*New Idea***The nine classes of plant-plant replacement****Randall W. Myster**

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Abstract

Current models of plant community dynamics have fallen short both of conceptualizing plant communities well and of giving researchers a tool that accurately predicts their dynamics. Here I present a new idea of how that conceptual model should be constructed. I begin with the observation that space is a critical component of plant life and how it changes determines—to a large extent—how individual plants change. I then define that space as consisting of the phyto-space, which the phyto-mass (biomass plus necromass) occupies, and the neighborhood space around that phyto-space where a plant can influence, and be influenced by, other plants. I posit that it is how plants that make up a community replace themselves over time, as their phyto-spaces and neighborhood spaces change, that is the fundamental process of plant community dynamics. Those plant-plant replacements fall into nine distinct classes that extend the concept of replacement to include new space created not just by whole plant mortality, but also by plant tissue loss. Finally, I suggest that because most plant-plant replacements involve seeds, seedlings and saplings, the mechanisms and tolerances of predation, pathogens, germination, herbivory and seedling/sapling competition will be most critical in determining the plant-plant replacements in any plant community and its resulting dynamics.

Keywords: neighborhood space; phyto-space; plant community dynamics

sorting where environmental gradients affect population vital rates and species interactions, (2) mass-effects where dispersal results in source-sink relations between populations in different patches, and (3) patch dynamics (Leibold et al. 2004). In patch dynamics (Pickett and White 1980), discrete disturbances occur in plant communities and create discrete patches, so that any plant community is a mosaic of patches each created by a disturbance in the past. Each of these disturbances has a regime that includes characteristics such as its severity, size, timing and duration. Severity, for instance, can be measured as the amount or proportion of plant biomass removed. In addition, multiple disturbances may occur in a patch over time and so patches can be a “palimpsest” showing lingering (i.e. legacy: Cramer et al. 2008, Elgersma et al. 2011) effects of several past disturbances. A good example of a lingering effect is when an agricultural field is no longer in use but the crop: (i) that was previously planted in that field persists; (ii) is no longer present itself but has facilitated the lingering presence of other plants; or (iii) is no longer present itself but has affected the soil or other ecosystem properties now found in the old field (that crop’s signature: Myster and Pickett 1994). Plant species within patches respond to the environmental changes brought on by disturbances, and those responses—recruitment, growth, reproduction, death—create any and all plant population and community patterns within that patch and, collectively, for the entire plant community.

Introduction

Researchers continue to try to conceptualize plant community dynamics. Current models include (1) species

Past models of plant community dynamics

Those models—species sorting, mass effects, patch dynamics—and other recent models of plant community dynamics have significant limitations (Leibold et al.

2004) and contain a host of false assumptions and oversimplifications (Tilman 2004, Gaston and Chown 2005, Gravel et al. 2010, Hart et al. 2016). They have also been dichotomized (Buchi et al. 2009) into “niche” models (Vandermeer 1972, Silvertown 2004) that investigate species differences vs. “neutral” models (Bell 2000, Hubbell 2001) which treat all species the same and instead emphasize the probabilistic processes of dispersal and plant death (Gravel et al. 2006).

One common modeling approach has been matrix models of tree species replacement (Horn 1976, Van Hulst 1979, Van Hulst 1992, Frelich et al. 1998). These models predict how tree species are replaced over time by generating probabilities found by sampling stems underneath the canopy of living individual trees or in their tree-fall gaps after they die (one possible definition of neighborhood space). Each tree species then has a vector of probabilities that represent how that species is replaced by each tree species found. These species vectors are then combined to form a matrix and, through matrix multiplication starting at an initial abundance matrix, may predict—but not explain through mechanism—the abundances of each tree species for any sampling time period into the future. This model assumes that the probabilities are constant, that is the matrix stays the same over the different life history stages of the canopy trees, within a given species, and over time.

Another approach has been unified neutral theory (Hubbell 2001). Here, species diversity (the major concern) is determined by a process similar to how genetic diversity is maintained in a gene pool, by drift or random prevalence among neutral loci. The model is a “zero-sum” game where each individual plant occupies just one space or unit of limiting resources as replacement proceeds. It assumes that all species are equivalent in their recruitment ability, in their competitive ability, etc. While individuals are treated equally regardless of species, however, the probability of replacement is positively correlated with the number of individuals within a species (p. 56 in Hubbell 2001). So, for example, a species with a large number of seeds arriving at a patch that is available for colonization would have a greater chance of colonizing that patch than a species with a smaller number of arriving seeds. Consequently, the number of species, the identity of those species, and their relative abundances, can all be maintained over time. Thus, neutral theory is similar to matrix replacement models, except that it counts seeds rather than stems.

A new paradigm

These models have been increasingly unable to explain plant community dynamics (e.g., in Neotropical forests, fields and grasslands: see chapters in Myster 2007, Myster 2012a, Myster 2017a, Myster in press) and so many researchers have turned to plant-plant

replacement (Horn 1976, Grubb 1977, Busing 1996, Poulson and Platt 1996, Balzter et al. 1998, Kneeshaw and Bergerson, 1998, Pacala et al. 1998) as a new and better paradigm (Myster 2012b). Plant-plant replacements are not large-scale events like disturbances, nor do they occur over entire patches, but instead happen at the scale of individual plants of potentially different sizes throughout plant communities (Myster 2012b). These replacements between individual plants combine to create plant community dynamics (Leibold et al. 2004, Buchi et al. 2009) and thus are its fundamental process.

Individual plant-plant replacements can occur whenever local space is released—by the death of a plant (Alcantara et al. 2015) or by other means such as loss of biomass or events that create new space, for example when a river changes its course and space that was underwater is now dry—and then re-occupied. That local space includes: (i) the space occupied by a plant’s living biomass and/or its dead necromass (together a plant’s phytospace: Myster 2012b); and (ii) the space outside a plant’s phytospace (a plant’s neighborhood space: Turkington & Harper, 1979) where the plant can influence, and be influenced by, other plants. The exact definition of the neighborhood space is a current research topic, but it has been estimated as: (i) circles of radius 12.5 cm with a herbaceous plant in the center (Naeem et al. 2000); (ii) circles of radius 25 times the diameter at breath height of a dead tree in the center or 15/25 m radius with a dead tree at the center (Canham et al. 2004); (iii) 5-10 m distances from a dying tree (Frelich et al. 1998); (iv) 0.001–0.1 ha (Frelich and Reich 1999); (v) a 0-25 m radius circle (Peters 2003); and (vi) radii of 5,10,15 and 20 m from the focal tree (Weiner et al. 2001).

Past models have often assumed that all replacements: (i) involve equal-sized spaces (considered as a surrogate for resources: Buchi et al. 2009, Hubbell 2001, Van Hulst 1992); and (ii) are one-to-one, that is one plant dies and is replaced with one, and only one, other plant. I believe that these assumptions are rarely true in plant communities and so I propose that the phyto-spaces and neighborhood spaces of all the plants involved in the replacements should be included in future models (Myster 2012b). I also propose that one-to-one replacement is but one of nine fundamental classes of plant-plant replacement (Table 1) which occur in plant communities (Pham et al. 2004, Myster 2017b, Yoda et al. 1963). The dynamics of any plant community then is defined by replacements among these nine different classes, operating over time in the phyto-spaces and neighborhood spaces of the plants involved.

This new more comprehensive, realistic and complete, paradigm for plant community dynamics contains replacements: (i) that don’t result from the death of a plant but from a loss of biomass and/or necromass or from release of phyto-spaces and/or neighborhood spaces by other means (the replacements: none→none,

Table 1. The nine classes of plant-plant replacement.

Replacement class	Description and example
none→none	No plant died and no new plant joined the neighborhood. New phyto-space and/or new neighborhood space may, however, have been released by a pre-existing plant and reoccupied by the same or another pre-existing plant. For example, when a branch falls off a tree and another tree grows a branch into that space(s).
none→one	No plant died and one new plant joined the neighborhood. The new plant may reoccupy space(s) that was released by a pre-existing plant. For example, when a branch falls off a tree and a tree seedling recruits into that space(s).
none→many	No plant died and more than one plant joined the neighborhood. These new plants may reoccupy space(s) that was released by a pre-existing plant. For example, when a branch falls off a tree and more than one tree seedling recruits into that space(s).
one→none	One plant died and no new plant joined the neighborhood. The space(s) released by the now dead plant may be reoccupied by a pre-existing plant. For example, when a tree dies and another tree grows a branch into that space(s).
one→one	One plant died and one new plant joined the neighborhood. The space(s) released by the now dead plant may be reoccupied by the new plant. For example, when a tree dies and another tree recruits into that space(s).
one→many	One plant died and more than one plant joined the neighborhood. The space(s) released by the now dead plant may be reoccupied by the new plants. For example, when a tree dies and more than one tree recruits into that space(s).
many→none	More than one plant died and no new plant joined the neighborhood. The combined or collective space released by the now dead plants may be reoccupied by a pre-existing plant. For example, when a tree dies and as it falls it pulls down another tree with it. Then, another tree grows a branch into that collective space.
many→one	More than one plant died and one plant joined the neighborhood. The combined or collective space released by the now dead plants may be reoccupied by this new plant. For example, when a tree dies and as it falls it pulls down another tree with it. Then, another tree recruits into that collective space.
many→many	Can be decomposed into the other replacement classes.

none→one and none→many: Table 1); (ii) where there is plant death but no resulting replacement (the replacements: one→none and many→none: Table 1) an example of which is the thinning phase of forest stand development (Grubb 1977); and (iii) involving more than one plant at a time (the replacements: none→many, one→many, many→none, many→one and many→many: Table 1) where the phyto-spaces and neighborhood spaces of those plants may overlap and/or combine (Kuuluvainen 1994) creating situations where plant-plant replacements may influence each other and create higher-level patterns within a plant community. Finally, the principle of parsimony suggests that the more complex a replacement is (moving down Table 1), the rarer it will be within a plant community.

Future research using this new paradigm

In this new paradigm, I extend the concept of replacement to include space created not just by whole plant mortality, but by plant tissue loss and other events as well. The new paradigm can help illuminate, and provide detail, for other models of plant community dynamics as well. As plant-plant replacements proceed within a patch, for example, they define how the patch changes, the mechanistic nature of those changes, and how the present composition of the patch was created. This new paradigm can also show how the species-species replacements of matrix models are a consequence of individual plant-plant replacements. As a species-species replacement model also, neutral models can be

decomposed into individual plant-plant replacement models where the use of phyto-spaces and neighborhood spaces is key. Indeed, plant-plant replacements can be used to test Neutral models by first ignoring the species of the individual plant-plant replacements, then not ignoring them, and comparing outcomes.

I posit that because plant communities have their greatest plant death at the post-dispersal (Myster 2017b) seed, seedling and/or sapling life stages (Grubb 1977) most plant-plant replacements will involve plants at these early stages of development as well. Therefore, mechanisms and tolerances that control those early plant life stages—predation, pathogens, germination, herbivory, competition—will be most critical in determining the majority of the plant-plant replacements in any plant community. Future modelers should be careful, however, not to assume panmictic replacement—that any species can be replaced by any other species—as was the case in both matrix and neutral models (see field data to refute that assumption in Alcantara et al. 2015, Verdu and Valiente-Banuet 2008, Gomez-Aparicio et al. 2008, Rother et al. 2013).

One corollary of this paradigm is that because any plant community is the consequence of past plant-plant replacements, we cannot see how plant communities are constructed if we only look at the current plant community. Therefore, future researchers need to establish permanent vegetation plots (Myster and Malahy 2008) and sample them over many years as spaces both inside (the phyto-space) and outside (e.g., the neighborhood space) plants are released and, potentially, reoccupied. This sampling should include plant death, biomass loss (e.g., a branch falling off a tree) or other events, which can make space available and any new plants or plant biomass that occupies that space (Table 1). Replacement patterns could include any of the nine different classes presented here, and analysis should examine correspondence between those patterns and (1) year of sampling, (2) plant species and (3) plant size (author, unpub. data).

Finally I suggest these five questions be part of future research: (1) Are some classes of individual plant-plant replacement more common than others? (2) Does that change over time? (3) Are patterns clear when we examine individual trees only, or are all the individuals of certain species/sizes replaced in the same way, so that we should examine species/size replacement patterns? (4) Do species/size replacement patterns suggest circularity or periodicity (Laird and Schamp 2006) which might then suggest maintenance of community patterns (e.g., richness) or maintenance of processes (e.g., species coexistence) over time? (5) Do patterns emerge when we put replacements into plant groups larger than species (strategies, “functional” groups) such as plant/stem size, dispersal vector (e.g., wind, bird, mammal), wood density or mycorrhizal association (Myster et al. 2013)?

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