

INVITED PERSPECTIVE

The third party

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Abstract. Spatial and temporal variation in interactions among plants, other species and the abiotic environment create context-dependency in vegetation pattern. We argue that we can enhance understanding of context-dependency by being more explicit about the kinds of direct interactions that occur among more than two living and non-living entities (i. e., third through nth parties) and formalizing how their combinations create context-dependency using simple conceptual models. This general approach can be translated into field studies of context-dependency in communities by combining: progressive sampling of local variation in vegetation pattern that encompasses variation in combinations of direct interactions; spatial and temporal measures of these direct interactions; locally parameterized versions of the conceptual models; and appropriately scaled experiments.

Keywords: Abiotic factor; Biotic factor; Competition; Context-dependency; Direct interaction; Ecosystem engineering; Facilitation; Indirect effect; Species interaction.

Context-dependency in vegetation pattern

Outcomes of direct competition between two or more plant species for an abiotic resource such as light can be changed by drought (Holmgren et al. 1997, 2000), additional plant competitors for light (George & Bazzaz 1999), mycorrhizal associations (Hartnett et al. 1993; Marler et al. 1999), herbivory (Hay 1986; Hambäck et al. 2000), and neighboring plant influences on salinity (Bertness & Shumway 1993) or microclimate (Callaway et al. 2002). Similarly, facilitative outcomes between two plant species may not occur because of increased resource levels (Tewksbury & Lloyd 2001), variation in structural architecture of a neighbor (Callaway et al. 1991), absence of herbivores or pollinators (Hambäck & Beckerman 2003; Feldman et al. 2004), or changes in abiotic stress intensity (Bertness & Callaway 1994). In



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all these and many other situations a living or non-living third through n th entity or 'party' intervenes to change the magnitude or direction of outcomes. Such conditionality or context-dependency in local vegetation pattern may be the norm, or at least very common. Context-dependency makes explaining or predicting vegetation patterns very challenging; many different kinds of interactions may have to be considered, along with their strengths and spatial and temporal configurations.

Here we argue that we can enhance understanding of context dependency in vegetation pattern by being more explicit about the kinds of direct interactions that occur among living and non-living parties, and we formalize how combinations of such direct interactions can change outcomes. We then present an approach based on this that can enhance field studies of context-dependency.

Outcomes, interactions and living and non-living parties

We use the term 'party' as informal parlance for any living or non-living entity (e.g., a species, an abiotic resource), and define a direct interaction as one in which one party affects another without any intermediary party. Ecological outcomes result from direct interactions among parties plus indirect influences arising because at least one of these parties also directly interacts with at least one another party. Thus if A affects B and B affects C, then A and C can influence each other through B, irrespective of whether A, B, or C are living or not. We often think of parties only as species. Indeed, indirect effects, which have received substantial attention as often subtle drivers of complex outcomes in communities (Miller 1994; Wootton 1994; Levine 1999; Callaway & Howard 2006), are defined as a third (through n th) species influence (Strauss 1991). However, it is well-recognized that such indirect influences are often mediated via third abiotic parties. We think more rapid progress in understanding context-dependency in vegetation outcomes can be made by being more explicit about these direct interactions among living and non-living parties.

Direct interactions among living and non-living parties

What kinds of direct interactions influence vegetation pattern? One can argue there are many, but we think it useful to consider just three general kinds: abiotic effects on species; species effects on the abiotic environment; and direct species interactions. It is worth noting that although indirect effects *sensu stricto* encompass the second and third kinds of direct interactions, species

effects on the abiotic environment are often subsumed into net species effects on species.

Abiotic effects on species include well-known resource and non-resource effects of many abiotic variables (e.g., light, precipitation, temperature, pH, soil nutrients, topography, fire, wind, salinity, landslides). Species effects on the abiotic environment arise in two ways. First, abiotic changes are caused by resource uptake (e.g., light, water, nutrients) and organic and inorganic material release into the environment (e.g., litter, mineralization). Second, there are ecosystem engineering effects of species on abiotic resources and non-resource factors (Jones et al. 1994, 1997; van Breemen & Finzi 1998) that arise independent of abiotic changes due to resource uptake or simple release. They include physical effects of organismal structures and organismally-induced structural change on abiotic variables (e.g., invertebrate burrowing and soil drainage; wind attenuation by canopies; litter effects on rain splash, temperature, soil gas exchange), and changes in abiotic chemical reactivity caused by certain materials that species release into the abiotic (e.g., H⁺ ions and pH, organic compounds causing complexation, flammable materials).

Direct interactions of species require a material or information transfer or exchange among them. Examples include trophic transfer from plants to consumers and from consumers to higher trophic levels; mycorrhizal/plant resource exchange; root graft resource exchange; plant/plant allelochemical inhibitors or stimulants; and reward-mediated animal vectoring (pollination and dispersal). It is worth noting that from this perspective plant competition for abiotic resources is not a direct species interaction; it arises from the coupling of the direct effects of each species on the same abiotic resource pool.

Combining direct interactions to assess context-dependency

How can the above kinds of direct interactions be combined to assess potential for context-dependency? We illustrate using two connected general conceptual models that can be used to create more specific models that incrementally incorporate conditional influences.

1. Limiting abiotic resources.

Given two or more plant species differentially using the same limiting abiotic resource, the following have the potential to cause context-dependency in vegetation pattern.

1.1. Externally driven variation in the abiotic resource (water or nutrients; light and CO₂ can be assumed to be externally invariant). Differential resource use results in different degrees of limitation depending on resource

amount. Although the basic interaction type is the same, the ‘dose-response relationship’ differs among plant species; thus variation in dose has differential effects (e.g., variation in initial resource availability in the R* hypothesis, Tilman 1985).

1.2. Variation in the number of plant species using the same resource (e.g., light, George & Bazzaz 1999). Here all species have the same type of direct interaction – uptake of a common resource. Whether or not outcomes change will depend upon where additional species sit in a resource use hierarchy.

1.3. Other species affect the recharge rate of the abiotic resource pool via local inputs (e.g. ‘resource supply points’, Tilman 1985, Fig. 1). For inorganic nutrients only, materials are added to the pool via species effects on the abiotic environment (a combination of organic matter abiotic inputs by plants and its microbial mineralization). The recharge rate influence operates as in 1.1 above.

1.4. Ecosystem engineering by species affects the size of the light, water or nutrient resource pool without using the resource, or in addition to any use. This is a different kind of species effect on the same abiotic variable (e.g., increasing water availability via runoff capture, Jones et al. 2006; or hydraulic lift, Dawson 1993).

1.5. Abiotic factors other than the limiting resource differentially affect plant species. Plant responses to these other abiotic factors (i.e., other resources or non-resource factors) affect the capacity to use the limiting resource with the influence being due to differential abiotic effects on species. When this other factor is a resource (e.g., how soil nutrients affect light interactions, Rice & Nagy 2000), then this limiting abiotic resource model can be used. If it is a non-resource factor then the second model (see 2 below) can be used.

1.6. Plant species have different direct interactions with other species (e.g., consumers, mycorrhizae, allelochemical inhibitors or stimulants) that then affect their resource use (e.g., arbuscular mycorrhizal fungi affecting phosphorus competition among grass species, Hartnett et al. 1993).

2. Abiotic non-resource constraints

Given two or more plant species differentially constrained (or enabled) by an abiotic non-resource factor, the following have the potential to cause context-dependency in vegetation pattern.

2.1. Externally driven variation in the abiotic non-resource factor (e.g., temperature, fire, humidity). This is similar to 1.1 above except that the “dose-response relationship” refers to non-resource factors (e.g., interactions among alpine plant species vary in direction and intensity with decreasing temperature, Choler et al. 2001).

2.2. Ecosystem engineering species alleviate or exacerbate the abiotic constraint. This is analogous to 1.4 above – e.g., *Pinus flexilis* effects on wind exposure of understory species, Baumeister & Callaway (2006; many nurse plant effects ameliorating temperature extremes via shading, e.g. Turner et al. (1966).

2.3. Other abiotic factors, either resources or another non-resource factor, differentially affect plant species. This is akin to 1.5 above because plant responses to other abiotic factors affect the capacity to deal with the abiotic constraint. When this is a non-resource factor then this abiotic non-resource constraint model can be used (e.g., the effect flooding appears to have on *Juncus roemerianus* tolerance to salinity, Pennings et al. 2005). If this factor is a resource then the first model (see 1 above) can be used.

2.4. Plant species have different direct interactions with other species (e.g., consumers, mycorrhizae, allelochemical inhibitors or stimulants) that then affect their capacity to deal with the abiotic constraint (e.g., mycorrhizal influence on plant heavy metal stress or tolerance, Hildebrandt et al. 2007). This is analogous to 1.6 above.

Different abiotic resources and non-resource factors vary in their effects on different species in the same community, both limiting resources and constraining non-resource factors may co-occur, and species vary in their effects on the abiotic environment. This makes the situation more complex, but does not preclude the use of the general models to assess possible causes of context-dependency. In real plant communities, complexity may well be reduced because some combinations of direct interactions will be more common than others, and any given locale is unlikely to have all possible combinations; this will simplify more specified local models.

Incremental understanding of context-dependency in space and time

Local spatial and temporal variation in vegetation pattern and in the combination of direct interactions, guided by local variants of the above general models, and accompanied by experiments, can be used to study context-dependency in vegetation communities. Most plant communities under the same baseline conditions (climate, gross topography, elevation, aspect, parent materials, regional colonist pool) nevertheless experience spatially and temporally heterogeneous abiotic resource and non-resource conditions at smaller scales of plant neighborhoods or vegetation patches (Ovington 1955; Jackson & Caldwell 1993; Canham et al. 1994, 1999). Vegetation composition between neighborhoods/patches or in the same locale over time can either be the same or different, and in the absence of stochastic variation, this similarity, or lack thereof, reflects local spatial and temporal conditionality in the coincident combination of direct interactions.

Similar community patterns can arise either because the kinds of direct interactions and their intensities among parties are the same (where intensity arises intrinsically from living and non-living parties interacting *and* the indirect influence of other connected direct interactions), or because different kinds of direct interactions somehow converge to produce the same pattern. In contrast, different patterns can arise either because the kinds of direct interactions are different or because the kinds of direct interactions are the same, but the interaction intensities differ. Thus areas with similar vegetation patterns can be used to test for causal uniformity vs. divergent causality with outcome convergence; whereas areas with different vegetation patterns can be used to test for divergent causality vs. differing interaction intensities of the same kinds of direct interactions. For any direct interaction to occur there must be spatial and temporal overlap of parties (where a legacy = temporal overlap), and for two or more direct interactions to influence each other the 'shared or common' parties must also overlap. Any given locale in space or over time that is characterized based on some vegetation pattern will have some combination of coincident direct interactions. Ubiquitous kinds of direct interactions will be found in most locales and times, whereas less frequent kinds will occur in fewer locations and times. Some of these locales and times will also have the same kinds of direct interaction but will vary in intensity.

If we incrementally sample locales and times with similar or dissimilar vegetation patterns we should frequently or rapidly encounter the most common causal combinations of direct interactions, and somewhere or periodically encounter the less frequent causal

combinations. We will also encompass greater variation in potentially influential direct interaction intensity. For example, if two plant species always use the same abiotic resource this should occur wherever and whenever they co-occur. In contrast, herbivory levels on one of those plant species that might be sufficient to affect a postulated competitive outcome among those species may well be found less often (Hambäck & Beckerman 2003). At some point sufficient locales and times will be sampled to collectively encompass enough variation in local vegetation pattern, combinations of direct interactions, and intensity of direct interactions to evaluate the robustness of outcomes and the conditions under which they change.

Measures of direct interactions and intensities (ecologists have many techniques for doing this; e.g., herbivory, engineering effects, resource use) in locales with similar or dissimilar vegetation pattern will generate correlations between pattern and combinations of local direct interactions (e.g., McCune & Allen 1985). For example, we might find similar vegetation where earthworms are abundant or herbivory is rare, suggesting divergent causality with outcome convergence. Such data can be used to evaluate competing, locally parameterized versions of the general models discussed above, including both the combinations of direct interactions and their measured intensities (e.g. Kikvidze et al. 2005). The most parsimonious explanatory models can then be tested by judicious, appropriately scaled manipulations of the identified direct interactions and their intensities (e.g., via species removal/addition, abiotic modification).

Depending on our ambition it is possible to progressively increase the number and kinds of direct interactions considered (e.g., Baumeister & Callaway 2006; Altieri et al. 2007). In the end we should emerge with a better understanding of which similar patterns have robust or variable cause, and which different patterns arise from different combinations of direct interactions versus variable intensity. We will also learn what kinds of direct interactions are most prevalent, which are most responsible for outcome change, and the frequency with which this occurs.

Summary and Conclusion

We have argued that we can enhance understanding of context dependency in vegetation pattern by: (1) being more explicit about the ways living and non-living parties can directly interact; and (2) formalizing how combinations of these may create context-dependency in simple conceptual models. We have further argued that we can translate this into a better understanding of context-dependency in vegetation communities by

combining: (1) incremental sampling of local variation in vegetation pattern that encompasses variation in combinations of direct interactions; (2) spatial and temporal measures of direct interactions; (3) locally parameterized versions of the general models; and (4) experiments manipulating the kinds of direct interactions and their intensities at appropriate spatial and temporal scales.

We recognize that our approach is not fully developed, not easy to do, and unlikely to always lead to unambiguous answers. Nevertheless, we think it logically extends and helps formalize what many vegetation scientists have been doing, as illustrated in many of the papers we cite. As pointed out in the introduction, there is now overwhelming evidence that species can positively or negatively affect each other in a surprisingly large number of ways via third parties. However, we need to move beyond this recognition and a tendency for outcome typology. We are simply arguing for a more explicit, comprehensive and integrative attack on the problem of context-dependency in vegetation pattern, and we hope that our framework will be a useful starting point.

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