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Vegetation change: a reunifying concept in plant ecology

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Abstract

Specialization can become detrimental to a discipline if it fosters intellectual isolation. A bibliographic analysis of several research areas in plant ecology (invasion biology, succession ecology, gap/patch dynamics, and global change effects on plants) 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. Invasion papers were least likely to be cross-linked (6%) with other fields, whereas gap/patch dynamics papers were most likely to be cross-linked (15%). This tendency toward intellectual isolation may be impeding efforts to achieve more powerful generalizations in ecology by reducing the number of potentially productive exchanges among researchers. In this paper, we illustrate this problem using the example of several speciality areas that study vegetation change. We argue that, 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. As an example, we propose that several speciality areas of plant ecology could be reunified under the term *ecology of vegetation change*. Individual researchers, journals, and ecological societies all can take specific steps to increase the useful exchange of ideas and information among research areas. Promoting rapid and more effective communication among diverse researchers may reduce the proliferation of narrow theories, concepts,

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and terminologies associated with particular research areas. In this way, we can expedite our understanding of the ecological mechanisms and consequences associated with plant communities.

Keywords: Climate change; Gap dynamics; Invasion ecology; Patch dynamics; Succession; 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).

In contemporary ecology, there are at least four prominent research speciality areas that study vegetation change: succession ecology, invasion biology, gap/patch dynamics, and global change effects on plant communities. The underlying processes studied in each of these areas are basically the same. First, colonization, establishment, turnover, persistence, and spread are fundamental events and processes that interact to produce vegetation change in all four subdisciplines; second, whatever the nature of vegetation change, it is often initiated or greatly influenced by, disturbance and/or changes in interactions with other trophic levels; third, local and long-distance dispersal allow new species to enter existing plant communities; fourth, facilitation and inhibition, as well as interactions with species from other trophic levels, strongly influence vegetation change; and fifth, 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 four research areas seek 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 there to be considerable information exchange among these research areas.

Examining communication among subdisciplines

One way to investigate whether such communication is in fact occurring is to examine keywords and the bibliographies of papers published in the different research areas. The selection of keywords for an article involves deliberate decisions on the part of the author to make the paper accessible to a particular group of researchers, e.g., through electronic searches. Thus, keywords should reflect an author's assessment of the paper's scope and relevance. An analysis of keywords in articles within a single speciality 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 keywords represents an explicit decision by the authors about how to present the scope of an article, a bibliography represents more an empirical documentation of the author's use of findings and ideas from the literature while writing the article. Thus, analyses of keywords 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

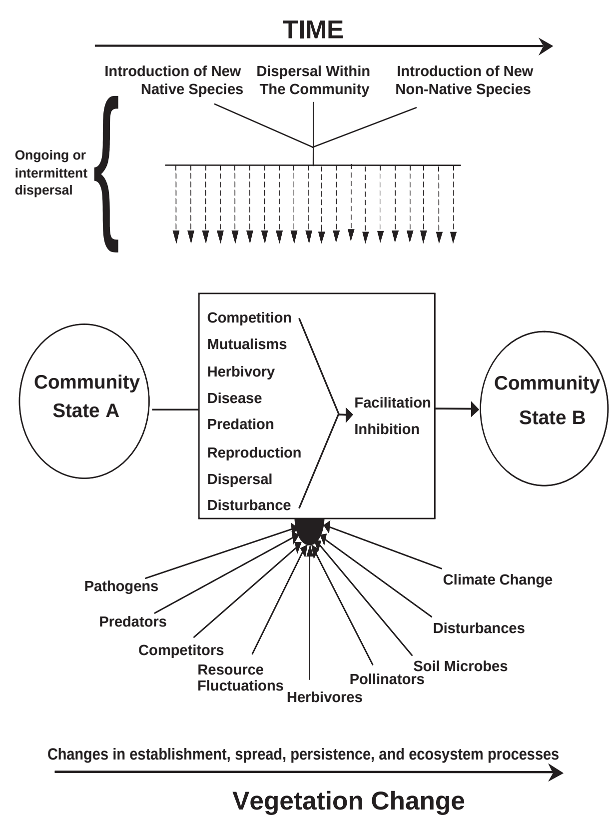

Fig. 1. The same factors change plant communities regardless of the speciality area in which the research is conducted.

Table 1. The combination of keywords used in the electronic search of the BasicBIOSIS database to identify a sample of articles in each of the four research speciality areas listed. The articles identified for a particular research area were then queried with the keywords 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

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

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 quite 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 keywords by searching the BasicBIOSIS electronic data base (http://www.biosis.org), which indexes 37 prominent botanical, ecological, and general science journals that regularly publish plant ecology articles. 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 keyword search (Table 1). These searches produced the following number of articles: invasion biology (499), succession (520), gap/patch dynamics (132), global/climate change (416). (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_2 levels, and rates of atmospheric deposition of nitrogen.) Each of the four samples were then queried using the keywords 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 biology 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 writing 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 keywords.

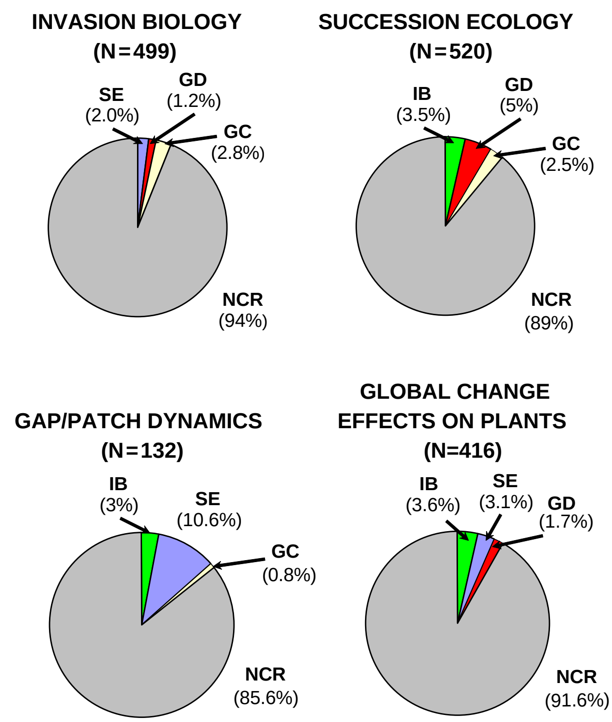

Fig. 2. Patterns of cross-referencing in articles from four research areas that study vegetation change; based on an analysis of keywords. Cross-referencing is defined as using keywords typically associated with one of the other research speciality areas. Analyses were conducted using the basicBIOSIS electronic database for articles published from January 1999 to December 2003. Percentages indicate the percent of the sample of articles that used a keyword typically associated with one of the other speciality area. Sample sizes (number of articles for which keywords were analyzed) are listed for each research speciality 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 keywords used).

Table 2. Examples of words used to assign sources to the respective four research speciality 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.

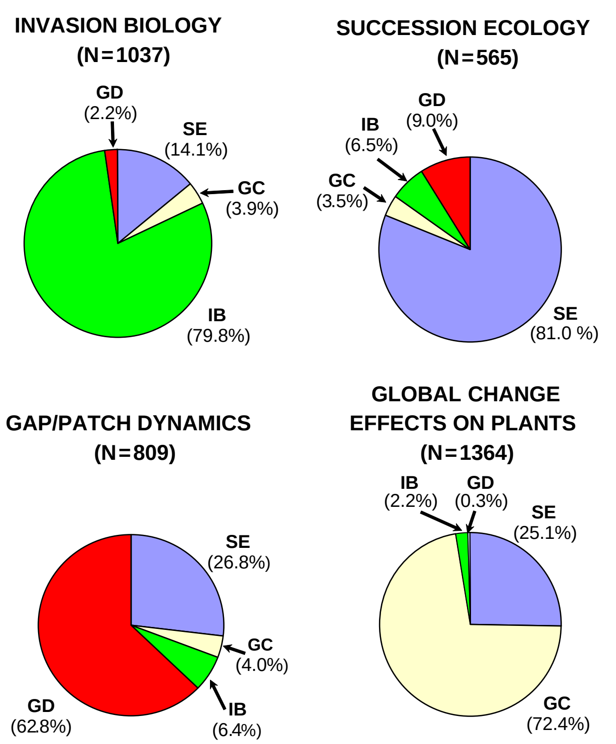

Fig. 3. The distribution of sources cited in bibliographies found in research speciality areas that could be assigned to one of the four research speciality areas based on their titles (IB, Invasion Biology; SE, Succession Ecology; GD, Gap/Patch Dynamics; GC, Global Change Effects on Vegetation).

Authors who consciously envisioned their paper as part of a particular research speciality area (as evidenced by their choice of keywords) overwhelmingly chose to consult sources within their speciality area in their papers (Fig. 3). Nevertheless, the authors' use of the research literature tends to be broader than the way they characterize the paper.

We can think of several reasons why authors might characterize their articles so narrowly. Some may want their articles strongly identified with a specific research speciality area because 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 and simply reflect a 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.

Four ways to close the gap

Our analyses indicate that most researchers who study vegetation change do so within a narrow conceptual framework. 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 speciality 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. The fourth step should be undertaken by the scientific community as a whole.

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 speciality area could be considered a part of a larger research initiative: *the ecology of vegetation change.* There is precedence for this perspective. Luken (1990) recognized vegetation change as the fundamental subject area relevant to all kinds of vegetation management. Thus, the first step is to be aware that related speciality areas exist. This step may be especially important for young researchers, such as doctoral students, who may have limited awareness of the scope of their and related research areas. If researchers began to envision themselves as studying vegetation change, rather than an invasion biologist, or succession ecologist, they would be less inclined to take a parochial perspective with respect to their research.

Pay more attention to the research in related speciality areas

The simplest step individual researchers can take to increase communication among speciality 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 (e.g., De Deyn et al., 2003). 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 (e.g., Christian and Wilson, 1999). Also, researchers can take simple steps to increase the likelihood that their own articles are read by researchers in other speciality areas. By carefully selecting keywords 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 keywords 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 keywords. Authors would construct the first set by selecting words from a standardized list of keywords representing general ecological concepts and phenomena. The second set would consist of more specific keywords, identified by the author and not standardized, that would reflect more specific aspects of the article. Taking these steps would enable researchers to increase the significance and impact of their own studies. They would also help to increase communication between subdisciplines and thereby facilitate efforts to understand causes and consequences of vegetation change.

Design studies that cross 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).

Role of the whole scientific community

This reassociation of research areas would also be facilitated by a few simple changes from journals and ecological societies. Explicit guidelines and standardization of keywords 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 speciality areas currently studying vegetation change, e.g., invasion ecology, succession ecology, gap/patch dynamics, global change impacts, restoration ecology, conservation biology, and weed biology.

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

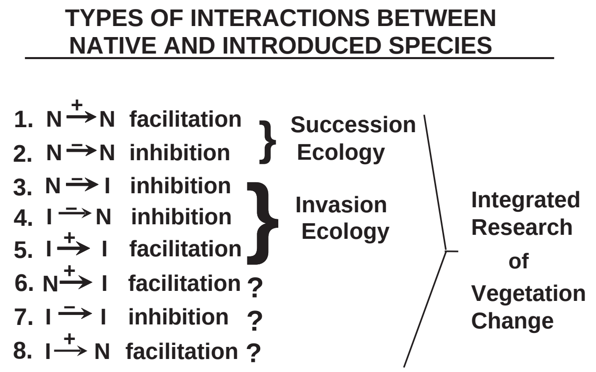

Fig. 4. Eight types of interactions among native (N) and introduced (I) species based on possible facilitation and inhibition among species. The first two types of interactions are addressed in most studies of succession. The next three types of interactions are typical subjects for invasion ecology 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.

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 among 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 consider 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 3, 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 nicitans*, 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, USA, 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). And, De Pietri (1992) showed that *Rosa rubiginosa*, a shrub introduced to Argentina, facilitated the re-establishment 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 accounting 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 (e.g., Lavorel et al., 1999).

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). Our analyses suggest that ecologists actually research and write their papers in a context that is

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
Interactions among plants and trophic levels influence the establishment and spread of native and introduced species.	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?	Comparative studies: phylogenetic studies (e.g., congener comparisons); geographic comparisons (e.g., gradients of latitude, altitude, climate, disturbance and land-use history).
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.	What are the mechanisms by which arriving species (native or introduced) affect the rate and direction of vegetation change?	For studies of mechanisms operating on a small scale, manipultative experiments (e.g., deletion/addition studies) focusing on the effects of: the resident populations, community, and ecosystem on arriving species; the arriving species on the resident populations, community, and ecosystem.
Species colonization, establishment, and spread are influenced by the spatial context and history of a site.	What are the mechanisms by which habitat patchiness influence dispersal success of native and introduced species?	For studies of large-scale systems and phenomena, observational and correlative studies of existing 'natural experiments' will be necessary.
Global change is influencing patterns of establishment and spread of native and introduced species.	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?	Modeling studies of establishment and spread of native and introduced species based on knowledge gained from field data.
The evolutionary history of species involved influences the establishment and spread of native and introduced species.	What are the mechanisms by which global change factors, individually and together, influence the establishment and spread of introduced and native species?	
Transient windows of opportunity are crucial for the establishment and spread of native and introduced plant species.	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?	
	What are the mechanistic explanations behind the 'windows' of opportunity that facilitate the establishment and spread of introduced and native species?	

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.

We believe that an effort to reunify several speciality areas in plant ecology can substantially enhance ecologists' ability to discover and generalize the mechanisms in the various specialties. In the case of vegetation change, rather than characterizing studies of vegetation change on the basis of what distinguishes them from one another, which tends to result too often in narrow theories, concepts, and terminologies associated with particular research areas, 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.

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