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**VEGETATION CHANGE: A REUNIFYING CONCEPT IN PLANT ECOLOGY**

Mark A. Davis, Jan Pergl, Anne-Marie Truscott, Johannes Kollmann, Jan P. Bakker,  
Roser Domenech, Karel Prach, Anne-Helene Prieur-Richard, Roos M. Veeneklaas, Petr Pysek, Roger del Moral,  
Richard J. Hobbs, Scott L. Collins, Steward T. A. Pickett, Peter B. Reich

Contact Information:

Mark A. Davis, Department of Biology  
Macalester College  
1600 Grand Avenue  
Saint Paul, MN 55105  
USA

**ABSTRACT**

Specialization can become detrimental to a discipline if it fosters intellectual isolation. A bibliographic analysis of several research areas in plant ecology revealed that plant ecologists do not regularly make use of the findings and insights of very similar studies being conducted in other research subdisciplines; nor do they try to make their findings and insights easily accessible to researchers in other areas. This tendency toward intellectual isolation may be impeding efforts to discover the mechanisms driving vegetation change by reducing the number of potentially productive exchanges among researchers. Rather than characterizing studies of vegetation change on the basis of what distinguishes them from one another, plant ecologists would benefit from concentrating on what such studies have in common. Individual researchers, journals, and ecological societies all can take specific steps to increase the useful exchange of ideas and information among research areas. By promoting rapid and more effective communication among diverse researchers, as opposed to narrow theories, concepts, and terminologies associated with particular research areas, we can expedite our understanding of the ecological mechanisms and consequences associated with plant communities in flux. Give a concrete example: e.g. journals suggest broad key words

**Key Words:** succession, invasion ecology, gap dynamics, patch dynamics, climate change, vegetation change

**Introduction**

As any discipline matures, it is expected and desirable that specialization will develop. This encourages more focused and efficient research among investigators with similar interests. As long as specialists in different groups communicate effectively with one another, knowledge can be pursued in depth while still permitting integration. However, specialization can become detrimental if it fosters intellectual isolation, resulting in investigators paying insufficient attention to ideas and findings in related subdisciplines (Davis et al. 2001).

Four prominent research specialty areas that study vegetation change are succession ecology, invasion biology, gap/patch dynamics, and global change effects on plant communities. These areas have much in common: (1) colonization, establishment, turnover, persistence, and spread are fundamental events and processes that interact to produce vegetation

change in all four subdisciplines; (2) whatever the nature of vegetation change, it is often initiated or greatly influenced by, disturbance and/or changes in interactions with other trophic levels; (3) local and long-distance dispersal allow new species to invade existing plant communities; (4) facilitation and inhibition as well as interactions with species from other trophic levels strongly influence vegetation change, and (5) in all cases, changes in community composition affect, and are affected by, ecosystem processes (Fig. 1). Essentially, these four research areas focus on different causes of vegetation change, e.g., species introduced from other regions of the world, disturbances that create gaps and initiate succession, and global change. Given that these research areas are trying to illuminate the mechanisms that cause vegetation change, and that the phenomena under study often interact (e.g., gaps and climate change may facilitate invasions), one would expect that considerable information exchange must occur among these research areas.

**Examining Communication Among Subdisciplines**

One way to test whether such communication is in fact occurring is to examine key words and the bibliographies of papers published in each research area. For example, selecting key words for an article represents a conscious and strategic decision on the part of the author to make the paper accessible to a particular group of researchers, through electronic searches. Thus, key words should reflect an author's assessment of the paper's scope and relevance. An analysis of key words in articles within a single specialty should reveal whether the researchers in that field tend to take a narrow or broad view with respect to the potential significance and impact of their studies.

If the selection of key words represents an explicit decision by the authors about how to articulate the scope of an article, a bibliography is a more empirical documentation of the author's use of findings and ideas from the literature. Thus, analyses of key words and bibliographies both should be informative, but in different ways. For example, authors may characterize their papers in a quite specialized way even though they use a much broader conceptual context to research and write their papers. Or, the reverse could be true; authors might tend to characterize their papers as being quite broad in their scope and significance, while they actually rely on a narrow body of literature to conceive and write them.

To assess the degree of dissociation that may exist among the four research areas listed above, we conducted both types of analyses on the literature in the respective fields. To assess how authors characterized their own articles, we analyzed key words by searching the BasicBIOSIS electronic data base (<http://www.biosis.org>), which indexes 37 botanical and ecological, and general science journals that regularly publish plant ecology articles (Table 1). Since we were most interested in assessing the recent status of the different research areas, we examined articles published between January 2000 and December 2003. We first identified a sample of papers in each research area using a key word search (Table 1). The term 'global change' has been used to describe a large number of processes occurring on a global scale, including everything from climate change to biological invasions to changing land-use patterns. For the purposes of this paper, we confined the focus of global change to atmospheric-related issues, specifically, changes in climate, CO<sub>2</sub> levels, and rates of atmospheric deposition of nitrogen. These searches produced the following number of articles: invasion biology (499), succession (520), gap/patch dynamics (132), global and climate change (416). Each of the four samples were then queried using the key words from the other three research areas to identify articles in which the author chose to connect his/her paper with one or more of the other research areas (Fig. 2). It is clear that authors in all four areas seldom choose to link their papers to the other research areas. Invasion papers were the least likely to be cross-linked (6%) while gap/patch dynamic papers were most likely to be cross-linked (15%).

To assess how extensively authors used findings and insights from other research areas in the writing of their papers, we analyzed the bibliographies from 50 randomly selected articles identified from each of the four subject area samples. Each source listed in a bibliography was evaluated, based on its title, as to whether it could be identified as a plant invasion

article, a plant succession article, a plant gap/patch dynamics article, or an article examining the impact of global change (as delimited above) on plant communities. Examples of words used to assign sources to the respective categories are listed in Table 2. The results of the bibliographic analysis were similar to that found for key words. Authors who consciously envisioned their paper as part of a particular research specialty area (as evidenced by their choice of key words) overwhelmingly chose to consult sources within their specialty area in their papers (Fig. 3). Nevertheless, authors' use of the research literature tends to be broader than the way they characterize the paper.

There are several reasons why authors might characterize their articles so narrowly. Some may want their articles strongly identified with a specific research specialty area if they are trying to establish or maintain a particular research identity. For these authors, the narrow characterization of their papers is a conscious decision. For others, the narrow depiction may be less intentional than simply a result of an already narrow perception of their research scope. Pressure to publish may prompt some investigators to formulate narrow questions or hypotheses, which may permit more rapid data collection and result in narrowly defined papers. Other investigators may respond to the same publishing pressures by spreading the results of one study in different papers, each focusing on a different specific aspect of the study. Another possible reason for narrowly conceived articles is that it is more difficult and time consuming to write a paper that draws substantively on different research traditions than to compose one that is more narrowly focused. It may also be more risky to expose a paper to the criticisms of divergent experts than a more focused community or reviewers. Thus, authors may choose to characterize their paper narrowly in order to restrict the pool or focus of reviewers.

**Three Ways to Close the Gap**

Our analyses indicate that most researchers are studying vegetation change within narrow conceptual frameworks. They do not regularly make use of the findings and insights of very similar studies being conducted in other research subdisciplines, nor do they try to make their findings and insights easily accessible to researchers in other areas. It seems obvious that plant ecology would benefit from better communication among the different research specialty areas. Indeed, communication across broad disciplinary horizons within ecology may be of value more generally (Pickett et al. 1994). We propose three steps that individual researchers can take to increase the useful exchange of ideas and information among these research areas.

*1. Step Back to Get the Larger View*

Invasion ecology, succession ecology, gap/patch dynamics, and studies of the effects of global change on plant communities all study vegetation in flux, that is, vegetation experiencing changes in species composition. Thus, each specialty area could be considered a part of a larger research initiative: *the ecology of vegetation change*. Vegetation change is recognized as the fundamental subject area relevant to all kinds of vegetation management (Luken 1990). If researchers began to envision themselves as studying vegetation change, rather than being an invasion biologist, or a succession ecologist, they would be less inclined to take a parochial perspective with respect to their research.

## 2. Attend More Carefully to Related Research.

The simplest step individual researchers can take to increase communication among specialty areas is to consciously seek out relevant ideas and data from related research areas. For example, an invasion ecologist investigating the community-wide consequences of an introduced species that is altering the soil-microbial community could recognize the value of seeking out findings obtained from similar studies conducted within a succession framework. Or, a researcher studying the effects of increases in nitrogen deposition on plant communities could recognize the relevance of the many invasion studies that have examined the impact of changing resource levels on plant community structure. Also, researchers can take simple steps to increase the likelihood that their own articles are read by researchers in other specialty areas. By carefully selecting key words for their articles, authors can maximize the probability that electronic searches by individuals from other research areas will identify their articles.

Currently, there is no standardized protocol for identifying key words for articles. The task is left entirely up to the author, who normally receives no instructions or guidance. To facilitate cross-fertilization and broader literature searches, journals might consider requiring authors to identify two sets of key words. Authors would construct the first set by selecting words from a standardized list of key words representing general ecological concepts and phenomena. The second set would consist of more specific key words, identified by the author and not standardized, that would reflect more specific aspects of the article. A more standardized protocol for selecting key words would help authors undertake broader and more effective literature searches as well as help them define their own work within broadly defined and widely recognized conceptual domains. For example, if the term 'vegetation change' was routinely used as a key word by researchers studying any form of vegetation change, electronic searches would be more effectively in identifying studies from other research specialty areas that investigated similar mechanisms of vegetation change. Taking these steps will enable researchers to increase the significance and impact of their own studies. They will also help to increase communication between subdisciplines and thereby facilitate efforts to understand causes and consequences of vegetation change.

## 3. Design Studies that Cross Across Research Boundaries

Another benefit of a general conceptual framework for studying vegetation change is that it would increase the number of studies intentionally developed to cut across traditional subdiscipline boundaries. It is becoming apparent that integrated studies will be increasingly more meaningful than additional studies conducted within narrow paradigms. For example, due to the global extent of climate change and introduced species, it is increasingly difficult (impossible in many cases) to study particular cases of vegetation change in isolation, e.g., to study succession or gap dynamics without also studying the impacts of introduced species and climate change (e.g., Meiners et al. 2001).

### Combining Invasion and Succession Ecology: An Example of More Integrated Studies

Newly arrived plant species affect community composition and ecosystem processes regardless of their origin. In

addition, studies of succession are increasingly incorporating introduced species into their analyses due to the ubiquity of these new species in some environments (e.g., Inouye et al. 1987, Meiners et al. 2002), prompting a call for more research focusing on the successional impact of introduced species (Walker and del Moral 2003).

A simple conceptual approach that could integrate succession and invasion ecology is to consider the various ways that species can facilitate and/or inhibit one another (Connell and Slatyer 1977, Pickett et al. 1987). Considering native and introduced species, and the possibility that each may inhibit or facilitate species in either group, eight types of potential interactions between the two groups of species can be identified (Fig. 4). The first two types of interactions shown in Fig. 4 (facilitation and inhibition of native species by other native species) are those typically studied during investigations of succession (Glenn-Lewin et al. 1992), although studies of old-field succession also typically study interactions with introduced species as well (Meiners et al. 2001). The next three types of interactions have been the subjects of most invasion studies. Studies of invasibility have shown that some native species are able to prevent, or at least slow, the establishment of introduced species (interaction type 5, fig. 4). For example, Wedin and Tilman (1993) showed that the native grass *Schizachyrium scoparium* can inhibit the establishment and spread of the introduced grass *Agropyron repens* by its ability to depress levels of soil nitrogen. Studies in disturbed New Zealand forests have shown that *Hakea sericea* (an introduced shrub) is inhibiting the reestablishment of the native shrub *Leptospermum scoparium* and native tree *Kunzea ericoides* (Williams 1992). The latter two examples exemplify the fourth type of interaction (Fig. 4). In a Hawaiian study, Carino and Daehler (2002) showed that an introduced legume, *Chamaecrista nictans*, facilitated the subsequent invasion of another introduced species, the grass *Pennisetum setaceum* (an example of the fifth interaction type, Fig. 4).

The final three types of interactions (Fig. 4) are not typical subjects of either succession or invasion ecology, yet they do occur. *Juniperus virginiana*, a native tree in the US, has been found to facilitate the establishment of *Rhamnus cathartica*, an introduced and invasive tree, on some Mississippi River bluffs through a nurse plant effect on *Rhamnus* seedlings (Ann Pierce, Minnesota Department of Natural Resources, pers. comm.; (type 6 interaction, Fig. 4). In the western United States, crested wheatgrass (*Agropyrum cristatum*), an introduced perennial, is known to impede the spread and establishment of the annual cheatgrass (*Bromus tectorum*), another introduced species (Johnson 1986; type 7 interaction, Fig. 4). Also, De Pietri (1992) showed that *Rosa rubiginosa*, a shrub introduced to Argentina, facilitated the reestablishment of several native woody species in disturbed subantarctic forests by reducing grazing herbivory on native seedlings growing beneath the thorny shrubs (type 8 interaction, Fig. 4).

This brief account of eight types of interaction between introduced and native species emphasizes that it is the nature of the impact of the species that is important, not the place of origin. Regardless of the interaction type under investigation, all these studies are trying to answer the same two basic questions: what are the mechanisms that facilitate or inhibit the establishment and spread of particular plant species over time, and what are the consequences of these changes on community structure

and ecosystem processes? Rather than the subdisciplines of succession and invasion ecology continuing down two parallel tracks, we think it makes more sense to take a common and integrated approach.

An overview of how succession and invasion ecology can be studied with an integrated approach is illustrated in Table 3, which lists over-arching principles that can help define such an approach, key questions that can drive integrated research, and the types of integrated studies needed to discover underlying mechanisms. Not surprisingly, once one begins to adopt an integrated approach, the tendency to integrate increases (Pickett 1999). For example, question 3 introduces issues of gap and patch dynamics, while question 5 introduces issues of global change. Finally, we believe it is essential that future studies represent *quantitative* efforts to illuminate the *mechanisms* of vegetation change.

### Conclusion

The dangers of parochialism in ecology and the need for collaboration among ecologists pursuing common questions in diverse ways are not new concerns (Bartholomew 1986, McIntosh 1987, Pickett et al. 1994). It is clear that ecologists need to be conscious of how we interact, or fail to interact, with one another. We believe that an effort to reunify several specialty areas in plant ecology can substantially enhance ecologists' ability to discover and describe the mechanisms responsible for vegetation change. Rather than characterizing studies of vegetation change on the basis of what distinguishes them from one another, plant ecologists would benefit from concentrating on what all the studies have in common. Vegetation change is the research focus for all the respective subdisciplines discussed in this article. We believe that to reconceptualize the various lines of research within a larger *ecology of vegetation change* would help to increase the effective dissemination of findings and ideas.

Individual researchers can facilitate this reassociation by consciously using the literature of related fields, by selecting key words that will increase the visibility of an article beyond the researcher's immediate specialty area, and by undertaking more integrated studies of vegetation change. Our analyses suggest that ecologists actually research and write their papers in a context that is broader than the one they use to describe their papers to others. Although the research context clearly needs to be broadened, a simple first step ecologists could take is to do a better job preaching what we practice.

This reassociation of research areas would also be facilitated by a few simple changes from journals and ecological societies. Explicit guidelines and standardization of key words in journals would be a start. This effort could use as a guide the recent efforts to develop an ecological metadata language (EML), which has been developed to facilitate the searching and retrieval of data (<http://knb.ecoinformatics.org/software/eml/>). Sessions and symposia at meetings, and even entire meetings, organized around the ecology of vegetation change would also accelerate the rate and extent of scientific exchange by attracting researchers from the diverse specialty areas currently studying vegetation change, e.g., invasion ecology, succession ecology, gap/patch dynamics, global change impacts, restoration ecology, conservation biology, and weed biology.

Researchers of vegetation change would benefit greatly from the intellectual synergy that would inevitably result from better communication among research specialty areas. It seems the subdisciplines that study vegetation change have been connected intellectually only tenuously. Communication has been uncertain and intermittent. We need broad, frequent interactions. By promoting rapid and more effective communication among diverse researchers, and by emphasizing shared mechanisms and common functional impacts of plants, as opposed to narrow theories, concepts, and terminologies associated with particular research areas, we can expedite our understanding of the ecological mechanisms and consequences associated with plant communities in flux.

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in which the research is conducted.

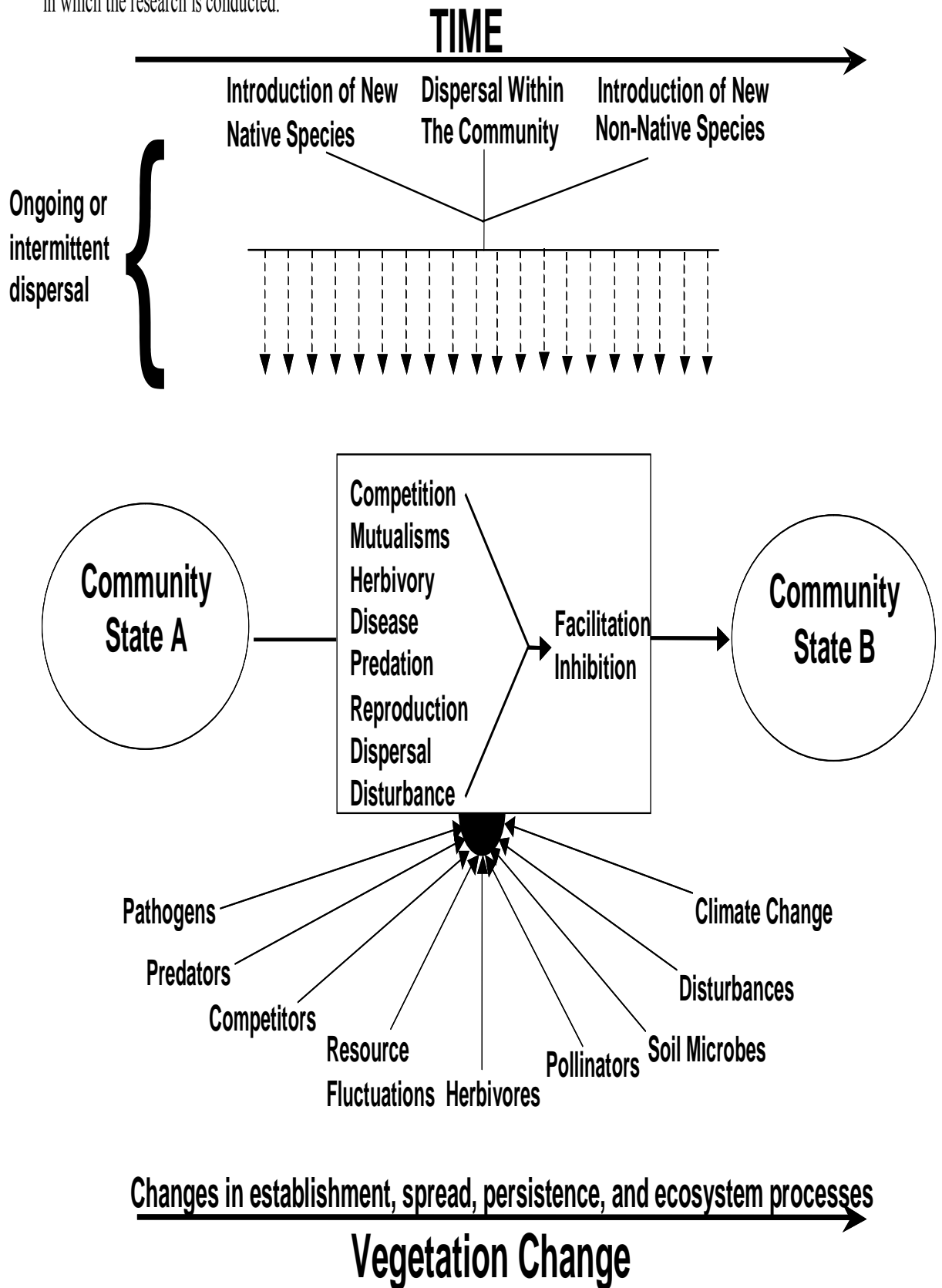


Figure 1. The same factors change plant communities regardless of the specialty area in which the research is conducted.

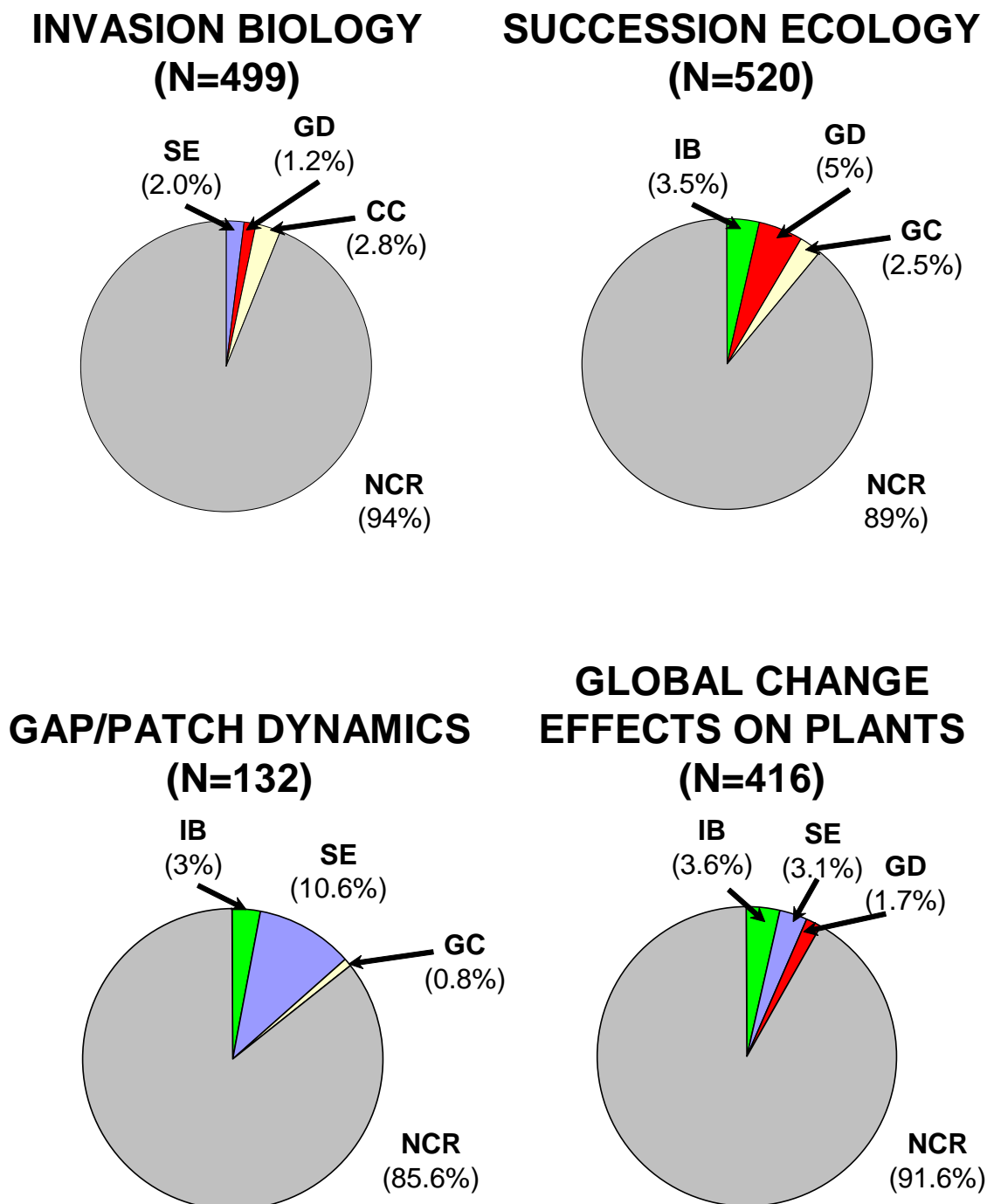


Figure 2. Patterns of cross-referencing in articles from four research areas that study vegetation change, based on an analysis of keywords. Cross-referencing is defined as using keywords typically associated with one of the other research specialty areas. Analyses were conducted using the BasicBIOSIS electronic database for articles published since January 1999. Percentages indicate the percent of the sample of articles that used a keyword typically associated with one of the other specialty area. Sample sizes (number of articles for which keywords were analyzed) are listed for each research specialty area. See Table 1 for a detailed description of the analysis methods used. IB=Invasion Biology, SE=Succession Ecology, GD=Gap/Patch Dynamics, GC=Global Change Effects on Vegetation, NCR=No Cross-Referenced Key Words Used.

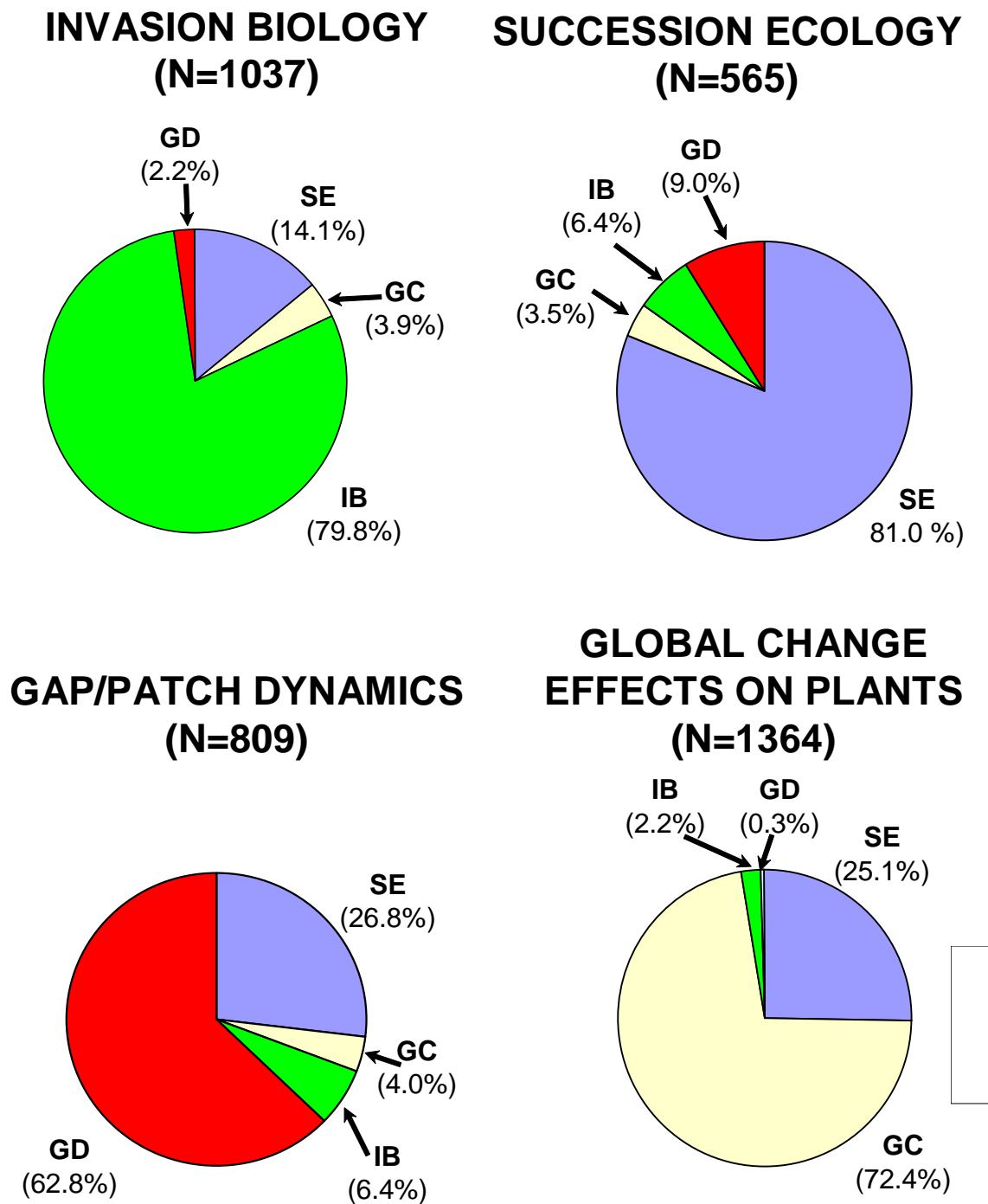


Figure 3. The distribution of sources cited in bibliographies found in research specialty areas that could be assigned to one of the four research specialty areas based on their titles. IB=Invasion Biology, SE=Succession Ecology, GD=Gap/Patch Dynamics, GC=Global Change Effects on Vegetation.

TYPES OF INTERACTIONS BETWEEN  
NATIVE AND INTRODUCED SPECIES

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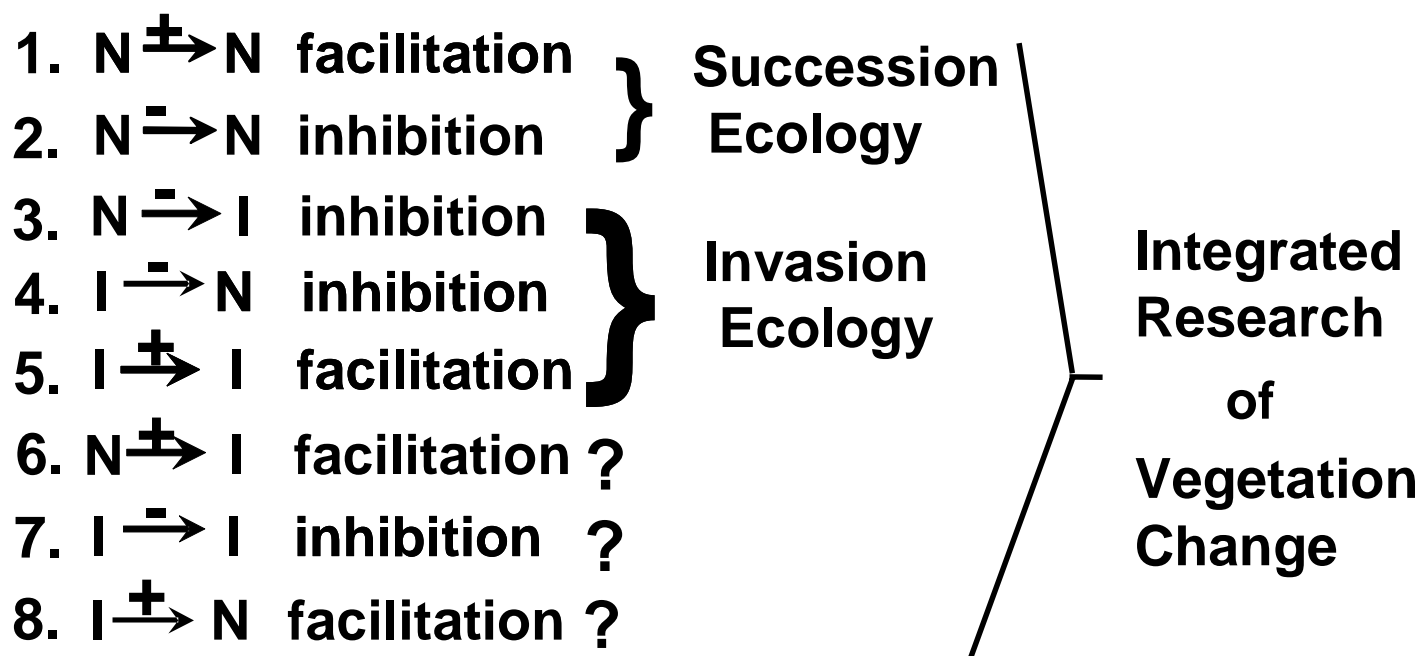


Figure 4. Eight types of interactions among native (N) and introduced (I) species based on possible facilitation and inhibition among species. The first two types of interactions are addressed in most studies of succession. The next three types of interactions are typical subjects for invasion ecology studies. The last three types of interactions have been studied less frequently and are not typical studies of either succession or invasion ecology, but they do occur. All eight types of interactions can be studied through an integrated approach organized around the notion of vegetation change.

Table 1. The combination of key words used in the electronic search of the BasicBiosis data base to identify a sample of articles in each of the four research specialty areas listed. The articles identified for a particular research area were then queried with the key words of each of the other respective areas in order to identify articles in which the author consciously chose to connect his/her paper with one or more of the other research areas. (BasicBIOSIS indexes more than 300 journals and other publications in the life sciences, including the following botanical, ecological, and general science journals that regularly publish plant ecology articles: *Advances in Ecological Research*, *Agriculture Ecosystems and Environment*, *American Journal of Botany*, *American Midland Naturalist*, *American Naturalist*, *Annals of Botany*, *Annals of the Missouri Botanical Garden*, *Annual Review of Ecology and Systematics*, *Applied Vegetation Science*, *Biodiversity and Conservation*, *Biological Conservation*, *Biological Reviews*, *Bioscience*, *Botanical Review*, *Canadian Journal of Botany*, *Conservation Biology*, *Ecological Monographs*, *Ecology*, *Environmental Conservation*, *Environmental and Experimental Botany*, *Evolution*, *International Journal of Plant Sciences*, *Journal of Applied Ecology*, *Journal of Ecology*, *Journal of Forestry*, *Journal of the Torrey Botanical Society*, *Nature*, *Oecologia*, *Oikos*, *Phytopathology*, *Plant Cell and Environment*, *Plant and Soil*, *Proceedings of the National Academy of Sciences of the United States of America*, *Proceedings of the Royal Society Biological Sciences Series B*, *Quarterly Review of Biology*, *Science*, *Trends in Ecology & Evolution*, *Trends in Plant Science*)

Invasion Ecology	Succession Ecology	Gap/Patch Dynamics	Global Change Effects
alien + plant	succession + plant	gap + plant	global change + plant
alien + vegetation	succession + vegetation	gap + vegetation	global change + vegetation
exotic + plant		patch + plant	climate change + plant
exotic + vegetation		patch + vegetation	climate change + vegetation

Table 2. Examples of words used to assign sources to the respective four research specialty areas in the bibliography analyses.

PATCH & GAP:	gap, patch, stand dynamics, canopy opening, treefall (pits, mounds), canopy damage, hurricane damage, vegetation dynamics, structural dynamics, canopy closure, vegetation change, small-scale disturbance, chronosequence
SUCCESSION:	succession, vegetation dynamics, successional, chronosequence, forest recovery in abandoned pasture, vegetation change, vegetation recovery, species turnover, shifting dominance
INVASION:	invasive, alien, invader, exotic, invasibility, introduced plant, invading adventitious species, non-indigenous species, bioinvasion
CLIMATE CHANGE:	climatic change, global change, changed nutrient levels, global warming, temperature change, environmental change, global desertification, atmospheric deposition.

Table 3. An overview of how succession and invasion ecology can be studied using an integrated approach to reveal the underlying population, community, and ecosystem processes that influence the establishment and spread of native and introduced species.

Over-Arching Principles	Key Research Questions	Types of Studies Needed
<ul style="list-style-type: none"> <li>• Interactions among plants and trophic levels influence the establishment and spread of native and introduced species.</li> <li>• The effects of the interactions between arriving and resident plants are due to the functional traits and relative abilities of species involved, not to the geographic origin of the species.</li> <li>• Species colonization, establishment, and spread are influenced by the spatial context and history of a site.</li> <li>• Global change is influencing patterns of establishment and spread of native and introduced species.</li> <li>• The evolutionary history of species involved influences the establishment and spread of native and introduced species.</li> <li>• Transient windows of opportunity are crucial for the establishment and spread of native and introduced plant species.</li> </ul>	<ul style="list-style-type: none"> <li>• To what extent do arriving species succeed because they inhibit resident species, or because they are tolerant of, or are facilitated by, the effects of residents?</li> <li>• What are the mechanisms by which arriving species (native or introduced) affect the rate and direction of vegetation change?</li> <li>• What are the mechanisms by which habitat patchiness influence dispersal success of native and introduced species?</li> <li>• What are the mechanisms by which the recent and historic disturbance and land-use history of a site influence the establishment and spread of introduced and native species?</li> <li>• What are the mechanisms by which global change factors, individually and together, influence the establishment and spread of introduced and native species?</li> <li>• To what extent, and in what way, does the evolutionary history of the species involved, both resident and arriving, influence the establishment and spread of introduced and native species?</li> <li>• What are the mechanistic explanations behind the ‘windows’ of opportunity that facilitate the establishment and spread of introduced and native species?</li> </ul>	<ul style="list-style-type: none"> <li>• Comparative studies               <ul style="list-style-type: none"> <li>--phylogenetic studies (e.g., congener comparisons)</li> <li>--geographic comparisons (e.g., gradients of latitude, altitude, climate, disturbance and land-use history)</li> </ul> </li> <li>• For studies of mechanisms operating on a small scale, manipulative experiments (e.g., deletion/addition studies) focusing on the effects of:               <ul style="list-style-type: none"> <li>--the resident populations, community, and ecosystem on arriving species</li> <li>--the arriving species on the resident populations, community, and ecosystem</li> </ul> </li> <li>• For studies of large-scale systems and phenomena, observational and correlative studies of existing ‘natural experiments’ will be necessary</li> <li>• Modeling studies of establishment and spread of native and introduced species based on knowledge gained from field data.</li> </ul>