

LETTER

Evolution and coevolution in mutualistic networks

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Abstract

A major current challenge in evolutionary biology is to understand how networks of interacting species shape the coevolutionary process. We combined a model for trait evolution with data for twenty plant-animal assemblages to explore coevolution in mutualistic networks. The results revealed three fundamental aspects of coevolution in species-rich mutualisms. First, coevolution shapes species traits throughout mutualistic networks by speeding up the overall rate of evolution. Second, coevolution results in higher trait complementarity in interacting partners and trait convergence in species in the same trophic level. Third, convergence is higher in the presence of super-generalists, which are species that interact with multiple groups of species. We predict that worldwide shifts in the occurrence of super-generalists will alter how coevolution shapes webs of interacting species. Introduced species such as honeybees will favour trait convergence in invaded communities, whereas the loss of large frugivores will lead to increased trait dissimilarity in tropical ecosystems.

Keywords

Coevolution, complementarity, convergence, ecological networks, evolutionary cascades, generalists, mutualisms, pollination, seed dispersal, small-world networks.

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INTRODUCTION

Coevolution is a key process producing, and maintaining, the complex networks of interacting species (Ehrlich & Raven 1964; Thompson 2005) that Darwin called the entangled bank: 'I am tempted to give one more instance showing how plants and animals, most remote in the scale of nature, are bound together by a web of complex relations' (Darwin 1859). A solid body of theory has explored the role of coevolution in shaping species traits in pairs or small groups of interacting species (Gandon & Michalakis 2002; Gomulkiewicz *et al.* 2003; Nuismer *et al.* 2008, 2010; Jones *et al.* 2009). An increasingly wide variety of empirical studies have shown that most evolving interactions involve at least a few groups of interacting species – e.g. seed predation by birds (Parchman & Benkman 2008), predation of amphibians by snakes (Geffeney *et al.* 2002) and pollination by insects (Thompson & Cunningham 2002; Gómez *et al.* 2009). These multispecific interactions are, in turn, embedded in even larger networks that often exhibit a predictable structure (Olesen *et al.* 2007; Vázquez *et al.* 2009). Within large mutualistic networks, some highly generalist species may have disproportionately large effects on evolution and coevolution (Thompson 2005; Guimarães *et al.* 2007; Olesen *et al.* 2007), but exactly how these species affect the coevolutionary process is still unclear.

Recent research has identified some of the ecological, evolutionary and coevolutionary processes that may shape ecological assemblages (Holoak & Loreau 2006; Rezende *et al.* 2007b; Santamaría & Rodríguez-Gironés 2007; Vázquez *et al.* 2009; Thébault & Fontaine 2010; Gómez *et al.* 2011). Coevolutionary models of two interacting species suggest that mutualisms often favour the evolution of trait complementarity, in which there is a high degree of trait matching

between interacting partners (e.g. Nuismer *et al.* 1999). Examples include the match between nectar concentration and pollinator's preferences (Baker *et al.* 1998), and seed size and body mass of frugivores (Jordano 1995). Moreover, trait convergence, in which trait similarity emerges as a response to similar selective pressures, is often observed in mutualisms, such as Müllerian mimicry rings (Meyer 2006), colour patterns in cleaning fishes (Côte 2000), and patterns of fruit design in unrelated plant species (Jordano 1995). Complementarity and convergence have been identified as potential factors that may shape the organization of large mutualistic networks (Thompson 2005; Rezende *et al.* 2007b; Santamaría & Rodríguez-Gironés 2007; Vázquez *et al.* 2009).

A major current challenge in coevolutionary research is therefore to understand the specific roles that coevolution plays in shaping trait evolution in interactions comprising up to hundreds of species (Thompson 2005). Understanding coevolution in multispecific assemblages requires more than adding up the outcomes of pair-wise interactions with specificity, reciprocity and simultaneity. One approach is to use tools derived from complex network theory to develop testable hypothesis about the role of network structure in coevolutionary dynamics (Guimarães *et al.* 2007), i.e. how indirect and cascading effects in diversified assemblages contribute to reciprocal pair-wise interactions.

We combined a model for single-trait evolution with network analysis and data for 20 empirical plant-animal assemblages to explore how short-term evolution and coevolution shape the spread of traits through mutualistic plant-animal networks. Our approach represents a first step to formalize models of coevolution in multispecific assemblages of mutualists by explicitly considering trait evolution within a complex network architecture. We focused on

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three central questions: (1) Does coevolution among species contribute significantly to the overall rate of evolution in complex networks? (2) Does coevolution result in a greater degree of complementarity and convergence within webs than expected in the absence of reciprocal selection? (3) Does the evolution of new lifestyles that rely upon species-rich webs (i.e. super-generalists) affect the patterns of trait evolution among species? Super-generalists are species, such as honeybees, quetzals, large cotingids, and some fruit-eating primates, that rely upon a local diversity of species and connect semi-independent groups of species within communities (Jordano *et al.* 2003; Thompson 2005; Olesen *et al.* 2007).

MODELLING APPROACH AND ANALYSIS

The evolutionary model

We used discrete-event simulations to model single-trait evolution in animals and plants linked to each other within a complex network of interactions. In the model, animal and plant phenotypic traits were modelled as real numbers (Z_i), in which i denotes a species. Initially, the trait values of all animals and plants were randomly assigned by sampling normal distributions with mean $\mu_Z = 0$ and variance $\sigma_Z^2 = 10^{-2}$. Trait evolution was modelled as discrete events of change caused by selective pressures imposed by mutualistic partners. In this approach, each node (species) has a state (trait value) and the state of each node is updated in each time step. This approach allowed us to follow specific trait changes, to quantify coevolutionary and evolutionary events, and to measure the degree of trait complementarity and convergence in simulations with and without some network properties, e.g. presence of super-generalist species.

Model dynamics

At each time step, a species may undergo trait evolution due to background evolution (e.g. responses to the abiotic environment) or network-derived evolution (i.e. responses to direct and/or indirect effects of biotic interactions). There was a fixed probability $p = 10^{-3}$ that the trait of a given species changes due to background evolution, which includes all evolutionary change not related to selective pressures imposed by patterns of mutualistic interactions, including genetic drift, fluctuating selection not related to the mutualistic interactions and the selective effects associated with other networks of biological interaction (Melian *et al.* 2009). Hence, we avoided the ecologically unrealistic assumption that all evolution in species was due to interactions within the network. If the trait value of species i , Z_i , evolved due to background evolution to a new state, Z'_i , then $Z'_i = Z_i + \varepsilon$, in which ε was randomly sampled from a normal distribution with mean $\mu_\varepsilon = 0$ and variance $\sigma_\varepsilon^2 = 10^{-4}$. Trait values might also change due to selection to maximize complementarity among interacting partners, hereafter referred to as network-derived evolution.

Network-derived evolution

In our model, there was a fixed probability $q = 10^{-2}$ that any species might show directional evolutionary change by increasing its complementarity to a randomly selected partner j . Thus, we assumed that selection due to the mutualistic interactions is stronger than in other selective pressures ($p > q$). Species j is selected with probability

equal to d_{ij} , the ecological dependences of species i on its interaction with j (Jordano 1987; Bascompte *et al.* 2006). If the trait value of species i evolved to a new state due to directional evolutionary change, then $Z'_i = Z_i + R_{ij}$, in which R_{ij} was the response to selection imposed by species j that interacts with i (see below).

Network-derived evolution may also occur due to evolutionary responses of species to background evolutionary change, direct evolutionary changes or previous evolutionary responses in their multiple partners, leading to several classes of evolutionary and coevolutionary events (Fig. 1). We defined f_{ij} as the probability of phenotypic selection imposed by a phenotypic change in a given partner translating into actual evolutionary change. Therefore, f_{ij} is the probability of phenotypic change in species i as a direct outcome of selection on individuals of species i imposed by a previous phenotypic change in species j . We assumed f_{ij} is mediated by the ecological dependence of species i on j , $f_{ij} = md_{ij}$, in which m is a scaling constant, $m = 0.5$. If the trait value of species i evolved in response to a shift in the trait value of species j to a new state, then $Z'_i = Z_i + R_{ij}$, as in the simple, directional evolutionary change described above.

Response to selection imposed by mutualistic partners

We used the breeder's equation from quantitative genetics to estimate the response to selection, but we placed it within an explicit network framework, $R_{ij(t)} = h_i^2 S_{ij(t)}$, in which h_i^2 was the heritability of trait Z_i and $S_{ij(t)}$ is the strength of selection (Lush 1937; Falconer & Mackay 1996; Beder & Gomulkiewicz 1998). Estimates of traits heritabilities were not available for the interacting species in the networks analysed. Nevertheless, there is evidence of a broad range of heritability values for traits mediating animal-plant interactions (Boag & Grant 1978; Wheelwright 1993). In our simulations, heritability was randomly sampled from a normal distribution with mean $\mu_{h^2} = 0.25$ and variance 0.1. We constrained the heritability values to vary between 0.05 and 1. If the randomly sampled value was < 0.05 , we set $h^2 = 0.05$ and if it was > 1 , we set $h^2 = 1$.

We assumed that selection imposed by mutualistic partners favours complementarity, which is the match between the phenotypic traits of interacting partners. There is strong evidence of selection favouring complementarity in mutualisms (Thompson 2005) and examples include the match between floral corolla depth and the length of hummingbird bills (Dalsgaard *et al.* 2008) or the tongue length of insects that pollinate the flowers (Borrell 2005; Anderson & Johnson 2008). Previous theoretical work has investigated how complementarity might affect network organization (Rezende *et al.* 2007a; Santamaría & Rodríguez-Gironés 2007). Here, we moved one step further to an understanding of how evolution shapes networks by allowing complementarity to emerge directly from selection among interacting species. We computed the strength of selection as $S_{ij} = O_i - Z_j$, in which O_i is the trait value that maximizes complementarity between i and j – defined as $O_i = Z_j$ for sake of simplicity – and corresponds to the mean trait value of species i after selection.

Each simulation ended after 10 000 time steps, a number sufficiently large to allow asymptotic results (Fig. S5). The model output quantified the number of evolutionary events leading to increased trait complementarity and/or increased convergence. We performed sensitivity analyses of the model, and the results were qualitatively similar across a broad range of values of the parameters

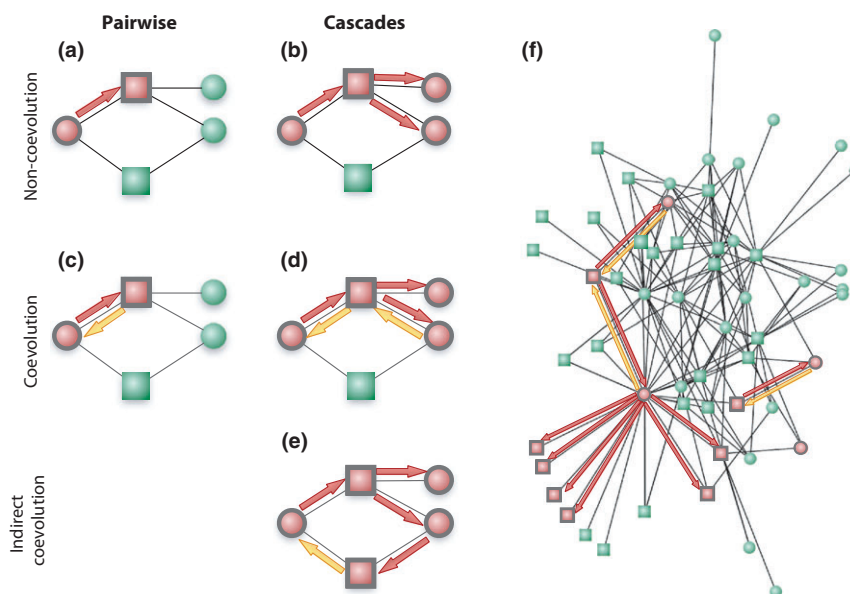


Figure 1 Evolution and coevolution within multispecific networks. (a–f) Squares represent animals, circles plants, red symbols with thick contours represent species that show shifts in phenotype, and arrows indicate which species are showing directional phenotypic change. Some of these events (red arrows) are (a) simple directional change related to a partner, which may lead to (b) evolutionary cascades. Other evolutionary responses may lead to coevolutionary events (yellow arrows), in which a species responds to changes in other species that were directly or indirectly caused by the first species, such as in (c) pair-wise coevolution or (d) direct and (e) indirect coevolutionary events within cascades. (f) Coevolutionary and evolutionary events may cascade through species-rich networks, affecting several species simultaneously. Network depicts interactions among plants and frugivorous animals in a local community, Nava de las Correhuellas, SE Spain.

(Supporting Information). The model was implemented in MATLAB 7.4.

Quantifying events of trait evolution, convergence and complementarity

The discrete-event structure of the model used to explore evolutionary dynamics allowed us to determine if a given event of trait evolution was triggered by a chain of previous events of trait evolution, such as $Z_i \rightarrow Z_j \rightarrow Z_k$, in which the selection imposed by trait value of species i , Z_i , on species j led to trait evolution of species j , $\rightarrow Z_j$, that, in turn, led to trait evolution in species k , $\rightarrow Z_k$. We classified each event of trait evolution into one of five classes of change, depending on whether or not the event involved a pair of species, three or more species (cascades), unidirectional evolution, or reciprocal evolution (i.e. coevolution) (Fig. 1). (a) *Simple evolutionary change* occurred if trait evolution recorded in species i , Z_i , was a result of $Z_j \rightarrow Z_i$ (Fig. 1a). (b) *A non-coevolutionary cascading event* occurred if trait evolution recorded in species i , $Z_{S(i)}$, was a result of a chain of events including at least two additional species, such as $Z_k \rightarrow Z_j \rightarrow Z_i$, in which no species was repeated (Fig. 1b). (c) *A pair-wise coevolutionary events* occurred if trait evolution in species i , Z_i , resulted from $Z_i \rightarrow Z_j \rightarrow Z_i$, closing a round of reciprocal selection. It was not a consequence of trait evolution involving other species than i and j (Fig. 1c). (d) *A direct coevolutionary cascading event* (DCCE) was similar to pair-wise coevolutionary event, but the chain of events that led to a DCCE, Z_i , included at least one additional species, $Z_k \rightarrow Z_i \rightarrow Z_j \rightarrow Z_i$ (Fig. 1d). (e) Finally, *an indirect coevolutionary cascading event* occurred if trait evolution observed in species i , Z_i , was separated from previous changes in species i by events of trait evolution in more than one intermediate species, such as $Z_i \rightarrow Z'_k \rightarrow Z'_n \rightarrow Z'_v \rightarrow Z'_i$ (Fig. 1e). Events of

type (a) and (b) were strictly non-coevolutionary events, as none of them involves reciprocal evolutionary change, whereas (c), (d) and (e) encompassed one set of reciprocal evolutionary events (coevolution) in the interacting species. In addition, events of type (b), (d) and (e) were cascading effects, whereas (a) and (c) did not involve cascades. Thus, the discrete-event structure of the model allowed us to assess and compare the complex ways in which evolutionary and coevolutionary changes can cascade through complex networks of interaction.

We quantified the degree of trait complementarity and/or convergence in each simulation. We computed the degree of complementarity as $-\log(\tau)$, in which τ was the mean pair-wise difference between traits of interacting animals and plants. The degree of convergence was defined as $-\log(\eta)$, in which η was the mean pair-wise difference between traits of species at same trophic level (e.g. fruit-eating animals).

Numerical simulations using empirical mutualistic networks

We then used the model to undertake an explicit analysis of the coevolutionary consequences of the structure of 20 empirically documented mutualistic networks in which the patterns of interaction and mutual ecological dependence (Jordano 1987; Bascompte *et al.* 2006) between species have been studied (9 plant-frugivore and 11 plant-pollinator networks, Supporting Information).

We first explored the relationship between evolution and coevolution in mutualistic networks by performing simulations on each empirical network. We assumed a fixed pattern of interaction among the species within the network to focus on trait evolution over short time scales. Trait evolution may lead to a shift in the patterns of interaction in mutualisms, but this simplifying assumption allowed us to explore how empirical patterns of interaction would influence how traits would evolve given a particular network structure. We then

relaxed the assumption of fixed patterns of interaction and explored how the evolution of super-generalists would affect subsequent coevolutionary dynamics (see below).

Coevolution and the rates of evolution

We first explored a scenario in which trait evolution occurs only due to background evolution. This scenario allowed us to describe how traits would evolve without the joint effects of reciprocal and non-reciprocal selection imposed by mutualistic networks. For each real network ($n = 100$ simulations per real network), we computed the average degree of complementarity and convergence of traits before and after a fixed number of time steps (10 000). We then averaged all values of complementarity and convergence across networks.

We then explored the role of coevolution in generating complementarity and convergence by using four different versions of our evolutionary model. We contrasted the outcomes of simulations of the evolutionary model with simulations in which we did not allow coevolutionary events and/or cascading events. Coevolution was prevented by setting $f_{ij} = 0$ in cases where selection imposed by species i led to trait evolution in j . Cascades were prevented using a similar approach. If species j showed an evolutionary response due to selection imposed by species i , then we set $f_{kj} = 0$ for every partner k of species j other than i . By combining simulation scenarios with and without coevolution and with and without cascading effects, this factorial design allowed us to explore the role of coevolution and cascades in shaping evolutionary dynamics.

We investigated how the temporal dynamics of complementarity and convergence were affected by coevolution and cascading effects using a repeated-measures general linear model (GLM) ($n = 100$ simulations of each model per network), in which coevolution and cascading effects are factors that can be either present or absent. In a second run of simulations, we used another GLM to test the effects of coevolution and cascades on complementarity, convergence and the rates of trait evolution, measured as the number of events of trait evolution recorded in different classes of evolutionary change ($n = 1000$ simulations of each model per network) in a fixed number of time steps (10 000). In all analyses we controlled for network-specific effects using the identity of network as an additional factor. We used the residuals of GLMs between network identity and evolutionary outcomes in a simple linear regression to investigate if, after controlling for network-specific effects, there was an association between complementarity and convergence.

The impact of super-generalists

Modules, groups of interacting species that are semi-independent of other groups within larger networks, are a common feature of many ecological networks (Guimarães *et al.* 2007; Olesen *et al.* 2007). The diversity of potential mutualistic partners available among the distinct modules may allow the evolution of super-generalists (Thompson 2005; Olesen *et al.* 2007). These species often have a set of eco-morphological, behavioural, or physiological adaptations that allow them to interact not only with many species, but also with species that strongly differ in their biological features (Thompson 2005). Thus, super-generalists not only interact with many partners, they rely on and connect multiple modules within networks (Jordano *et al.* 2003; Thompson 2005; Olesen *et al.* 2007). Therefore, the super-generalist lifestyle is only possible after the emergence of large networks

of interacting species. We explored how the evolution of super-generalists affects trait evolution and influences the coevolutionary process within networks. We identified super-generalists by following the definition and approach provided by Olesen *et al.* (2007) (see Supporting Information).

We simulated the evolutionary model in real networks (scenario 1, with super-generalists) and in two related scenarios ($n = 100$ simulations per scenario/real network). In scenario 2 (without super-generalists), we decreased the among-module connectivity of super-generalists, i.e. they did not differ from other species in connecting species from different modules (Supporting Information). Thus, scenario 2, trimming just those interactions of super-generalists that 'glue' the modules together, can be viewed as a description of how the structure of a mutualistic network would look like prior to the emergence of the super-generalist lifestyle.

Differences in evolutionary dynamics between networks with and without super-generalists might indicate the role of this lifestyle in driving evolution and coevolution. However, super-generalists may affect network structure in two different ways: by increasing the number of interactions among modules or simply by increasing the number of interactions in the network. We disentangled the evolutionary and coevolutionary consequences of both structural shifts by creating a third scenario (control) in which we randomly reduced the overall number of interactions (Supporting Information). We tested the effects of super-generalists on the evolutionary dynamics through a GLM, using the three different scenarios (with super-generalists, without super-generalists and control) as levels of the same factor. In addition, we used network identity as an additional factor to account for network-specific effects. We performed paired comparisons among these three scenarios using the Tukey HSD test.

RESULTS

In the absence of network-derived evolution, the degrees of complementarity before and after the evolutionary dynamics were very similar (mean degree of complementarity across networks: -0.113 ± 0.014 vs. -0.116 ± 0.018 , mean \pm SD). In fact, eleven networks (55%) showed lower degrees of complementarity after the evolutionary dynamics. Background evolution decreased the degree of convergence both in plants (before vs. after: -0.103 ± 0.025 vs. -0.113 ± 0.024) and animals (before vs. after: -0.111 ± 0.015 vs. -0.122 ± 0.015). In all networks, degrees of trait convergence for both animals and plants after evolutionary dynamics were lower than the initial degree of trait convergence. In contrast, network-derived evolution often led to higher degrees of complementarity (2.097 ± 0.438) and convergence both in plants (1.691 ± 0.633) and animals (1.728 ± 0.612 , $n = 1000$ simulations per network, 10 000 time steps).

In the presence of network-derived evolution, the simulated dynamics led to a greater frequency of evolutionary events than coevolutionary events (Fig. 2a), with coevolutionary events representing only a small percentage ($9.8 \pm 1.2\%$, mean \pm SE, $n = 1000$ simulations per network) of all directional changes. Nevertheless, evolution and coevolution both contributed to the increased convergence and complementarity among traits within the network. In fact, coevolution significantly sped up the evolutionary rate within networks (repeated measures GLM, $F_{1, 7977} > 60.89$, $P < 0.001$), and significantly increased both complementarity and convergence (GLM, $F_{1, 7977} > 81.84$, $P < 0.001$ for all evolutionary outcomes; Fig. 2b). The distribution of initial traits among species did not affect the emergence of complementarity and

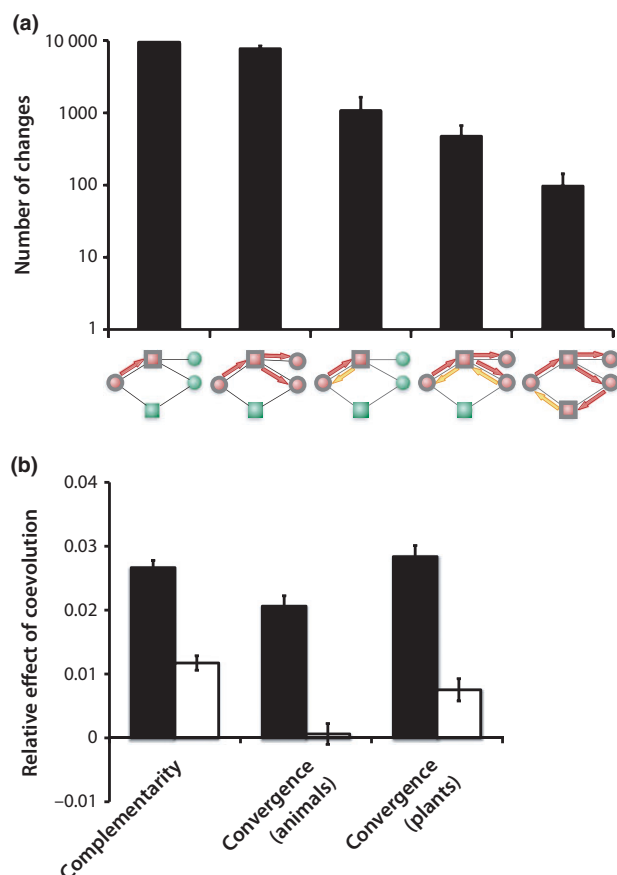


Figure 2 Coevolution and the emergence of complementarity and convergence. (a) The frequency (mean \pm SD) of the different classes of evolutionary and coevolutionary events (Fig. 1) at the end of the simulations. (b) After the end of simulations, we computed the effects of coevolution for simulations in which cascading effects were allowed (black bars) or not (white bars) to occur. The effects of coevolution were estimated as the ratio between the least squares means of complementarity and convergence for simulations allowing or not coevolution. Positive ratios indicate that coevolution increases the values of the metric of interest, whereas negative values indicate decreases in the values. Error bars depict SD.

convergence. Alternative trait distributions, including those based on real phenotypic traits, led to no qualitative difference in the simulation outcomes (see Supporting Information).

Changes in complementarity and convergence, however, did not occur in lock-step. Selection for complementarity led to convergence, indicating dependence of these two evolutionary outcomes, but the degree of convergence varied widely among networks with similar degrees of complementarity. After controlling for particulars of each network, convergence was partially correlated with complementarity ($R^2 = 0.493$, $F = 7776.68$, d.f. = 7999, $P < 0.001$ for convergence among animals; $R^2 = 0.432$, $F = 6092.23$, d.f. = 7999, $P < 0.001$ for convergence among plants). Hence, as species coevolve within large networks, the evolutionary convergence of a trait within trophic levels only partially depends on the patterns of evolutionary complementarity of traits between trophic levels.

Coevolution fuelled convergence and complementarity by increasing the total number of directional changes (GLM, $F_{1\ 79977} = 448124.80$, $P < 0.001$) and the number of non-coevolutionary, directional changes occurring within cascades (GLM, $F_{1\ 39979} = 439766.30$, $P < 0.0001$). Coevolution increased the num-

ber of cascading evolutionary events in which species showed an evolutionary response to a partner that was coevolving with other species within the network. In fact, the effects of coevolution depended strongly on the presence of cascading effects (Fig. 2b). In simulations in which cascades were allowed to occur, coevolution led to much higher degrees of complementarity (coevolution \times cascading effects, $F_{1\ 79977} = 108.39$, $P < 0.0001$), and convergence within animal (GLM, $F_{1\ 79977} = 74.23$, $P < 0.0001$) and plant species assemblages (GLM, $F_{1\ 79977} = 79.27$, $P < 0.0001$). Thus, by generating cascading effects and speeding up the overall rate of evolutionary change, coevolution generates additional non-coevolutionary events.

The impact of super-generalists

Super-generalists occurred as a small percentage of species within the twenty empirical networks ($3.5 \pm 3.8\%$ of all species, mean \pm SD, $n = 20$ networks). They significantly increased in frequency with increasing species richness in the networks (log-log regression, $R^2 = 0.639$, $F = 31.83$, d.f. = 19, $P < 0.001$) and were absent in 5 of the 20 networks.

Super-generalists had two clear impacts on simulated coevolutionary dynamics. Their presence led to a significant increase in the frequency of non-coevolutionary cascading events (GLM, $F_{2\ 4455} = 870.08$, $P < 0.001$; Fig. 3a) and a decrease in the frequency of coevolutionary events (GLM, $F_{2\ 4455} > 2669.71$, $P < 0.001$, for all types of coevolutionary events; Fig. 3a). These two effects arose from the asymmetries that occur in interactions among super-generalists and other species in mutualistic networks (Bascompte *et al.* 2003, 2006): species that interact with super-generalists are more likely to evolve in response to them, whereas super-generalists will seldom respond to an evolutionary shift in one of their many partners (Guimarães *et al.* 2007). Therefore, although coevolutionary events are important to the dynamics of species-rich mutualisms (Fig. 2), their direct effects may be most apparent prior to the emergence of super-generalists. Once there are super-generalists in the network, there is a significant increase in complementarity (GLM, $F_{2\ 4455} = 224.63$, $P < 0.001$; Fig. 3b) and, especially, convergence (for animals: $F_{2\ 4455} = 855.48$, $P < 0.001$; for plants: $F_{2\ 4455} = 699.02$, $P < 0.001$; Fig. 3b).

We studied the underlying causes for change in the evolutionary dynamics when super-generalists are present by investigating how variation in the degree of dependence of species on super-generalists affects evolution and coevolution. We calculated the strength of super-generalists as the fraction of all ecological dependences among species in the network that are dependencies of other species on super-generalists. We used a GLM to investigate if the strength of super-generalists explains differences between simulations in networks with and without super-generalists (scenario 1 and 2). As the degree of dependency of other species on super-generalists increased, so did the differences in complementarity (GLM, $F_{2\ 2996} = 88.43$, $P < 0.001$; Fig. 3c) and convergence (for animals: $F_{2\ 2996} = 244.21$, $P < 0.001$; for plants: $F_{2\ 2996} = 280.37$, $P < 0.001$; Fig. 3d) between simulations with and without super-generalists.

Super-generalists, by altering network structure, therefore drove the dynamics of the entire assemblage by increasing both complementarity and, especially, convergence (Fig. 3b). The increase in convergence and complementarity was not simply a consequence of super-generalists increasing the total number of interactions within the network. Rather, it resulted from the connections that

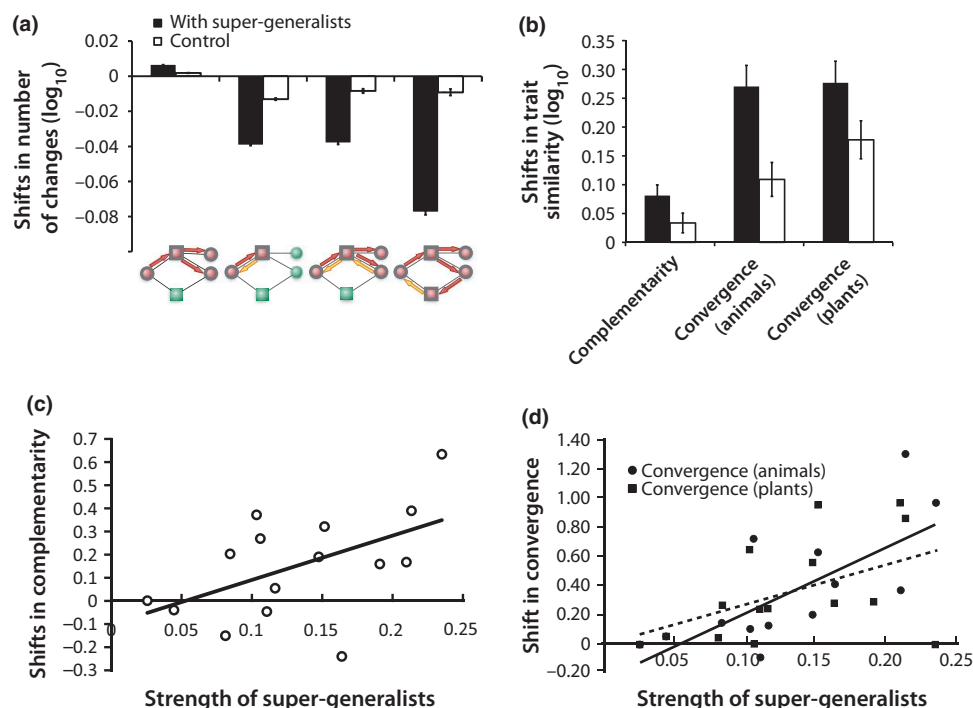


Figure 3 Super-generalists and the organization of evolution and coevolution. (a–b) Black columns depict the relative effects of super-generalists on evolutionary rates and outcomes. Effects were estimated as the ratio between the least squares means for simulations using real networks with super-generalists (scenario 1) and networks in which super-generalists were transformed into ordinary species (scenario 2, see text for further details). White columns depict the ratio between simulations using real networks (scenario 1) and a control for shifts in connectance (control). Positive ratios indicate that super-generalists increased the evolutionary rates and outcomes, whereas negative values indicate decreases. (a) Super-generalists increased the number of non-coevolutionary cascading events, but they caused a decrease in the frequency of coevolution. (b) The presence of super-generalists increased the complementarity and convergence within networks. (c–d) Effects on evolutionary outcomes varied across networks with the strength of super-generalists. Shifts in the outcomes are the difference in the mean complementarity or convergence between networks with and without super-generalists. Complementarity in (c) is shown as circles and solid lines, convergence in (d) is shown among animals as circles and solid lines and plants as squares and dashed lines.

super-generalists create among modules (Fig. 3a–b), i.e. their role in glueing subsets of species that otherwise would remain unconnected (Olesen *et al.* 2007). Hence, super-generalists shifted the evolutionary dynamics by increasing the cascading effects of each evolutionary event among modules (Fig. 4). In fact, in the presence of super-generalists, the average short path length, ℓ , between any pair of species within a network decreased by 16%. For real networks $\bar{\ell} = 2.87 \pm 0.43$ links, whereas for networks without super-generalist $\bar{\ell} = 3.42 \pm 0.94$ links (paired *t*-test, $t = -3.50$, $P = 0.002$, $n = 15$ networks). The simulations help visualize how this small-world effect of super-generalists acts, organizing subsequent evolution and coevolution (Fig. 4).

DISCUSSION

Interactions among free-living species are sometimes viewed as so ‘diffuse’ that it is difficult to understand how natural selection and coevolution shape these highly complex webs of interaction. Part of the challenge of coevolutionary biology is to get beyond that view and find ways of probing how coevolution acts within large networks (Thompson 2005). Coevolutionary network models based on the structure of real webs of interaction, as analysed herein, have the potential to aid in the development of specific hypotheses on multispecific coevolution.

Our results identify three central points about how evolutionary change might occur in large networks. First, coevolution is likely to be

a key process shaping trait evolution within mega-diversified communities, through direct and indirect influences on the rates and pathways of evolutionary change. Our results generalize to species networks the notion that coevolution speeds up trait evolution in interacting species, as suggested by mutually specific pair-wise models (Nuismer *et al.* 1999) and studies of experimental evolution (Forde *et al.* 2008; Paterson *et al.* 2010). In species-rich networks, coevolutionary and non-coevolutionary changes are intrinsically interwoven, with coevolutionary events generating non-coevolutionary events through a complex set of cascading effects. Therefore, the importance of coevolution in shaping traits in large species-rich networks cannot be assessed simply by determining the relative proportion of current selection that involves reciprocal selection between pairs of species. By generating cascading effects and speeding up the overall rate of evolutionary change, coevolution generates additional non-coevolutionary events. Hence, as networks develop, coevolution may appear to be increasingly rare within species-rich mutualisms specifically because it fuels further non-reciprocal, evolutionary events.

In our simulations we kept the network structure fixed, but the coevolutionary process may actually change the patterns of interaction within communities (Thompson 2005). Future work should investigate how coevolution would affect the dependences of interacting species, leading to shifts in network structure that ultimately could change the role of coevolution in shaping trait patterns. These results, however, together with those showing the unexpected effects of adding species in pair-wise, eco-evolutionary models (reviewed in

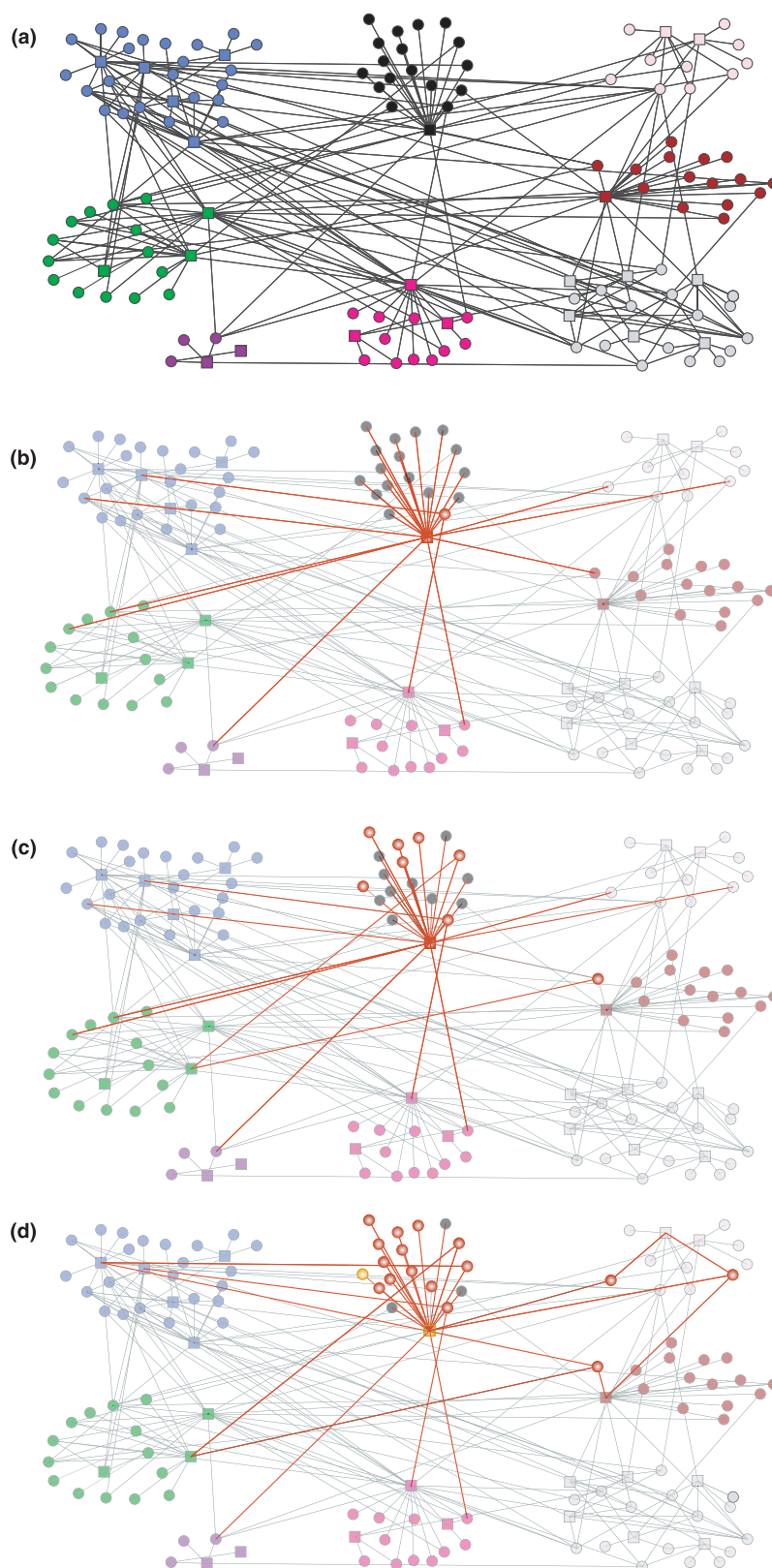


Figure 4 Super-generalists mould trait evolution in mutualistic networks. (a) The network describing interactions between plants (squares) and their pollinators (circles) in the subarctic alpine zone of Latnjajaure, in Sweden (Elberling & Olesen 1999). Colours indicate different groups of interacting species (modules). (b–d) Snapshots of a simulated coevolutionary cascade. Red lines indicate selective pressures imposed by species that show trait evolution. (b) The super-generalist plant *Saxifraga aizoides* responds to an evolutionary change in one of its pollinators (both in red). (c) Several species (red) respond to the trait evolution of the super-generalist species, including a species in a second module. (d) This cascade led to *S. aizoides* (yellow square) to coevolve to one of its partners. This coevolutionary event (yellow) fuelled new non-coevolutionary (red) changes in species in different modules of the network.

Fussmann *et al.* 2007) and the destabilizing role of evolution on ecological dynamics of species-rich communities (Loeuille 2010), suggest the utility of studying evolution and coevolution in a multispecies context.

Second, our results indicate that two broad classes of coevolutionary dynamics, namely coevolutionary complementarity and convergence, which are often considered as independent processes (Thompson 2005), are correlated yet semi-independent processes. Our results predict that coevolutionary convergence in a trait within a trophic level may, at least in part, emerge as a consequence of selection for complementarity of traits between trophic levels. Additional studies, however, will be needed to assess how the relationship between convergence and complementarity is altered amid more complex structures of multivariate phenotypic selection (Iwao & Rausher 1997; Gómez *et al.* 2009).

Third, our results highlight that not all species are equally important for the evolutionary dynamics of multispecific interactions (Bascompte *et al.* 2003; Jordano *et al.* 2003; Guimarães *et al.* 2007). Rather, a small proportion of species, the super-generalists, may play a central role in organizing evolution and coevolution in species-rich assemblages, driving them toward high complementarity, and above all, convergence. Thus, the emergence of the super-generalist lifestyle is a fundamental component of the maintenance of convergence at the community-level within highly diversified mutualistic assemblages, which, in turn, may be essential for the addition and persistence of more specialized species (Bascompte *et al.* 2003). The altered dynamics resulting from the emergence of super-generalists can be viewed as a small-world effect (Watts & Strogatz 1998; Olesen *et al.* 2006), as has been observed in ecological, molecular, technological and social networks, in which a given node (species) creates short paths connecting modules within the network (assemblages), which, in turn, may favour the emergence of cascading effects. Our model suggests that super-generalists might trigger analogous dynamics in ecological networks, and help explain why cascading effects can be so pervasive.

Our findings may have direct consequences for the conservation of endangered ecosystems (Kiers *et al.* 2010). Recent work on invasive dynamics by exotic species in mutualistic assemblages (Lopezaraiza-Mikel *et al.* 2007; Aizen *et al.* 2008) has shown that introduced species may quickly become generalists at the core of the network of interactions (Aizen *et al.* 2008). The worldwide introduction of some super-generalist species such as honeybees may therefore generate far-reaching alteration of the coevolutionary process within native assemblages, driving species traits towards higher complementarity and convergence in assemblages that previously lacked super-generalists. On the other hand, the local extinction of endangered super-generalist species, such as large frugivores (Hansen & Galetti 2009), may lead not only to significant losses of mutualistic services by restriction of interactions to less efficient mutualists, but also to fast-paced evolutionary diversification in species traits. Under either scenario, evolution and coevolution are likely to alter the traits of many species as the presence of super-generalists continues to change in many major ecosystems worldwide.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Mean degree of complementarity and convergence for three sets of initial conditions of trait values: traits sampled from normal distribution (green), from uniform distributions (red) and from distributions based on actual data on species-specific phenotypic values (yellow). Error bars represent the associated 95% confidence intervals.

Figure S2 Mean degree of complementarity (a), convergence among animals (b) and plants (c) for different ratios between rates of directional (q) and random (p) phenotypic changes. Error bars represent 95% confidence interval. The red circles represent the benchmark value for the parameter.

Figure S3 Mean degree of complementarity (a), convergence among animals (b) and plants (c) for different values of m (relationship between ecological and evolutionary dependence). Error bars represent 95% confidence interval. The red circles represent the benchmark value for the parameter.

Figure S4 Mean degree of complementarity (a), convergence among animals (b) and plants (c) for different values of heritability. Error bars represent 95% confidence interval. The red circles represent the benchmark value for the parameter.

Figure S5 Mean complementarity (a), convergence (animals, b; plants, c) for simulations with different number of time steps. Time steps were measured using the number of independent events of change (IEC, the sum of events by p and q). Error bars, 95% confidence interval. The red circles, benchmark value for the parameter.

Table S1 Mutualistic networks used in the coevolutionary simulations. The matrices describing the networks analysed are available under request. Network labels follow (Bascompte *et al.* 2006; Rezende *et al.* 2007b).

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