

# An emerging synthesis between community ecology and evolutionary biology

Marc T.J. Johnson<sup>1,2</sup> and John R. Stinchcombe<sup>1,3</sup>

<sup>1</sup> Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, M5S 3B2, Canada

<sup>2</sup> Present address: Department of Biology, Box 90338, Duke University, Durham, NC, 27708, USA

<sup>3</sup> Centre for the Analysis of Genome Evolution and Function, University of Toronto, Toronto, ON, M5S 3B2, Canada

A synthesis between community ecology and evolutionary biology is emerging that identifies how genetic variation and evolution within one species can shape the ecological properties of entire communities and, in turn, how community context can govern evolutionary processes and patterns. This synthesis incorporates research on the ecology and evolution within communities over short timescales (community genetics and diffuse coevolution), as well as macroevolutionary timescales (community phylogenetics and co-diversification of communities). As we discuss here, preliminary evidence supports the hypothesis that there is a dynamic interplay between ecology and evolution within communities, yet researchers have not yet demonstrated convincingly whether, and under what circumstances, it is important for biologists to bridge community ecology and evolutionary biology. Answering this question will have important implications for both basic and applied problems in biology.

## Bridging community ecology and evolutionary biology

Community ecology and evolutionary biology are disciplines typically studied in relative isolation from one another. Community ecology examines how interactions among species and their environment affect the abundance, distribution and diversity of species within communities. Most theoretical and empirical studies within community ecology ignore genetic variation and evolutionary change within species, and instead assume that species comprise homogeneous non-evolving populations. By contrast, evolutionary biology considers genetic variation and the mechanisms that result in genetic and phenotypic changes within populations. Although there is a long tradition within evolutionary biology to investigate how ecological factors govern evolution [1], the role that community processes and patterns (community context) have in affecting evolution has received little attention outside of studies of coevolution [2–6] and the ecology of adaptive radiations [7].

By taking community interactions and evolution into account within a single study, it might be possible to gain new insight into questions typically asked by ecologists and evolutionary biologists. Community ecology has been

described as ‘...a mess with so much contingency that useful generalizations are hard to find’ [8], whereas the main factors in microevolutionary studies often account for a small fraction of the observed variation [9]. Bridging questions and approaches from community ecology and evolutionary biology will lead to new insight if evolution in one species affects some ecological property of a community (e.g. species richness) or, alternatively, the ecological properties

## Glossary

**Allopatry:** geographical separation between populations.

**Co-diversification:** evolutionary diversification that occurs in parallel between two or more lineages over macroevolutionary time (i.e. thousands to millions of generations). Co-diversification can involve coevolution, co-adaptation and/or co-speciation between interacting lineages of species, and it can arise as a result of reciprocal or non-reciprocal interactions among species.

**Community heritability ( $H^2_c$ ):** the proportion of variation of a community variable (e.g. species richness, evenness or community composition) that is explained by genetic variation within a single population of a focal species.

**Co-speciation:** synchronous speciation in two or more interacting populations.

**Diffuse coevolution:** reciprocal natural selection and responses to selection between two or more species that is dependent on community context (i.e. the presence or absence, abundance or behaviour of other species).

**Effect size:** the magnitude of a standardized difference in mean values between treatments, groups or genotypes.

**Environmental filtering:** a process in which the distribution and abundance of species within a habitat is governed by whether each species has traits that enable it to colonize and establish viable populations.

**Geographic mosaic of coevolution:** geographic variation in the outcome of coevolutionary interactions and adaptations among interacting populations within communities. Across a landscape, local communities can exhibit either reciprocal selection and adaptation among interacting populations, or non-reciprocal selection, leading to no adaptation of populations, or adaptation in only one or a subset of the interacting populations.

**Pairwise coevolution:** reciprocal natural selection and evolutionary response between two interacting species, which is independent of the presence or absence of other species.

**Phylogenetic scale:** the degree of genetic divergence observed between two species, between clades, or across an entire phylogeny.

**Phylogenetic clustering:** closely related species that are found in the same habitat more often than by chance.

**Phylogenetic overdispersion:** closely related species being found in the same habitat less often than expected by chance.

**Natural selection:** the differential survival or fecundity of individuals that vary in a phenotypic trait. Natural selection can be estimated from: (i) the partial regression coefficients from a multiple regression of relative fitness on several phenotypic traits (selection gradients); or (ii) the difference in the mean value of a trait before and after selection acts on a population, which is equal to the covariance between a trait and relative fitness (selection differential).

**Niche conservatism:** the tendency for species to retain ancestral traits that influence their distribution, abundance and interactions within communities.

**Vicariance:** geographical separation of a population that leads to allopatric speciation. Vicariance can result in a pattern of co-speciation among several evolutionary lineages when multiple ancestral species are geographically separated in the same manner by the same geographical barrier.

Corresponding author: Johnson, M.T.J. (johnson@eeb.utoronto.ca).  
Available online 12 February 2007.

of a community influence the evolutionary dynamics within one or more populations [2]. A flurry of recent studies in four research areas combines the approaches from community ecology and evolutionary biology to understand whether and how frequently these types of interaction occur in nature (Box 1).

Here, we assess the potential advantages of combining community ecology and evolutionary biology into a single research program, and offer a conceptual framework, synthesis and avenues for future research. We conclude by considering how far biologists have come in answering the question: does combining community ecology and evolutionary biology lead to a better understanding of the complexity of communities and populations, or can we obtain accurate conclusions when these disciplines proceed independently?

### Community-level consequences of genetic variation and evolution

Theoretical and empirical research in community ecology typically assumes that genetic variation and evolution within species has negligible effects on communities. However, rapid evolution within populations does occur [10] and can influence community dynamics if the phenotypic trait undergoing evolutionary change affects the fitness or behaviour of one or more species in the community [11]. This phenomenon has been best explored for simple predator–prey communities, where theory and microcosm experiments show that evolution in the resistance of the prey to predators can influence predator–prey population cycles [12–14].

Although theory and experiments support the hypothesis that evolutionary dynamics affect community processes and patterns (Box 1), it is unclear how important these phenomena are in nature. No study has convincingly demonstrated that rapid evolution in one species affects community dynamics in the field. However, for

evolution to have community-level effects, intraspecific genetic variation must itself affect community properties (e.g. community composition or multitrophic interactions). Plants offer an ideal system for testing whether there are community-level effects of genetic variation, because as the basal resource in most food webs, plants can have cascading effects throughout communities. Recent theory and experimental work shows that genotypic differences among individual plants, and the amount of genetic diversity within plant populations, influences the coexistence of competing plant species [15–17], the structure of arthropod communities [18–23] and ecosystem processes [24,25]. Generalizing from these studies, we propose several conditions that influence the effects of genetic variation and evolution on communities (Table 1).

### Community heritability

The influence of genetic variation on community patterns can be quantified as the proportion of total variation in a community variable ( $V_t$ ) explained by genetic variance within a focal population ( $V_g$ ) of the community [22]. Based on its similarity to the heritability of phenotypic traits, this statistic has been called broad-sense ‘community heritability’ or  $H^2c$  ( $H^2c = V_g/V_t$ ) [26]. Several recent studies report that genetic variation within plants leads to significant ‘community heritability’ in the composition, diversity and trophic interactions within consumer communities [22,26,27].

Estimates of community heritability provide a basis for predicting whether evolution in one population can cause changes in the ecological properties of a community variable. If, for example, genetic variation in plant defense shows a negative genetic correlation with herbivore species richness (resulting in a significant  $H^2c$  for species richness), and selection acts to favor increased plant defense,

### Box 1. A basic synthesis of community ecology and evolutionary biology

Four rapidly developing areas of research bridge the questions and methods typically ascribed to community ecology and evolutionary biology: (i) the effects of genetic variation and rapid evolution in one species on the ecological characteristics of communities (community genetics) [2,21]; (ii) the role of evolutionary history (phylogeny) versus contemporary ecological forces in structuring communities (community phylogenetics) [34]; (iii) the influence of community context on the direction and rate of evolution [diffuse (co)evolution] [5,6]; and (iv) the study of whether multiple species coexist and co-diversify over macroevolutionary timescales (co-diversification of communities) [56]. We propose that two general hypotheses underlie these emerging areas of research:

Hypothesis 1: evolutionary processes and patterns causally affect community patterns (i.e. species diversity, relative abundance and distribution), and the dynamics associated with species interactions (e.g. predator–prey cycles).

Hypothesis 2: species interactions (e.g. host–parasite, plant–herbivore, predation, competition and mutualisms) and community context influence the direction, rate and outcome of evolutionary processes.

The areas of research that address these hypotheses are summarized by a basic conceptual framework that differentiates whether research is motivated by ecologically focused questions that address the causal effects of evolutionary processes and patterns on community dynamics and patterns (evolution→community ecology), as well as evolutionary focused questions that investigate how community ecology governs

evolution within populations (community ecology→evolution). These questions can be examined over short timescales (one to several generations: microscale) or longer timescales (thousands to millions of generations: macroscale) (Figure 1).

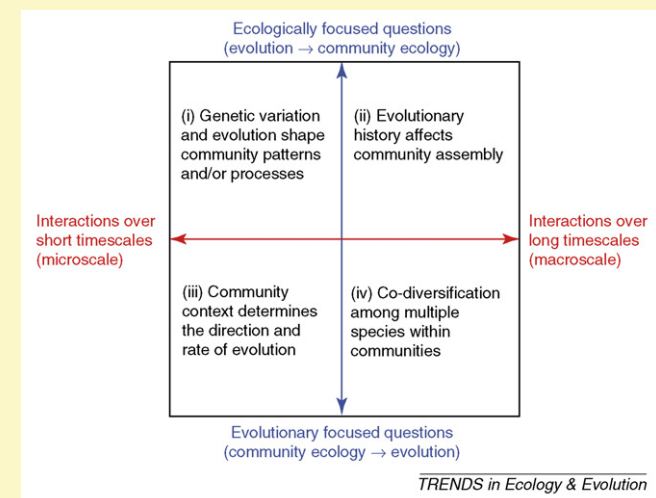


Figure 1.

**Table 1. Conditions that affect support for the hypotheses that bridge community ecology and evolutionary biology<sup>a</sup>**

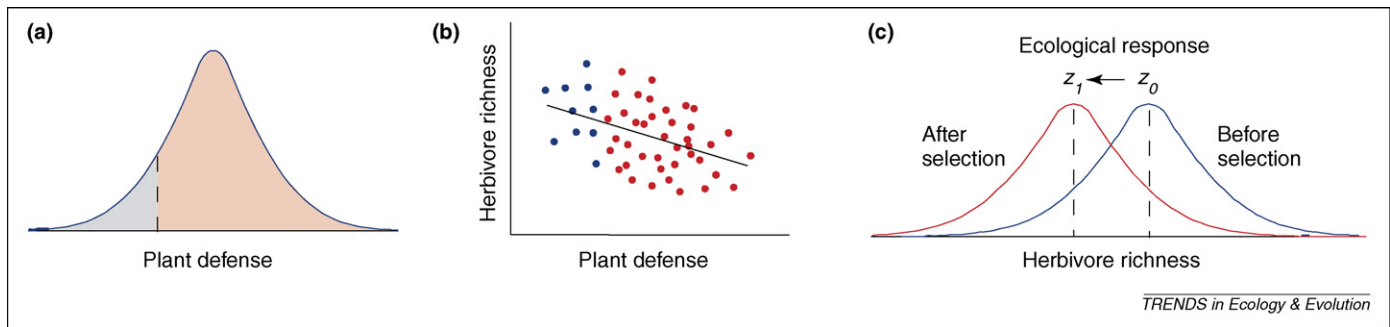
Category	Condition and/or property	Explanation	Refs
<b>(i) Genetic variation and microevolution affect community properties</b>			
Ecological	Dominance	Genetic variation and evolution in dominant or keystone species will have the strongest impact on communities	[21]
	Spatial scale	Genetic variation and evolution in local populations will have the strongest effect relative to other ecological factors at local spatial scales	[22]
Evolutionary	Genetic variance	Any factor that increases genetic variation within and between populations (e.g. population size, sexual system, hybridization, etc.) will lead to greater ecological effects of genetic variation	[26,67]
	Specialization	Species engaged in specialized interactions with a host or mutualist are most likely to be affected by genetic variation and evolution in the host or mutualist	
<b>(ii) Evolutionary history influences community assembly</b>			
Ecological	Spatial scale and environmental heterogeneity	Environmental heterogeneity increases with spatial scale, which can lead to greater phylogenetic clustering	[41]
	Interaction strength	Phylogenetic overdispersion increases with greater interspecific competition among species with phylogenetically conserved traits	[34]
	Enemies and mutualists	Natural enemies and mutualists increase the strength of phylogenetic signals on community structure when their attraction to species correlates with phylogeny; they decrease phylogenetic patterns if their action is uncorrelated with phylogeny	[42]
Evolutionary	Stochastic processes	Stochastic disturbance and drift reduce the strength of phylogenetic signals	[43]
	Adaptive radiation and dispersal limitation	<i>In situ</i> adaptive radiations coupled with dispersal limitations result in phylogenetic clustering at large spatial scales	[39]
	Time since divergence	Recently diverged taxa are most likely to show phylogenetic overdispersion	[45]
	Speciation mode and secondary contact	Positive correlations between phylogenetic distance and co-occurrence are more likely for congeneric species and groups that speciated in allopatry and recently came into secondary contact	(See text)
<b>(iii) Community context affects the direction and rate of evolution</b>			
Ecological	Indirect interactions	Direct interactions among two species can indirectly alter the nature of selection on a third species via density- and trait-mediated mechanisms. The importance of indirect interactions can increase with increased diversity in the community and increased interaction strength among species	[68]
	Phenotypic plasticity	Species interactions that cause a plastic response in a trait of a focal organism can alter the strength or type of selection on the trait (e.g. in the case of non-linear fitness surfaces)	[68,69]
	Spatial and temporal variation	Spatial and temporal changes in abiotic conditions and community composition can cause variable selection	[4,53,54]
Evolutionary	Genetic variance	(See above)	
	Genetic constraints	Genetic correlations between traits can constrain evolution in response to multiple selective agents	[5,6]
<b>(iv) Multiple species within communities co-diversify</b>			
Ecological	Robustness or stability	The presence and nature of species interactions must remain consistent across time and space	[70]
	Vicariance	Repeated events that geographically isolate communities can lead to co-speciation through allopatry	[64]
	Vertical transfer of communities	Vertical transfer of community members from generation to generation links the evolutionary history and increases stability of communities. Asexual reproduction further limits gene flow among diverging populations	[71]
Evolutionary	Specialization	Obligate associations among interacting species can increase the long-term ecological and evolutionary stability of interactions within communities	[56]
	Reciprocal natural selection	Consistent reciprocal natural selection among community members can lead to co-adaptation and co-speciation	[51]

<sup>a</sup>Support for hypotheses 1 and 2 at the microscale and macroscale (Box 1) will depend most strongly on the above ecological and evolutionary conditions and properties. These conditions are based on empirical and theoretical results and are not always necessary or sufficient to support the hypotheses.

the response to selection in the plant population is predicted to lead to fewer herbivore species on those plants (Figure 1). This does not imply that the herbivore community evolves as a superorganism, but that evolutionary changes in the plant population lead to ecological changes in the herbivore community over time. These changes in the community can be caused by the direct effects of plant evolution on multiple species, and by indirect effects resulting from interactions between the affected species. Although a few studies have measured community heritability [22,26,27], no studies have yet determined whether community variables change in response to evolution in one species (Figure 1c).

### Relative importance

Little is known about the relative importance of genetic variation and the ecological factors most commonly studied in community ecology [11]. Variation in the abiotic environment, competition, predation and mutualisms are key factors that determine the structure of communities. The primary objective of recent studies in community genetics has been to determine whether genetic variation in a population has a statistically significant effect on some aspect of the community. We argue that this approach is no longer sufficient, and the next step is to partition the variation explained by ecological and genetic factors, including the interactions between these sources of variation.



**Figure 1.** The community-level consequences of evolution by natural selection illustrated by a hypothetical example of how evolution by natural selection in plants can lead to ecological changes in a herbivore community. Consider a plant population that contains additive genetic variation in a plant defensive trait (e.g. secondary compounds, trichomes or leaf toughness) (a), and exhibits a negative genetic correlation with insect herbivore richness on individual plants (b), resulting in a significant 'community heritability'. If truncation selection leads to an increase in plant defense (i.e. plants in the blue-shaded portion of the curve (a) do not reproduce [blue points in (b)]), there should be an evolutionary response towards increased plant defense. This evolutionary response in the plant is predicted to lead to an ecological response in herbivore richness (c), whereby mean herbivore richness decreases from a mean of  $z_0$  before selection (blue curve: distribution of arthropod richness on plants before selection) to a mean of  $z_1$  after selection (red curve: distribution of arthropod richness after selection).

Multifactorial experiments that include multiple genotypes and manipulate at least one ecological factor make it possible to quantify the relative importance (e.g. with effect sizes or proportion of variance explained) and interactions between genetic variation and ecological factors that affect communities. The few studies that have taken this approach [22,25,28,29], show that genetic variation in plant traits, and the interaction between plant genotype and ecological factors, can be as important as spatial and temporal environmental variation, competition among insects and the effects of predation on individual arthropod populations and communities. Hairston *et al.* [11] also outline a general framework that can be used to measure the relative contributions of evolutionary change and ecological factors in driving community dynamics.

### Evolutionary history and the structure of contemporary communities

The notion that phylogenetic relationships between species can affect the structure of contemporary communities has a long history in ecology [30,31]. Given common descent, and a trend for phylogenetic niche conservatism, one might expect positive relationships between phylogenetic relatedness, the traits of species and habitat preferences [32]. Indeed, several studies on plants find clear phylogenetic signals of habitat preferences and ecologically important traits such as leaf characteristics [33]. On the one hand, these observations suggest that a positive relationship between phylogenetic history and co-occurrence in communities should exist, especially if phylogenetically conserved traits contribute directly to the distribution and abundance of species. On the other hand, if ecological interactions such as competition are a dominant force in structuring communities, one might predict that communities have an under-representation of closely related species [30]. Recent advances in molecular phylogenetics and statistical methods enable broader assessment of the intersection between evolutionary history and contemporary ecological interactions in structuring communities [34], and we suggest several conditions that make detecting phylogenetic signatures on communities most likely (Table 1).

Similar numbers of studies have found evidence for phylogenetic clustering versus phylogenetic overdispersion.

Studies detecting phylogenetic clustering [35–39] support the role of environmental filtering, where related species live in the same habitat because they share ecologically important traits. By contrast, evidence for phylogenetic overdispersion [40–42] implicates competition as a potential force driving the structure of communities. Perhaps not surprisingly, some studies have found a mixture of both patterns, either depending on habitat [43], spatial and temporal scale, or phylogenetic scale [42,44,45]. For instance, Lovette and Hochachka [44] found a pattern of overdispersion for wood-warblers at the local community scale, suggesting that competition leads to exclusion of closely related bird species. They also found phylogenetic clustering on the regional scale, indicating a role for environmental filtering. A few studies also found no phylogenetic signal on community structure [46–49], showing that the assembly of communities is not always influenced by phylogenetic relatedness. Determining the spatial scale at which a phylogenetic signal will be most relevant remains an important problem.

### Strength of phylogenetic and ecological forces

Despite these promising starts, several weaknesses exist for community phylogenetic approaches, which represent exciting avenues for future research. In our opinion, the next generation of studies must move beyond testing for a significant signal of phylogeny on communities, and towards assessing the strength of these associations, both in their own right and relative to traditional ecological factors [42]. We need a better understanding of the intersection between evolutionary history and contemporary ecological forces, such as competition, predation, mutualism, disturbance and stochastic processes. That is, what proportion of variation in community similarity, niche overlap and co-occurrence can be explained by phylogenetic distance? And, is the variation explained of greater or lesser magnitude than the abiotic and biotic factors identified above?

These questions need to be addressed not only in retrospective studies, but also in experimental studies that manipulate phylogenetic distance and ecological factors simultaneously. In addition, the dominant conceptual view in community phylogenetics is that environmental filtering and competition for resources are responsible for patterns



of phylogenetic clustering and overdispersion [34]. Are these predictions altered for communities structured by predation, stochastic disturbance, and so on? Some of these factors can act in ways that are dependent on phylogeny, whereas others act independently of phylogeny and can obscure phylogenetic signals (Table 1). Finally, if most speciation occurs in allopatry [50], one would expect that closely related species with smaller amounts of genetic distance between them would co-occur less often than would distantly related species. As such, a positive relationship between phylogenetic distance and co-occurrence should be the null hypothesis for studies of closely related species.

### The influence of community context on the rate and direction of microevolution

The importance of ecological interactions within communities in driving evolution within a focal population, and coevolution among populations, has been intensely debated for over 40 years [3–6,51]. Given that most species interact with numerous other species in a community, a series of questions at the intersection of community ecology and evolutionary biology naturally follow: does the presence of multiple interacting species in a community alter evolutionary and coevolutionary processes and patterns? If it does, is this due primarily to genetic or ecological factors? And, when community context alters evolutionary relationships among species, how does this manifest itself on a geographical scale?

There are two straightforward ways that community context can affect the rate of microevolutionary change within populations. If it alters either the expression of genetic variation, or the strength of natural selection on a focal population, microevolution will necessarily be linked to variation in the community. Although the effects of community context on evolution can involve reciprocal natural selection and evolutionary change between two or more populations, such reciprocity is not necessary for it to influence evolution within one or more populations. We use the short-hand ‘(co)evolution’ to refer to both reciprocal and non-reciprocal evolutionary interactions in communities.

#### *Pairwise and diffuse (co)evolution*

Although the distinction between pairwise and diffuse (co)evolution has been criticized as an artificial dichotomy and a distinction that should be abandoned [4], we believe that it is important. Distinguishing between these patterns of evolution provides direct insight into whether a consideration of community interactions among multiple species is necessary to understand evolution [52]. If evolution within a population is typically driven by independent pairwise interactions between species, an understanding of more complex community interactions is not needed. If selection is usually diffuse, an understanding of complex community processes and patterns is essential to the study of evolution. Theoretical models and experimental designs for distinguishing between pairwise and diffuse selection and coevolution have been well developed [5,6,52].

Despite the attention that has been paid to coevolution, and the intuitive notion that changes in community composition necessarily alter evolutionary interactions within

communities, there are few supporting data [6]. We propose that two additional gaps in our knowledge remain. First, studies have attempted to predict whether evolution is pairwise or diffuse by studying selection on a single species within the community [5,53,54]. Whether pairwise or diffuse selection typically involves reciprocal selection [55] and evolutionary change among populations is little studied.

The second gap relates to whether geographic mosaics of selection and (co)evolution are caused by variation in the biotic or abiotic environment. Empirical work that bridges community ecology and evolutionary biology could synthesize Thompson’s [4] mosaic approach with approaches that assess whether evolution is driven by pairwise or diffuse selection. A ubiquitous feature of interspecific interactions is that they are spatially variable [4]. Are changes in these interactions driven by variation in the abiotic environment, or are they driven by variation in the biotic environment, where variable community context might alter natural selection on the interactions among species (diffuse selection)? To date, studies that implicate changes in community composition in creating geographic mosaics of coevolution have relied on observational comparisons of the traits of species and interactions across broad geographical regions. This approach is important but limited by the confounding factors that are inherent to observational techniques (i.e. patterns among species might be caused by variation in unmeasured factors). A pairing of reciprocal transplant experiments with experimental manipulations of community composition would further help to disentangle the relative importance of abiotic and biotic mechanisms of geographic mosaics of coevolution.

### Co-diversification of communities over macroevolutionary time

Given the ‘mess’ [8] that is the reality of community ecology, is it foolhardy to ask whether there are ancient communities in which multiple interacting species co-evolved or co-speciated over millions of years? The emerging paradigm is that evolutionary interactions among species vary in both space and time and, for this reason, the conditions that lead to co-diversification over macroevolutionary timescales are thought to be highly restrictive. It is perhaps surprising then, that numerous recent studies detect co-speciation between evolving lineages of species (e.g. rodents and lice, pollinators and plants, etc.) [56–60], and we propose conditions that are most likely to lead to such patterns (Table 1).

#### *Multispecies co-diversification*

Studies of the macroevolutionary patterns of communities have focused on interactions between pairs of species, whereas most communities contain multiple interacting species. Can multiple species within communities co-diversify? The best evidence for multispecies co-diversification comes from the over 50-million-year-old communities of fungus-farming ants, ant-cultivated fungi, parasitic fungi and antibiotic-secreting bacteria that reduce parasitism on cultivated fungi [61]. The four-way interactions in these communities are highly specialized and have an ancient origin. The association among ants, cultivated fungi and

parasitic fungi exhibit deep phylogenetic congruence, with host switching among more recently diverged symbionts [61]. Furthermore, the interactions between the ants and their cultivated fungus arose just twice, whereas the ant–parasite interaction is strictly monophyletic, and the association with bacteria evolved multiple times [62]. Thus, this community shows evidence for co-speciation among three of the four community members.

Examples of multispecies co-diversification are rare, but it is unclear whether this is because co-diversification in complex communities is evolutionarily unstable, or insufficient effort has been devoted to finding such patterns. Given the numerous examples of long-term co-diversification between pairs of species [56–58,63], and the knowledge that many of these interactions also involve intimate associations with additional taxa, it seems probable that multispecies co-diversification is more common. We suggest that a starting point for testing this prediction is within systems that already show evidence of co-speciation and contain additional symbionts. For example, it might be the case that the co-speciation exhibited by aphids and their bacterial symbionts *Buchnera* [63] also involves the diversification of plant hosts, secondary bacterial symbionts and aphid parasitoids.

#### *Ecology of co-diversification*

The comparative phylogenetic methods used to study the evolutionary history of communities provide no information about the ecological mechanisms underlying macroevolutionary patterns. Although it is often assumed that co-diversification implicates a long history of coevolution, comparing phylogenies does not provide evidence for reciprocal natural selection and adaptation among species [3]. Co-diversification can result from non-coevolutionary mechanisms, such as vicariance, asymmetric selection resulting from host tracking by commensal symbionts, and rapid colonization and diversification of a parasite following the radiation of a host [64].

Although the ecological interactions that led to co-diversification are lost in time, experiments that utilize extant communities can help reject alternative mechanisms of co-diversification. Once co-speciation has been detected among multiple species, a series of experiments can elucidate the nature of ecological interactions within extant communities. In the simplest case of interactions between two species, one of three patterns might exist: (i) reciprocal positive or negative fitness effects between species; (ii) unidirectional fitness effects of one species on a second species; or (iii) no fitness effects on either species. Only (i) is consistent with a coevolutionary hypothesis of diversification, whereas (ii) and (iii) are most congruent with commensal interactions and vicariance leading to co-diversification, respectively. When this approach is applied to interactions among three or more species, further insight will be gained from measuring the direct and indirect fitness effects of species interactions. Although such experiments do not provide definitive proof of how ecological mechanisms shaped macroevolutionary patterns, the information from these and similar experiments [65] offer the best approach to understanding the ecological mechanisms of co-diversification.

The ecological interactions within co-diversified communities are rarely studied [65]. Reciprocal fitness effects consistent with coevolved interactions have been detected among two to three symbiotic species within a single community [55,60,66]. Despite the importance of these results, these studies have only considered interactions within a single community. As such, it is difficult to determine whether these patterns are generalizable among diverged communities. For example, are the reciprocal fitness effects observed in a single bird–louse community representative of the effects between other bird and louse species from the same clade? Idiosyncratic interactions between species across the phylogeny would suggest that there is no common mechanism to co-diversification, whereas consistent reciprocal fitness effects would imply that the birds and louse have coevolved.

#### **How important is it for biologists to bridge community ecology and evolutionary biology?**

An increase in recent research that bridges community ecology and evolutionary biology provides mounting evidence in support of the hypotheses proposed here (Box 1). Evolutionary processes over short and long timescales can influence community dynamics and patterns. Likewise, ecological interactions among species within communities can influence micro- and macroevolutionary processes and patterns. As is often the case in new areas of research, the focus has been on documenting the presence or absence of an ecological or evolutionary effect in experiments. In this regard, there is no question: there is frequently an effect. It is therefore tempting to conclude that bridging community ecology and evolutionary biology is essential, as it provides at least some additional explanatory power in answering questions within both community ecology and evolutionary biology. However, this conclusion is premature.

Despite the exciting results reviewed here, the importance of bridging community ecology and evolutionary biology has not yet been convincingly demonstrated. There is a lack of evidence that compares the interactions and relative importance of different factors contributing to ecological and evolutionary variation within communities. We propose that it is crucial for future research to determine how important it is, and under what conditions biologists should bridge community ecology and evolutionary biology. Moreover, researchers that seek to understand the relative importance of different factors must conduct experiments that simulate natural levels of variation. We anticipate that it is the results of these experiments and their application to both basic and applied problems in biology (e.g. conservation, agriculture or epidemiology), that will ultimately determine whether community ecologists, evolutionary biologists and applied biologists will see the utility of adopting each others perspectives and approaches.

#### **Acknowledgements**

We thank P. Abrams, A.A. Agrawal, A.F. Agrawal, S. Barrett, C. Currie, W. Godsoe, S. Heard, L. Rowe and three anonymous reviewers for comments on the ideas conveyed in this article. Our research is funded by the Natural Sciences and Engineering Research Council of Canada and the University of Toronto Connaught Fund.

## References

- 1 Ford, E.B. (1964) *Ecological Genetics*, John Wiley & Sons
- 2 Antonovics, J. (1992) Toward community genetics. In *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics* (Fritz, R.S. and Simms, E.L., eds), pp. 195–215, University of Chicago Press
- 3 Janzen, D.H. (1980) When is it coevolution? *Evolution* 34, 611–612
- 4 Thompson, J.N. (2005) *The Geographic Mosaic of Coevolution*, University of Chicago Press
- 5 Stinchcombe, J.R. and Rausher, M.D. (2001) Diffuse selection on resistance to deer herbivory in the ivyleaf morning glory, *Ipomoea hederacea*. *Am. Nat.* 158, 376–388
- 6 Strauss, S.Y. *et al.* (2005) Toward a more trait-centered approach to diffuse (co)evolution. *New Phytol.* 165, 81–90
- 7 Schluter, D. (2000) *The Ecology of Adaptive Radiation*, Oxford University Press
- 8 Lawton, J.H. (1999) Are there general laws in ecology? *Oikos* 84, 177–192
- 9 Møller, A.P. and Jennions, M.D. (2002) How much variance can be explained by ecologists and evolutionary biologists? *Oecologia* 132, 492–500
- 10 Kinnison, M.T. and Hendry, A.P. (2001) The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* 112–113, 145–164
- 11 Hairston, N.G. *et al.* (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* 8, 1114–1127
- 12 Abrams, P.A. and Matsuda, H. (1997) Prey adaptation as a cause of predator-prey cycles. *Evolution* 51, 1742–1750
- 13 Yoshida, T. *et al.* (2003) Rapid evolution drives ecological dynamics in a predator-prey system. *Nature* 424, 303–306
- 14 Bohannan, B.J.M. and Lenski, R.E. (2000) Linking genetic change to community evolution: insights from studies of bacteria and bacteriophage. *Ecol. Lett.* 3, 362–377
- 15 Booth, R.E. and Grime, J.P. (2003) Effects of genetic impoverishment on plant community diversity. *J. Ecol.* 91, 721–730
- 16 Vellend, M. (2006) The consequences of genetic diversity in competitive communities. *Ecology* 87, 304–311
- 17 Proffitt, C.E. *et al.* (2005) *Spartina alterniflora* genotype influences facilitation and suppression of high marsh species colonizing an early successional salt marsh. *J. Ecol.* 93, 404–416
- 18 Crutsinger, G.M. *et al.* (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* 313, 966–968
- 19 Johnson, M.T.J. *et al.* (2006) Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecol. Lett.* 9, 24–34
- 20 Fritz, R.S. and Price, P.W. (1988) Genetic variation among plants and insect community structure: willows and sawflies. *Ecology* 69, 845–856
- 21 Whitham, T.G. *et al.* (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* 84, 559–573
- 22 Johnson, M.T.J. and Agrawal, A.A. (2005) Plant genotype and environment interact to shape a diverse arthropod community on Evening Primrose (*Oenothera biennis*). *Ecology* 86, 874–885
- 23 Hughes, A.R. and Stachowicz, J.J. (2004) Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc. Natl. Acad. Sci. U. S. A.* 101, 8998–9002
- 24 Schweitzer, J.A. *et al.* (2004) Genetically based trait in a dominant tree affects ecosystem processes. *Ecol. Lett.* 7, 127–134
- 25 Madritch, M. *et al.* (2006) Genetic identity of *Populus tremuloides* litter influences decomposition and nutrient release in a mixed forest stand. *Ecosystems* 9, 528–537
- 26 Shuster, S.M. *et al.* (2006) Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. *Evolution* 60, 991–1003
- 27 Bailey, J.K. *et al.* (2006) Importance of species interactions to community heritability: a genetic basis to trophic-level interactions. *Ecol. Lett.* 9, 78–85
- 28 McGuire, R.J. and Johnson, M.T.J. (2006) Plant genotype and induced responses affect resistance to herbivores on evening primrose (*Oenothera biennis*). *Ecol. Entomol.* 31, 20–31
- 29 Karban, R. (1992) Plant variation: its effects on populations of herbivorous insects. In *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics* (Fritz, R.S. and Simms, E.L., eds), pp. 195–215, University of Chicago Press
- 30 Elton, C. (1946) Competition and the structure of ecological communities. *J. Anim. Ecol.* 15, 54–68
- 31 Darwin, C. (1859) *The Origin of Species*, John Murray
- 32 McPeck, M.A. and Brown, J.M. (2000) Building a regional species pool: diversification of the *Enallagma* damselflies in eastern North America. *Ecology* 81, 904–920
- 33 Ackerly, D.D. (2004) Adaptation, niche conservatism, and convergence: comparative studies of leaf evolution in the California Chaparral. *Am. Nat.* 163, 654–671
- 34 Webb, C.O. *et al.* (2002) Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* 33, 475–505
- 35 Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *Am. Nat.* 156, 145–155
- 36 Tofts, R. and Silvertown, J. (2000) A phylogenetic approach to community assembly from a local species pool. *Proc. R. Soc. B* 267, 363–369
- 37 Ødegaard, F. *et al.* (2005) The importance of plant relatedness for host utilization among phytophagous insects. *Ecol. Lett.* 8, 612–617
- 38 Weiblen, G.D. *et al.* (2006) Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology* 87, S62–S75
- 39 Horner-Devine, M.C. and Bohannan, B.J.M. (2006) Phylogenetic clustering and overdispersion in bacterial communities. *Ecology* 87, S100–S108
- 40 Silvertown, J. *et al.* (2001) Phylogeny and the niche structure of meadow plant communities. *J. Ecol.* 89, 428–435
- 41 Cavender-Bares, J. *et al.* (2004) Phylogenetic overdispersion in Floridian oak communities. *Am. Nat.* 163, 823–843
- 42 Webb, C.O. *et al.* (2006) Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology* 87, S123–S131
- 43 Kembel, S.W. and Hubbell, S.P. (2006) The phylogenetic structure of a neotropical forest tree community. *Ecology* 87, S86–S99
- 44 Lovette, I.J. and Hochachka, W.M. (2006) Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. *Ecology* 87, S14–S28
- 45 Cavender-Bares, J. *et al.* (2006) Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87, S109–S122
- 46 Losos, J.B. *et al.* (2003) Niche lability in the evolution of Caribbean lizard community. *Nature* 424, 542–545
- 47 Gillespie, R. (2004) Community assembly through adaptive radiation in Hawaiian spiders. *Science* 303, 356–359
- 48 Ives, A.R. and Godfray, H.C.J. (2006) Phylogenetic analysis of trophic associations. *Am. Nat.* 168, E1–E14
- 49 Silvertown, J. *et al.* (2006) Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proc. R. Soc. B* 273, 39–44
- 50 Coyne, J.A. and Orr, H.A. (2004) *Speciation*, Sinauer Associates
- 51 Ehrlich, P.R. and Raven, P.H. (1964) Butterflies and plants: a study in coevolution. *Evolution* 18, 586–608
- 52 Rausher, M.D. (1996) Genetic analysis of coevolution between plants and their natural enemies. *Trends Genet.* 12, 212–217
- 53 Lau, J.A. (2006) Evolutionary responses of native plants to novel community members. *Evolution* 60, 56–63
- 54 Stinchcombe, J.R. and Rausher, M.D. (2002) The evolution of tolerance to deer herbivory: modifications caused by the abundance of insect herbivores. *Proc. R. Soc. B* 269, 1241–1246
- 55 Clayton, D.H. *et al.* (1999) Reciprocal natural selection on host-parasite phenotypes. *Am. Nat.* 154, 261–270
- 56 Page, R.D.M. ed. (2003) *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*, University of Chicago Press
- 57 Peek, A.S. *et al.* (1998) Cospeciation of chemotrophic bacteria and deep sea clams. *Proc. Natl. Acad. Sci. U. S. A.* 95, 9962–9966
- 58 Rønsted, N. *et al.* (2005) 60 million years of co-divergence in the fig-wasp symbiosis. *Proc. R. Soc. B* 272, 2593–2599
- 59 Farrell, B. and Mitter, C. (1990) Phylogenesis of insect/plant interactions: have *Phyllobrotica* leaf beetles (Chrysomelidae) and the *Lamiales* diversified in parallel? *Evolution* 44, 1389–1403
- 60 Currie, C.R. *et al.* (2003) Experimental evidence of a tripartite mutualism: bacteria protect ant fungus gardens from specialized parasites. *Oikos* 101, 91–102
- 61 Currie, C.R. *et al.* (2003) Ancient tripartite coevolution in the attine ant-microbe symbiosis. *Science* 299, 386–388
- 62 Cafaro, M.J. and Currie, C.R. (2005) Phylogenetic analysis of mutualistic filamentous bacteria associated with fungus-growing ants. *Can. J. Microbiol.* 51, 441–446



- 63 Moran, N.A. (2001) The coevolution of bacterial endosymbionts and phloem-feeding insects. *Ann. Miss. Bot. Gard.* 88, 35–44
- 64 Brooks, D.R. and McLennan, D.A. (1991) *Phylogeny, Ecology and Behavior: A Research Program in Comparative Biology*, University of Chicago Press
- 65 Clayton, D.H. *et al.* (2003) The ecological basis of coevolutionary history. In *Tangled Trees: Phylogeny, Cospeciation, and Coevolution* (Page, R.D.M., ed.), pp. 310–341, University of Chicago Press
- 66 Koga, R. *et al.* (2003) Changing partners in an obligate symbiosis: a facultative endosymbiont can compensate for loss of the essential endosymbiont *Buchnera* in an aphid. *Proc. R. Soc. B* 270, 2543–2550
- 67 Hartl, D.L. and Clark, A.G. (1989) *Principles of Population Genetics*, Sinauer Associates
- 68 Inouye, B. and Stinchcombe, J.R. (2001) Relationships between ecological interaction modifications and diffuse coevolution: similarities, differences, and causal links. *Oikos* 95, 353–360
- 69 Kraft, P.G. *et al.* (2006) Predator-induced phenotypic plasticity in tadpoles: extension or innovation? *J. Evol. Biol.* 19, 450–458
- 70 Axelrod, R. and Hamilton, W.D. (1981) The evolution of cooperation. *Science* 211, 1390–1396
- 71 Bull, J.J. *et al.* (1991) Selection of benevolence in a host-parasite system. *Evolution* 45, 875–882

## Forthcoming Conferences

Are you organizing a conference, workshop or meeting that would be of interest to *TREE* readers? If so, please e-mail the details to us at [TREE@elsevier.com](mailto:TREE@elsevier.com) and we will feature it in our Forthcoming Conference filler.

### 5–8 June 2007

ESEE 2007. Integrating Natural and Social Sciences for Sustainability, Leipzig, Germany  
<http://www.esee2007.ufz.de>

### 12–15 June 2007

5th Meeting of the Australasian Evolution Society, The University of New South Wales, Sydney, Australia  
<http://www.evolutionau.org>

### 16–21 June 2007

Evolution Annual Meeting, held jointly by the Society for the Study of Evolution, the American Society of Naturalists and the Society of Systematic Biologists, Christchurch, New Zealand  
<http://www.evolutionsociety.org/meetings.htm>

### 25–27 June 2007

International Symposium sponsored by the Botanical Society of Scotland on the 'History, Evolution and Future of Arctic and Alpine Flora', St Andrews, UK  
<http://biology.st-andrews.ac.uk/aafcon>

### 1–5 July 2007

Society for Conservation Biology Annual Meeting, Port Elizabeth, South Africa  
<http://www.nmmu.ac.za/scb/>

### 16–18 July 2007

ENTO '07: RES Annual National Meeting and RES Symposium on Aquatic Insects, Edinburgh, UK  
<http://www.royensoc.co.uk/>

### 29 July–2 August 2007

13th Symposium on Insect-Plant Relationships (SIP13), Uppsala, Sweden  
<http://www-conference.slu.se/sip13>

### 5–10 August 2007

92nd ESA Annual Meeting, held jointly with SER, San Jose, CA, USA  
<http://www.esa.org/meetings/FutureAnnualMeetings.php>

### 12–18 August 2007

30th Congress of the International Association of Theoretical and Applied Limnology, Montréal, Canada  
<http://www.sil2007.org>

### 20–25 August 2007

11th Congress of The European Society for Evolutionary Biology, Uppsala, Sweden  
<http://www.eseb.org/>

### 28–31 August 2007

6th Biennial Meeting of the Systematics Association, Edinburgh, UK  
<http://www.systass.org/biennial2007/>

### 2–5 September 2007

MEDECOS XI 2007: 11th International Mediterranean Ecosystems Conference, Perth, Western Australia, Australia  
<http://www.medecosxi2007.com.au>

### 9–13 September 2007

Seed Ecology II 2007: 2nd International Society for Seed Science Meeting on Seeds and the Environment, Perth, Western Australia, Australia  
<http://www.seedecology2007.com.au>

### 10–12 September 2007

British Ecology Society Annual Meeting, Glasgow, UK  
<http://www.britishecologicalsociety.org/articles/meetings/current/>

### 10–13 September, 2007

10th International Colloquium on Endocytobiology and Symbiosis" Gmunden, Austria.  
<http://www.endocytobiology.org/>

### 13–14 September 2007

Systems Biology and the Biology of Systems: how, if at all are they related? Buxton, Derbyshire, UK  
<http://www.newphytologist.org/systems/default.htm>

### 17–20 October 2007

67th Annual Meeting of the Society of Vertebrate Paleontology, Austin, Texas USA  
[http://www.vertpaleo.org/future\\_meetings.htm](http://www.vertpaleo.org/future_meetings.htm)