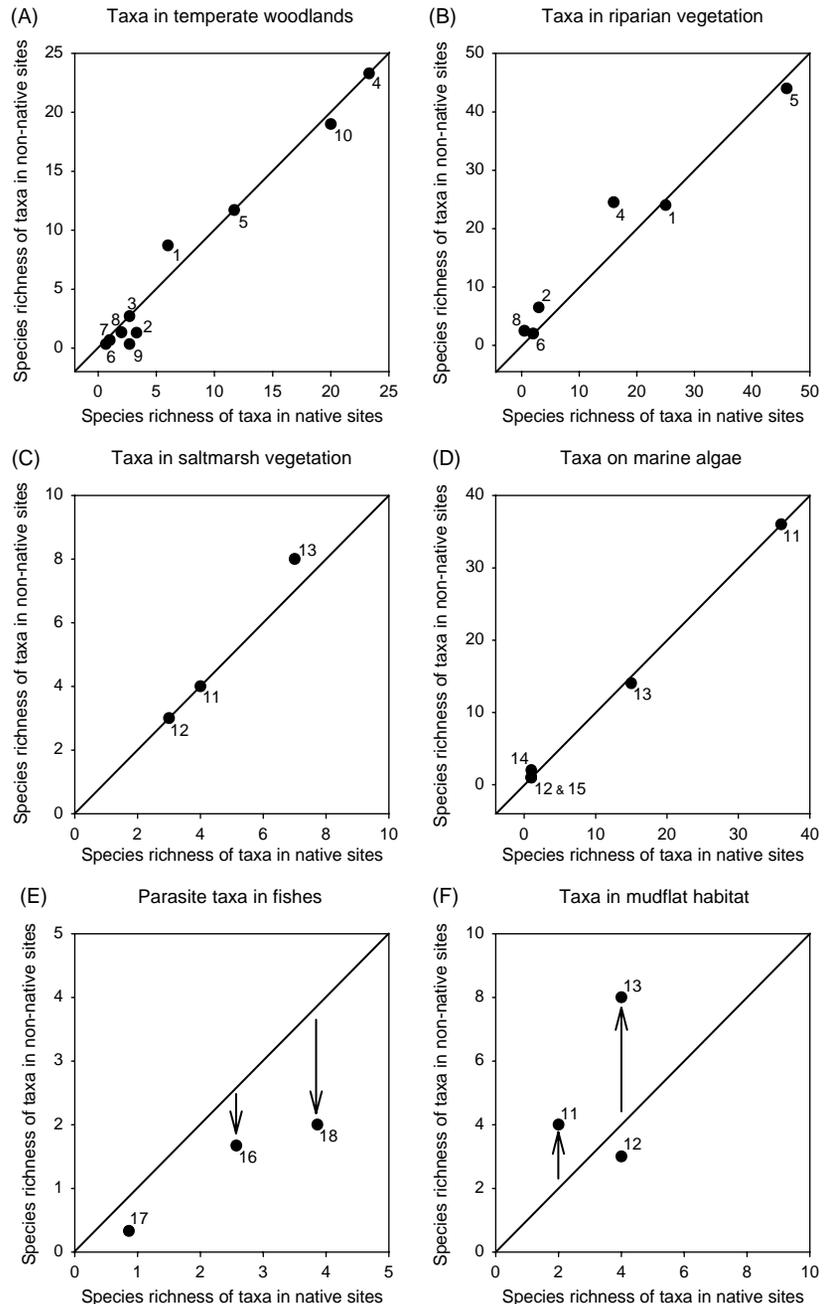
Fishes as hosts for parasites

Pérez-Ponce de León et al. (2000) compared species of helminth parasites in seven native and three exotic fish species in Lake Patzcuara, Mexico. It is unclear when these exotic fish species were introduced to this lake. Roughly equal numbers of individuals of each species of native and exotic fish were collected, with a mean of 60.4 and 58.3 individuals respectively. The organs (gills, eyes, brain, muscle, mesentery, liver, spleen, heart, gonads and gastrointestinal tract) of each individual were examined for helminth parasites using a dissecting microscope. The richness values reported are mean values for native and exotic species of fishes.

Results

We found examples of the first categorical response (equivalency) in woodland, riparian, saltmarsh, and intertidal studies (Fig. 2A–D). Specifically, evidence for this response came from comparisons of native oak woodlands and exotic eucalypt plantations in California, native riparian vegetation and invasive saltcedar vegetation in New Mexico, invasive *Spartina anglica* and native saltmarsh vegetation in Tasmania, and invasive seaweed and native seaweed assemblages in the low intertidal–shallow subtidal zone in Spain (Ellis 1995, Ellis et al. 1997, 2000, Viejo 1999, Hedge and Kriwoken 2000, Sax 2002b). We found an example of the third categorical response (inhibition) in a study of parasite richness in fishes of Lake Patzcuara, Mexico (Pérez-Ponce de León et al. 2000). In this study, the average number of parasite species inhabiting host populations of naturalized fish species was much less than that found in host

Fig. 2. The species richness values of multiple taxonomic components of species assemblages in native and exotic habitats. (A) Native woodlands and exotic *Eucalyptus globulus* woodlands in California showed roughly equivalent values for compared taxonomic components, animal classes: birds¹, mammals², amphibians³, arachnids⁴, insects⁵, malacostraca⁶, millipedes⁷, centipedes⁸, and plant divisions: ferns⁹ and seed plants¹⁰. Data are from Sax (2002a) and corresponding unpublished records. (B) Native riparian vegetation and non-native *Tamarix ramosissima* vegetation in New Mexico showed roughly equivalent values for compared animal classes: birds¹, mammals², arachnids⁴, insects⁵, malacostraca⁶, and centipedes⁸. Data are from Ellis (1995), Ellis et al. (1997, 2000), and corresponding unpublished records. (C) Native saltmarsh vegetation and invaded *Spartina anglica* vegetation in Tasmania showed roughly equivalent values for compared animal phyla: arthropods¹¹, annelids¹², and mollusks¹³. Data are from Hedge and Kriwoken (2000). (D) Native seaweed habitat and invasive *Sargassum muticum* habitat in Spain showed roughly equivalent values for compared epibiotic animal phyla: arthropods¹¹, annelids¹², mollusks¹³, cnidarians¹⁴, and echinoderms¹⁵. Data are from Viejo (1999). (E) Native populations of fish species showed greater average values than non-native populations of fish species in Lake Pátzcuaro, Mexico, for compared parasite phyla: nematoda¹⁶, acanthocaphalla¹⁷, and platyhelminthes¹⁸. Data is from Pérez-Ponce de León et al. (2000). (F) Native mudflat habitat showed lower values than invasive *Spartina anglica* habitat in Tasmania for compared animal phyla: arthropods¹¹, annelids¹², and mollusks¹³. Data are from Hedge and Kriwoken (2000).



populations of native fish species (Fig. 2E). We found an example of the fourth categorical response (facilitation) in a study that compared native mudflat habitats with invaded ones dominated by *Spartina anglica* (Hedge and Kriwoken 2000). In this study, the species richness of various invertebrate phyla was much greater in invaded vegetation than in native mudflat habitat (Fig. 2F). Examples of facilitation are also noted in other studies that investigated exotic species invasions of estuaries and

coastal shores. For example, Crooks (1998) reports greater species richness of invertebrate phyla in mudflat habitats invaded by the mussel, *Musculista sehousia*, de Montaudouin and Sauriau (1999) report greater species richness of invertebrate phyla in mudflat habitat invaded by the gastropod, *Crepidula fornicata*, and Castilla et al. (2004) report greater species richness of invertebrate phyla in intertidal habitat invaded by the ascidian, *Pyura praeputialis*.

We did not find evidence to support the second categorical response, compensation. We suspect that a thorough examination of quantitative characteristics other than species richness, such as species abundance, may reveal evidence to support this response. Our failure to find evidence for compensation, with regards to species richness, may have occurred for three reasons. First, compensation among taxonomic groups may not occur in nature. Second, we may have missed studies (in our review of the literature) that show this response. Third, compensation may occur, but be unreported in the literature. We believe that this last possibility is particularly likely given that few studies are known to the authors that examine multiple components of species assemblages in native and exotic habitats. We hope that future studies will examine multiple taxonomic groups, as we believe these data are needed to develop a holistic understanding of how species assemblages have been affected by exotic species.

Discussion

It is important to emphasize that species can be divided into groups for multiple component comparisons in many ways. Here we took the simplest approach and divided species into groups based on taxonomy, but divisions based on trophic or functional groups are also conceivable. Regardless of the type of grouping selected, however, it is important to note that the level of these groupings is a critical component of the analysis. In the empirical examples we discussed above, the taxonomic level used to group species differed from study to study. For example, in the comparisons of native and *Spartina anglica* habitats, we divided species by phyla, while in the comparisons of native and *Tamarix ramosissima* vegetation, we divided species by classes (Fig. 2). Different taxonomic levels must often be used in order to optimize the utility of multiple component comparisons. Choosing the most appropriate taxonomic level for these comparisons should be based on at least three considerations. First, using too high of a taxonomic level will reduce the among-component resolution of the analysis, e.g. examining the *S. anglica* invasion at the level of Kingdom would have provided only one data point. Second, using too low of a taxonomic level will reduce the within-component resolution, e.g. examining the *S. anglica* invasion at the level of species would have reduced this technique to a presence/absence analysis. Third, when multiple taxonomic levels offer sufficient resolution then it is important to be sure that the levels chosen do not qualitatively change the results. Future research efforts should attempt to clarify these issues, and should attempt to establish causal links between the categorical responses discussed here and

specific aspects of community alteration by exotic species.

In spite of the need for additional research, it is clear that taxonomic components of species assemblages can vary in a number of ways between native and exotic habitats. First, measures of taxonomic components within species assemblages can be equivalent between native and exotic habitats. While the commonness of this response may seem surprising (as evidenced by assemblages in woodland, riparian, saltmarsh and intertidal habitats), these results are consistent with work by Brown et al. (2001) who show that the species richness of many assemblages can remain unchanged in spite of large changes in species composition. Second, measures of all components can be lower in exotic habitats. Such reductions in species richness should perhaps be expected whenever complex coevolutionary relationships are disrupted by the absence of native species, e.g. when parasite species cannot complete their life histories without a specific chain of host species (Pérez-Ponce de León et al. 2000). Third, measures of all components can be higher in exotic habitats. Such increases in species richness should be expected whenever an invading species (regardless of whether that species is native or exotic) increases the complexity and/or heterogeneity of a habitat. For example, nearshore marine environments of California that are colonized naturally by giant kelp, *Macrocystis pyrifera*, are structurally diverse and contain many associated species, whereas nearby sites that are suitable for kelp colonization, but where kelp is absent are structurally simple and contain fewer species (Foster and Schiel 1985). Finally, as discussed above, it is unclear whether a compensation response between components in assemblages should be expected, and further work will be necessary to determine whether this occurs.

The graphical method described here can be used in two distinct ways. First, in temporally explicit comparisons that examine changes that occur at a single site (or set of sites) over time, e.g. as a native habitat-providing species is replaced by an exotic one. Second, in spatially explicit comparisons that examine two sites (or sets of sites) that are located nearby each other, e.g. where one habitat is formed by native species and the other by exotic species. Spatially explicit comparisons are ideal for evaluating many applied conservation problems, such as the efficacy of artificially created (or restored) habitats in mimicking patterns of diversity found in intact native habitats. Temporally explicit comparisons are ideal for evaluating how patterns of diversity have changed over time as a native habitat-providing species is replaced by an exotic one. Although temporally explicit comparisons are the only means by which to conclusively determine the effects of such habitat conversions at a particular site, relevant data (that records changes through time) will often be

unavailable. In such cases, space-for-time substitutions, i.e. comparing nearby sites that have been modified with those that have not, can provide evidence that is suggestive of how particular sites have changed over time; this type of evidence was examined in the studies featured in Fig. 2. When this is done the validity of three assumptions must be considered. First, that the area currently occupied by an exotic habitat was formerly occupied by the same type of native habitat that it is being compared to, e.g. that an exotic forest plantation, which is being compared to a particular type of native forest, was in fact historically occupied by that same type of native forest. Second, that the native habitat being compared has not been modified or degraded in a significant way. Third, that the habitats compared have identical environmental conditions, e.g. slope, aspect, elevation, etc. The degree to which these assumptions are invalidated corresponds inversely with the degree of confidence we should ascribe to these space-for-time substitutions. Finally, when making comparisons across time or space it is important to note that repeated sampling over time is necessary to determine whether any observed pattern of community response is transient or stable. It is conceivable, for example, that an observed pattern of inhibition may be replaced over time by one of equivalency, compensation or facilitation if low rates of species colonization of newly created or altered habitats create significant lags in the accumulation, and hence number, of species present. Similarly, it is worth emphasizing that active management of exotic habitats (such as the removal of understory vegetation in many forest plantations) may reduce the capacity of those habitats to support species-rich assemblages, complicating the interpretation of comparisons made between native and exotic habitats.

On a final note, we believe it is important to stress that studies of the impacts of exotic species should be oriented whenever possible towards an understanding of the full range of potential outcomes for any particular subject of concern. Recent work by Sax et al. (2002) and Sax and Gaines (2003) has stressed that species diversity may change as a consequence of exotic species invasions in different ways (increasing, decreasing or remaining unchanged), at different spatial scales (global, regional and local), for different taxonomic groups (e.g. birds, fishes and plants), and that each of these types of changes may have a host of significant ecological impacts on native biota. Recent work by Olden and Poff (2003) has stressed that biotic homogenization may occur in many distinct ways, and that the opposite of biotic homogenization, biotic differentiation can occur as well. We hope that the conceptual framework described here for comparing native and exotic habitats may also serve to broaden the range of possible changes generally considered and studied by ecologists, and

thereby lead to a more complete understanding of the impacts of exotic species.

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