

An evolutionary perspective on the biogeography of species interactions

T. Poisot, K. Cazelles, D. Gravel

Introduction

Arguably the biggest challenge faced by community ecologists is to understand, and predict, how ecosystem properties will change in the face of large-scale disturbance events. Ecosystems functions emerge from both the identity of local species, and the way they interact, in a given environmental context. Species range shift, micro-evolutionary changes, and rapid environmental variation, is therefore expected to disrupt the current state of communities, and thus change the way ecosystems function. Although hypotheses have been generated, and data gathered, regarding the relationship between community structure and ecosystem properties, it is not clear whether they are sufficient to *predict* the outcome of large-scale changes. The core issue lies in the fact that emerging communities, rather than being an additive combination of existing ones (*e.g.* species from site A relocate to site B to track their temperature optimum), will be entirely novel ones. This novelty will emerge through a variety of ecological and micro-evolutionary mechanisms. **(i)** Species will use different tactics to cope with change, that can result in any combination of range shift, and rapid adaptation. **(ii)** Because of the precedent point, this will result in either new species entering existing interaction networks, or establishing different interactions within them. Finally, **(iii)**, the environmental conditions themselves will change, affecting the traits, abundances, and presence of different species. Because all of these mechanisms are interwoven in feedbacks, the way we approach them should incorporate concepts and elements from separate bodies of work, and focus on understanding which are well-articulated, and which are not.

1. Literature on species interactions at the community level neglected variation in either species, or the way they interact
2. Accounting for species interaction is needed to predict biogeodistribution and response to global changes
3. Accounting for micro-evolutionary changes is important to predict response to global changes as well
4. The establishment of interactions relies on traits (mis)matching, so the consequences of biogeodistribution/evo changes must be done in a trait-explicit framework

Last paragraph: In this paper, we discuss aspects of ecological network theory, environmental and historical biogeography, and coevolution, that can be integrated in order to predict and describe the dynamics of interaction networks. Interestingly, most of the groundwork is already present, and we call for a synthesis effort, aiming at the integration of disparate elements of theory, models, and data. We propose that future research on the dynamics of networks, be it temporal, spatial, or evolutionary, be guided by the role of species trait in determining the existence of interactions.

Box:: venn diagram

Box: case studies (if any)

The state of the art

In this part, we showcase the elements of network theory, biogeography, and coevolution studies that are necessary to achieve an integration between the three fields.

we don't discuss the overlap yet: think of this as the basic ingredients of the integration, not how we will integrate them

Network theory:

Dom

Constraints on species presence / absence, species dynamics, involve functional traits

Jenn / Memmott : robustness, species extinction cascades, pressure to select the more robust network (indirectly) – the probability of extinction of one species varies with the risk of extinction of other species below it

Biogeography:

D.J. Kev'

large scale variations, species presence f(environment), predicts community composition, spatial heterogeneity, consequences for species evolution (at the single species scale)

evolutionary/historical biogeography: Dom will do a synthesis of the TREE paper

Discuss Pillai, Gonzalez & Loreau: interactions constrain co-distribution

Coevolution:

In its contemporary incarnation, coevolution studies the interactions between pairs of species composed of (potentially) genetically differentiated populations, which may be connected by gene-flow (dispersal). Theory surrounding coevolutions aims at finding mechanisms that links traits and their genetic architecture to the distribution of interaction outcomes (Thompson 1999), so as to predict the impact of trait distribution on species interactions, and the impact of interactions on the evolution of trait distribution. Of particular interest to our goal is the central concept that (i) covariance in trait species will determine the distribution of interaction outcomes (that is the distribution of interaction strenght, in a network perspective), and (ii) the covariance between interaction outcome and trait distribution will drive the evolution of the trait in one or both species (Gomulkiewicz *et al.* 2007).

%TODO review examples

Although the notion that traits drive the existence and strength of species interactions in networks, there has been extremely few studies that attempted to understand the consequences of network structure on trait distribution in the different species. As we discuss in a later section, this is in part because most studies focused on understanding how network structure emerged from evolutionary processes and trait distribution, without going full circle to asking the question of how network structure drives coevolutionary dynamics. Yoder & Nuismer (2010) makes the proposition that the ability of coevolution to trigger an increase in diversity was contingent upon the type of ecological interactions, with mutualistic interactions generating the least diversity. However, it is worth noting that this model, as most empirical studies, focused on situations in which species richness is low, and it is therefore worth asking how the multiple interactions that a species establishes within a network represents different selection pressures and diversification opportunity. The idea that multi-species interactions affect both coevolutionary dynamics (Thrall *et al.* 2007) and the number of interaction partners (Poisot *et al.* 2011) has been well established in the recent years, offering the rationale and opportunity to further understand how network structure and coevolutionary dynamics interact.

The current overlap

The good: biogeographic perspectives on coevolution

TP – GMTC, Nuismer models

Since Thompson (2005) proposed the concept of a *geographic mosaic of selections*, that is the fact that selection varies across space as a function of local environmental conditions, the concepts of coevolution have been well understood in a spatial context. **REVIEW main concepts of GMTC**

Emblematic systems: crossbills, yucca moth

The bad: understanding network variation over space

DG/KC – TTIB, beta

The ugly: evolution of networks, evolution in networks

TP – Loeuille, web world, Cattin, Allesina

Evolution *of* networks (as macro-ecological objects) and evolution *in* networks (as the consequences of species interactions on evolutionary dynamics) have been considered so far as distinct fields. Yet, as evolutionary changes in species through interactions within a network will also influence their distribution and trait values (**Figure 1a TODO**), it would make sense to understand how these two scales interact. Long-term evolutionary dynamics have been studied in a number of different ways, including looking for phylogenetic conservatism in species roles [@daniel] or interactions [@allesina]; comparing emergent properties of paleo-networks [@dunne; @roopnarine]; and more generally by studying the phylogenetic signal in species interactions [@various-refs]. On the other hand, short-term evolutionary dynamics introduced by ecological dynamics have been studied in smaller community modules. A variety of models described, for example, co-evolutionary dynamics of antagonistic [@poisot-ProcB] or mutualistic [@NuismerJordano] networks.

– models of network evolution: also disconnected

– nuismer and jordano

discuss micro-evolution / macro-evolution (phylo Daniel, paleo Jenn, Roopnarine, taxo Allesina)

The road to synthesis

Scaling-up coevolutionary concepts

limitation as a micro-evo perspective

Scaling-down the species interaction network paradigm

interactions are complex probabilistic processes

Perspectives

How do we switch from no network (autotrophs) to a network (heterotrophy): important qualitative change, intermediate steps?

Discuss the relevance of fundamental/realized versus Grinnell/Elton niches (ugly Ecol Lett figure)

Traits are the future, all hail the traits

No grand theory of everything

new family of questions vs. re-visiting standing questions

References

- Gomulkiewicz, R., Drown, D.M., Dybdahl, M.F., Godsoe, W., Nuismer, S.L., Pepin, K.M., Ridenhour, B.J., Smith, C.I. & Yoder, J.B. (2007) Dos and don'ts of testing the geographic mosaic theory of coevolution. *Heredity*, **98**, 249–258.
- Poisot, T., Bever, J.D., Nemri, A., Thrall, P.H. & Hochberg, M.E. (2011) A conceptual framework for the evolution of ecological specialisation. *Ecology Letters*, **14**, 841–851.
- Thompson, J.N. (1999) The raw material for coevolution. *Oikos*, **84**, 5–16.
- Thompson, J.N. (2005) *The Geographic Mosaic of Coevolution*. University Of Chicago Press.
- Thrall, P.H., Hochberg, M.E., Burdon, J.J. & Bever, J.D. (2007) Coevolution of symbiotic mutualists and parasites in a community context. *Trends in Ecology & Evolution*, **22**, 120–126.
- Yoder, J.B. & Nuismer, S.L. (2010) When does coevolution promote diversification? *The American Naturalist*, **176**, 802–817.