

Rethinking plant community theory

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Plant communities have traditionally been viewed as either a random collection of individuals or as organismal entities. For most ecologists however, neither perspective provides a modern comprehensive view of plant communities, but we have yet to formalize the view that we currently hold. Here, we assert that an explicit re-consideration of formal community theory must incorporate interactions that have recently been prominent in plant ecology, namely facilitation and indirect effects among competitors. These interactions do not support the traditional individualistic perspective. We believe that rejecting strict individualistic theory will allow ecologists to better explain variation occurring at different spatial scales, synthesize more general predictive theories of community dynamics, and develop models for community-level responses to global change. Here, we introduce the concept of the integrated community (IC) which proposes that range from highly natural plant communities individualistic to highly interdependent depending on synergism among: (i) stochastic processes, (ii) the abiotic tolerances of species, (iii) positive and negative interactions among plants, and (iv) indirect interactions within and between trophic levels. All of these processes are well accepted by plant ecologists, but no single theory has sought to integrate these different processes into our concept of communities.

Preamble

Many ecologists have expressed concern that progress in ecology is insufficient (Wilkinson 1998, Austin 1999, O'Connor 2000, Swihart et al. 2002). Among the most compelling, Austin suggests that progress is limited by fundamental inconsistencies between paradigms within ecology (Austin 1999). Our perception of plant community organization is affected by a historical dichotomy of individualistic versus organismal classifications. Clements likened the plant community, or association, to an organism, "able to essentially reproduce its component parts" (Clements 1916), whereas Gleason argued that a plant community is "scarcely even a vegetational unit, but merely a coincidence" (Gleason 1926). Gleason's view prevailed and various permutations of the individualistic paradigm now permeate our thinking as ecologists (i.e. species as neutral, Hubbell 2001); however, very few clear and non-controversial definitions of the theory exist. For example, a recent apologetic for

Gleason clearly presents modern misinterpretations of his ideas but does not conclude with a call to an appropriate definition of individualistic theory (Nicholson and McIntosh 2002).

While it is tempting to dismiss this legacy as ancient history and argue that we have moved beyond this, the bottom line is that although modern experiments are much more multifactorial and often consider many species within a community, there is still a bias in plant ecology to structure research and interpret results from an individualistic perspective. Certainly, the study of individualistic attributes such as physiological tolerance or competitive ability has led to very successful research on the importance of the environment and competition as factors structuring plant communities. Also without question, facilitation and its importance has also been clearly demonstrated (Bruno et al. 2003). Nonetheless, both processes are still interpreted primarily in the context of single species. We suggest that community ecology is ready to synthesise new empirical success. Bruno et al. (2003) proposed that the inclusion of facilitation into ecological theory "...will fundamentally challenge some of our most cherished paradigms" and "...that current theory emphasizing competition or predation paints an incomplete, and in some cases misleading picture of our understanding of the structure and organization of ecological systems". We take this one step further and submit that part of the solution to the old debate on individualistic versus organismal communities and recent experimental efforts to understand the relative importance of positive or negative interactions is to explicitly reconsider what most ecologists appear to have done implicitly; our formal conceptual theory of the fundamental nature of communities. Furthermore, we are confident that the adoption of a broader perspective for the concept of community will help circumvent the temptation to argue that one type of process, i.e. 'positive' versus 'negative'

interactions between plants, is more important than another (Shouse 2003).

Synthesis

Literally hundreds of recent studies conducted in virtually every biome on Earth have shown that plant species can have strong direct and indirect positive effects (i.e. facilitation) on other plant species (Hunter and Aarssen 1988, Bertness and Callaway 1994, Callaway 1995). In addition to facilitation, the recent emergence of indirect interactions among competitors is also at odds with a dichotomous view of communities. Indirect interactions among plants demonstrate that simple pair-wise competition among multiple species can produce webs of positive and negative effects with profound effects on community organization (Wilson and Keddy 1986, Miller 1994, Li and Wilson 1998, Levine 1999, Callaway and Pennings 2000). Interestingly, these complex webs of positive and negative interactions can be produced by competitive effects alone, such as when at least one species of lower rank outcompetes one or more species of higher rank (Karlson and Jackson 1981, Aarssen 1983, Berlow 1999). Not only do changes in potential chains of

interactions refute a strictly individualistic interpretation, but 'interaction modification', where direct pair-wise interactions between species are modified by the presence or density of other species (Adler and Morris 1994, Wootton 1994, Inouye and Stinchcombe 2001), suggests that interdependence may be the norm within communities particularly (but not exclusively) when multiple trophic levels are considered. Clearly, an informal paradigm shift is occurring towards communities as an integrated assemblage of species in which a continuum of independent and interdependent relationships exists.

In the light of these subtle changes, we propose a simple model for plant communities which we term the 'integrated community concept'. We predict that community structure is inclusively determined by synergistic (non-linear) interactions among (i) stochastic processes, (ii) the specific tolerances of species to the suite of local abiotic conditions, (iii) positive and negative direct and indirect interactions among plants, and (iv) direct interactions with other organisms (Fig. 1, adapted from a schema used to illustrate the factors that limit geographic ranges, Krebs 2001, and a previously proposed general concept of biological filters, Grime 1998, Laakso et al. 2001). This schema is just one of many possible ways that these different processes might inter-

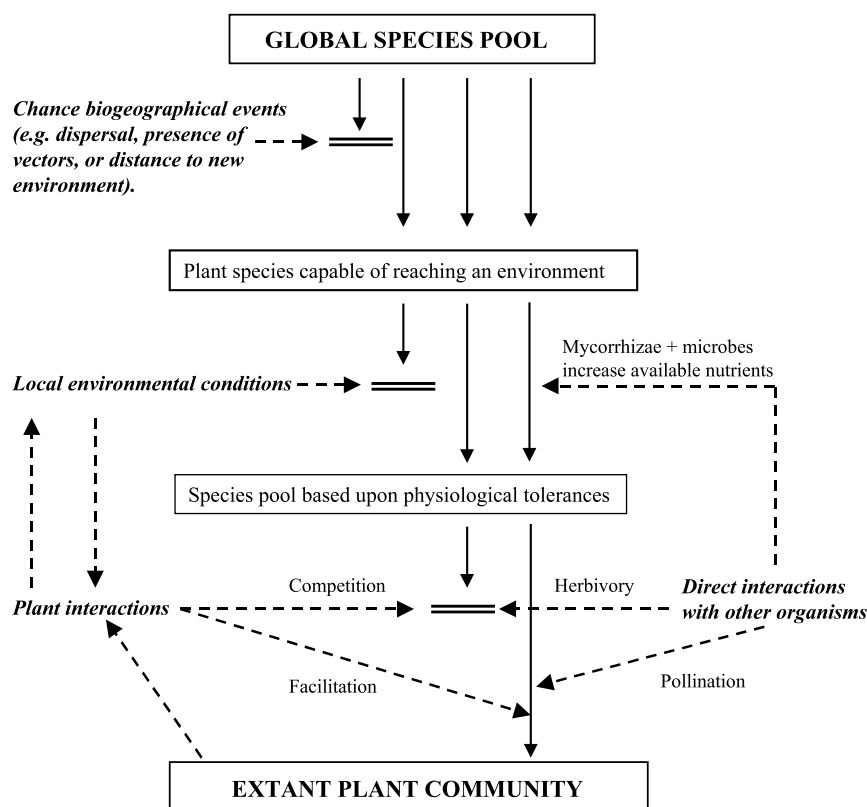


Fig. 1. The main processes or filters that structure a plant community. The IC concept proposes that all four processes can be important in determining the extant plant community at a given site but that the relative importance of each process will vary in space and time. Each process/filter is represented by a pair of horizontal lines and the corresponding description is in bold italics adjacent to the symbol (sub-sets of a process such as herbivory or competition are labeled in plain text). Solid arrows depict the movement of species through the filters, and hatched lines illustrate where each process might influence the plant community.

act to determine the composition of a community. Nonetheless, if communities are determined by complex interactions among these different categories of processes, and not just singly by competition or herbivory for instance, communities will function both as a collection of independent individual species and as assemblages of species. Hence, communities can be dualistic in nature being both individualistic and integrated to some degree. Similarly, others have previously proposed that communities can vary numerically in two distinct, possibly independent ways; in species composition within the community and in aggregate measures such as total abundance or biomass (Micheli et al. 1999). However, real communities are likely never functioning fully as either groups of individual species (present only due to individual tolerances) or as assemblages of perfectly integrated species (facilitating one another or directly interacting). Therefore, communities (and even a single community) will encompass a range of different dependencies among species – or degrees of integration – determined by the relative importance, and variation in space and time, of each of the filters we proposed. Again, the concept of filters is not crucial to our reconceptualization of community but rather serves as a convenient means to articulate the intersection of different processes in determining the representation of species. The crucial aspect of this visualization of the potential variation within a community is that every community will have a vertical component of depen-

dence (Fig. 2). While it is tempting to isolate only one sub-set of processes at a time such as competition and facilitation or even erroneously debate which type of interaction is more important – positive versus negative (Shouse 2003), this simplification can lead to faulty conclusions about the relative importance of a single process and overlooks the possibility of interactions between different types of processes. The real challenge is instead to determine when and where different processes are important, and to do this, we need to credit communities with more complexity, i.e. as a dynamic collection of species integrated to varying degrees (through competition and facilitation) inextricably linked to biotic and abiotic drivers.

Applications

Neutrality

Neutral models view all species as equal or at least as near neutral (Hubbell 2001), but niche-based models ascribe particular properties to species (Chave et al. 2002). Neutrality-based and niche-based concepts have radically different interpretations for mechanisms that promote and maintain diversity while assigning dramatically different levels of importance to specific species effects (Whitfield 2002, Ricklefs 2003), creating a modern dichotomy with fascinating parallels to the historical individualistic–organismal conflict. The IC allows us to reconcile these two views of the importance of species. Using our schema of how different processes might interact to determine the representation of species within a given community, random processes such as dispersal (the first process depicted in Fig. 1) can initially determine who arrives at a particular point in space (Hubbell 2001) but relatively non-random processes such as plant-plant interactions (positive and negative) determine who persists (Fig. 1, the third process). This suggests to us that both neutral and niche-based models (Chave et al. 2002) have conceptual power for predicting plant community composition, and the success of each will vary depending on influence the relative importance of species particularly at different points in space or in different types of habitats (Fig. 2). This is not to say that the neutral model proposed by Hubbell and the concept of niche are always correct interpretations of the importance of species to the community, but simply that different types of processes vary in relative neutrality or species specificity (perhaps viewed on a continuum of randomness) are important in determining the representation of species in a given community.

Similarly, in a recent comparison of the zero-sum multinomial distribution (ZSM) of Hubbell's neutral model versus the log-normal distribution (as null) by model fitting of two empirical data sets, the neutral model failed to fit the data better than the null the vast

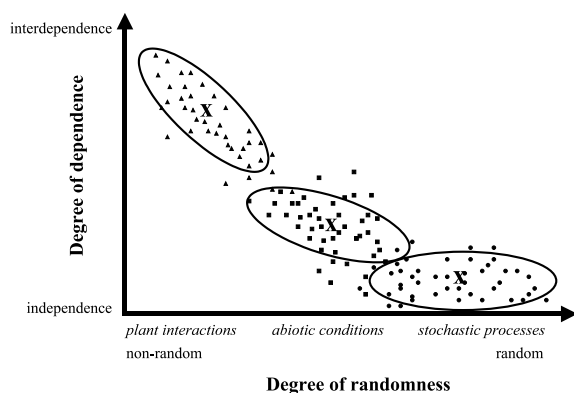


Fig. 2. The degree of dependence of individuals within a plant community as a function of the degree of randomness of processes that influence plant community structure. Different symbols represent individual species from different plant communities and each point is a value for a single species. Hypothetically, dependence for each species could be based on relative competitive intensity calculated from neighbor removal experiments, and randomness could be based on the relative importance of each of the three processes or filters that determine geographical ranges for each species. The ellipses represent a possible analysis of grouping of species within a community (such as through principal component analyses) which essentially describes the integration of the plant community. The centroid of each ellipse is shown with an 'x' and is equivalent to the hypothetical mean degree of integration for that community.

majority of the time (McGill 2003). McGill then concludes that "... the success of the lognormal does not mean that community structure is random; it simply means that community structure is a function of several multiplicative processes (the number of processes need not be large...)" Here, we also suggest that a number of processes influence community structure and that perhaps they can even be integrated into one framework when considering their relative importance, i.e. Fig. 1. Will the response of communities and ecosystems to large-scale changes be better explained by the reductionist consideration of individual species, the purely synergistic analyses of whole communities, or as we are suggesting, both?

Climate change

Currently, predictions of community change are based primarily on the 'climate envelopes' of species in which the future distribution of a species is projected from its adaptations to a particular set of climatic conditions (Davis et al. 1998, Walther et al. 2002). However, Davis et al. (1998) warn that most attempts to predict biotic responses to climate change may fail if species interactions are not explicitly considered. If both facilitative and competitive interactions are important in determining community structure, then design and interpretation of studies of community response must not be constrained by the assumption of species independence.

This is certainly the case in sub-alpine environments where the distribution of plant species is governed both by the physiological tolerances of species (their climate envelopes) and by facilitative and competitive interactions. Positive interactions appear to extend the upper elevational limits of many alpine plant species beyond their climate envelopes and competitive abilities (Choler et al. 2001, Callaway et al. 2002); while climate envelopes would predict that many high-altitude alpine species have the capacity to survive at low altitudes, their lower altitudinal limits are actually set by negative, competitive interactions from low-altitude species (Callaway et al. 2002). Hence, at least in the sub-alpine, interactions between species can strongly influence distribution along with the traits of specific species.

Using the IC, we might also predict that the indirect effects of species will change with perturbations in global climate. In general, weak interactions within communities have important effects by magnifying spatiotemporal variation in community structure (Berlow 1999). Therefore, the greatest variation in species effect may occur for the weakest interactions such as through the changes in the amelioration effect of neighboring species on high elevation target species (Callaway et al. 2002) or through indirect or 'apparent facilitation' (Levine 1999) by suppression of a competitor at lower elevations now

being released. Under either scenario, the new distribution of species will clearly be a product of changes in individual species tolerances plus the indirect interactions between species. Furthermore, the indirect interactions between species may even be more sensitive to climate change than the climate envelopes of individual species. In a recent review of climate change effects, Walther et al. (2002) similarly pointed out that "the complexity of ecological interactions renders it difficult to extrapolate from studies of individuals and populations to the community or ecosystem level." It could therefore be extremely productive to apply the IC concept to future studies of global climate change and include measurement and manipulation of species interactions (and interdependence) through species additions/removals concurrently with changes in abiotic conditions (a scenario which is likely to occur in time).

Invasive species dominance

If plant communities are organized only by stochastic processes, adaptation to the abiotic environment, and resource competition, how can a minor species from Eurasia arrive in North America and competitively exclude virtually all natives in an environment that the invader has never experienced? We may turn to trophic levels for explanations, and certainly the release from natural enemies is a crucial component of invasive plant success as illustrated by the success of some biocontrol herbivores (Blossey and Notzold 1995, Adler 1999, Willis et al. 2000, Maron and Vila 2001). However, a complete explanation of invasive success based solely on consumers assumes topdown control of communities at a level not yet realized by ecologists.

If plant-plant interactions are also an important process, then the regular exposure of species to each other (perhaps initial similar environmental tolerances and random events generate co-occurrence) may allow for co-evolution within communities. This may occur through competitive niche partitioning, development of tolerance to particular root exudates, or development of tolerance to how neighbors alter soil microbial communities. This does not mean that co-evolution leads to organismal utopia. Factors such as limited time, environmental variability, competitive equivalence (Aarssen 1983), or limited evolutionary potential in the initial species pool must provide strong limitations. Therefore, the IC can provide an alternative explanation to invasive species dominance. Invasive species disturb the (albeit imperfect) integration when introduced to a community, and there is generally room for new species (Shea and Chesson 2002) depending on how tightly the community is integrated.

For instance, Callaway and Aschehoug (2000) compared the competitive effects of *Centaurea diffusa*, an

invasive Eurasian forb, on three bunchgrass species that co-exist with *C. diffusa* in Eurasia to the effects of *C. diffusa* on three bunchgrass species from North America. If communities are integrated to some degree, than the original source community should be less affected by the invasive species due to long-term exposure to each other than the new community. This was the case both directly and indirectly; *Centaurea diffusa* had much stronger negative effects on North American species than it had on Eurasian species. Correspondingly, none of the North American grass species (nor all species analyzed collectively) had a significant competitive effect on the biomass of *C. diffusa*, but the Eurasian species *K. laerssenii*, and all Eurasian species analyzed collectively, significantly reduced *C. diffusa* biomass. Addition of activated carbon, which ameliorates the chemical effects of the invader on the grasses, also demonstrated that the indirect interactions between *C. diffusa* and the grass species differed with biogeographical region. This suggests that *C. diffusa* produces chemicals that long-term and familiar Eurasian neighbors have adapted to but that *C. diffusa*'s new North American neighbors have not. Hence, at least this study supports the position that considering the integration of a plant community can provide novel experiments that test for interdependence to better understand invasion ecology.

Conclusions

In light of the general importance of plant–plant interactions, our formal concept of a community should catch up with recent theory and experiments and move beyond the historical dichotomy. Ecologists do not believe that plant communities are either individualistic or organismal. If the reality of our functional paradigm of plant communities has progressed beyond this, then we need to explore and synthesize this perspective so that we can move forward experimentally and begin to investigate broad issues in community ecology and to communicate more effectively with other disciplines such as conservation biology. The synthesis we have applied here is hopefully a step towards this by providing a coherent causal explanation of the concept of a plant community. The IC states that plant communities can simultaneously function both individualistically with species being mainly independent to assemblages of different species which function interdependently. Given the complexity of natural systems, it is only reasonable to assume that the degree of integration between and within communities will vary in time and space. This does not imply that variation in community structure and composition is not predictable, and as such, we have applied the IC to several issues in ecology to demonstrate that the adoption of this framework only strength-

ens our ability to test how plant communities function. Explicitly recognizing the balance between independence and interdependence within communities will also allow us the conceptual freedom to better understand resistance and susceptibility of natural communities to human-induced change. While the integrated community concept may not be the only solution to encompass all the processes we now consider important in communities, at least the IC allows interdependence between species – a key focus of much ecological research. In short, the IC should not be viewed as yet another framework in which all new results must fit, but rather an attempt to break down the old paradigms for community, open new avenues of investigation with greater breadth, and serve as a reminder that often we progress more quickly experimentally and mathematically than we do conceptually.

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