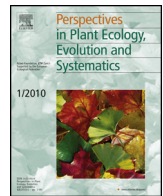




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## Review

# Structural constraints on novel ecosystems in agriculture: The rapid emergence of stereotypic modules



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## ABSTRACT

Agricultural ecosystems are, by their very nature, a cauldron of novel ecosystems, emerging with exotic species at the core of their very existence and followed by invasions of other species, so-called associated biodiversity. Within that framework similar ecosystem modules become assembled very rapidly with native and non-native species, a consistency that reflects deep ecological principles at both local and landscape levels. Here we describe three such modules: trophic levels and food webs, natural enemies in space and time, and trait-mediated trophic cascades and the accumulation of non-linearities. We propose that diverse agroecosystems are bound to contain such modularities and therefore have similar ecological structures as natural systems in spite of their novelty. We use examples from the coffee agroecosystem in Mexico to illustrate these modules.

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## Introduction

The central goal of ecology as it evolved into a distinct recognizable science, was effectively to understand the details of Darwin's "force of selection." Many notable biologists of the late nineteenth century were steeped in the new Darwinian paradigm, the paradigm that seemed to make all of biology make sense in a way that it had not before. Anatomists and paleontologists took on the task of verifying the gradual changes from one form to another through evolutionary time, systematists formulated their already well-established tradition of hierarchical classification within a newly sensible paradigm, both effectively continuing traditional work styles, but with new-found meaning. Ecologists engaged with

the other part of the paradigm. Not with the facts and results of evolution, but with Darwin's mechanism, his "force of selection."

Viewed as the fundamental mechanism underlying the whole enterprise, details of the environment, both physical and biological, needed to be understood for reasons that had never been fully appreciated before, although, as with the other biological disciplines, the particular methods employed were little changed—anatomists described anatomy, paleontologists described fossils, and "ecologists" described natural history. As each of these fields burgeoned, their connection with Darwinism grew ever stronger. And while the extreme dryness of the desert or reduced salinity of the estuary clearly generated a force to which selection would respond, the assemblage of other organisms, the biotic environment, was evidently just as significant a force. Its importance was clear. But its nature was evidently transient, at least in most places where naturalists and ecologists were inclined to study in the late nineteenth century. Thus, the fantastic voyages

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of the early naturalists, especially to tropical lands, offered a picture of “nature” that was uninterrupted, a nature that could be imagined as the biological side of Darwin’s “force of selection.”

It is in those exotic tropical lands that a bit of romanticism in the science of ecology emerged—the pristine forest, the virgin habitat, the untrammelled wilderness. Although the European environment had been so altered by one particular species in the past (*Homo sapiens*) so as to be unfit for proper study of the true force of selection, what existed before that species so massively and destructively intervened seemed to be available in the newly discovered lands of America, Africa and Asia. A constant, Newtonian-like, equilibrium could be imagined there. Consequently the “natural” emerged as a social construct of the nineteenth century at least partially in response to the perceived need to study the force of selection in some sort of pure form.

Today, partially from the acknowledgment that many ecosystems are by their very elementary dynamics likely to be transient, the study of the Darwinian force of selection has become far more catholic, leading to the obvious question of how ecosystems come to be assembled in ecological time, especially when elements formerly isolated from one another are suddenly brought together. The growing interest in these “novel” ecosystems is thus a welcome trend (Hobbs et al., 2006; Seastedt et al., 2008; Hobbs et al., 2009). Indeed, one wonders, in light of modern ecological theory, whether there are truly any non-novel ecosystems, and if there were, how we might recognize them. As Dutch ecologists Huismann and Schilthuizen (2013) noted in a popular article.

Of course it is painful to see that familiar species are becoming rarer and unsolicited newcomers more common. But we must realize that nature is not a fixed diorama and that the pursuit of a constructed nature of predefined composition is a potentially disastrous course. It would be better for nature conservation to consider more general goals: what should be the extent of biodiversity and what limits are acceptable within which it is allowed to fluctuate? What should be the nature of the overall food web? Such global indicators would enable us to develop monitoring programs and not suggest that we immediately panic if an alien species invades or a native species plummets. It would be of more value to conservation if we were to shed the idea of a fixed blueprint of ‘Dutch nature’ and acknowledge the dynamic aspects of that Dutch nature.

We echo their call for a new and more scientific appreciation of nature, and especially emphasize that vast swaths of the world are similar to the Netherlands in that they are carved out of something that was, into an agroecosystem that either is, or is in transition to something else.

#### *Agroecosystems as novel ecosystems*

Agricultural ecosystems are, by their very nature, a cauldron of novelty and thus perhaps the world’s most evident novel ecosystems, although this is not always acknowledged. Most frequently they emerge with exotic species at the core of their very existence, the crops and animals that are intentionally introduced, the planned biodiversity. However, this intentional collection of plants and animals is inevitably followed by subsequent colonization of other species, the so-called associated biodiversity, including pests and associated natural enemies of those pests, mutualists, competitors (weeds), diseases and decomposers (Perfecto et al., 2009). What seems to be the general pattern is that similar ecosystems become assembled very rapidly with similar dynamic structuring, but frequently with taxonomically diverse elements. We hypothesize that this consistency reflects general laws of ecology, operative in almost all agroecosystems. We further propose that these laws

are generally applicable to all other ecosystems, suggesting potential limitations on the modes of ecosystem organization.

There has long been an appreciation in community ecology that ecosystems are structured in a non-random fashion, with certain rules of organization that do not sort out along all possible configurations, but rather represent repeated modules of organization (Dupont and Olesen, 2009; Fortuna et al., 2010). Such modules are thought to result from structural limitations on the basic elements of community organization involving processes such as competition, predation and disease dynamics. It is thus a reasonable hypothesis that future and novel ecosystems will tend toward structures that contain similar modularities (Levin, 1999, 2005).

Agricultural ecosystems in particular are excellent model ecosystems for the study of novel ecosystems, being, by their very definition, novel. As has been observed many times in the past, the pest component of agroecosystems reflects a disturbing pattern of recurrence, much to the chagrin of agricultural planners, from the beginnings of agriculture to the present. Although this aspect of agroecosystems is well known, less fully appreciated is the more subtle ecosystem connections that also invariably arrive, not always with the inevitable pests, but frequently forming complex interactions among themselves and with the pests. Indeed, the practice of classical biological control effectively recognizes this fact in an overly simplified role (one natural enemy for every pest) and seeks to return the assumed population control of the new pest by finding a biological control agent from its native range, an implicit acknowledgement of the ubiquitous nature of the plant/herbivore/predator module, the classic three-level trophic chain of elementary ecology classes. As we note below, these structures become immensely more complex very quickly, even in overly simplified agroecosystems (the typical industrial monoculture), but dramatically so in more traditional diverse agroecosystems (Vandermeer et al., 2010).

It is likely that other modular designs (beyond the simple tri-trophic systems) are also recurring and thus likely to show up in novel ecosystems. In this paper we highlight three modular structures that we have uncovered in the course of our research in the coffee agroecosystem of Mexico, and suggest that they represent consistent patterns of modularity for ecosystems more generally.

We propose that these relatively consistent trends of modularity in agroecosystems suggest certain structural constraints might be expected in other novel ecosystems, and for that matter, in terrestrial ecosystems in general. By their very nature novel ecosystems are difficult to study, especially those in which the community assembly process has not had the time to reach any kind of stable status. Since many agroecosystems are novel ecosystems that have been around for some time, we could assume that whatever assembly rules are operative, they will have sorted out to some extent due to the relative age of these ecosystems, in contrast to other more recently established novel ecosystems. Ecosystem patterns, at both local and landscape level, may thus be viewed in a “close-to-equilibrium” state, thus suggesting potential predictive programs for the eventual assembly of the many other novel ecosystems currently being assembled around the world. We suggest that agroecosystems contain within their dynamics at least three basic modularities worthy of further study: (1) the trophic level/food web module, (2) predators and diseases in space and time, and (3) trait-mediated cascades. Other modules are undoubtedly evident to other researchers, including obvious ones like pollination networks (Olesen et al., 2007) and asymmetric plant competition (Weiner, 1990), but also, more importantly, less obvious ones that are potentially just as interesting and important as the three we highlight in this article. We also suggest that it is worth consideration that these modularities, which we argue represent commonalities in agroecosystems, may be general modularities that emerge in all novel and non-novel ecosystems.

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