



LETTER

Coevolution, diversification and alternative states in two-trophic communities

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Abstract

Single-trait eco-evolutionary models of arms races between consumers and their resource species often show inhibition rather than promotion of community diversification. In contrast, modelling arms races involving multiple traits, we found that arms races can promote diversification when trade-off costs among traits make simultaneous investment in multiple traits either more beneficial or more costly. Coevolution between resource and consumer species generates an adaptive landscape for each, with the configuration giving predictable suites of consumer and resource species. Nonetheless, the adaptive landscape contains multiple alternative stable states, and which stable community is reached depends on small stochastic differences occurring along evolutionary pathways. Our results may solve a puzzling conflict between eco-evolutionary theory that predicts community diversification via consumer–resource interactions will be rare, and empirical research that has uncovered real cases. Furthermore, our results suggest that these real cases might be just a subset of alternative stable communities.

Keywords

Coexistence, community structure, divergence, predator, prey.

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INTRODUCTION

Strong natural selection is expected to generate repeated, predictable patterns in diversification (Schluter, 1996; Orr and Smith, 1998; Webb *et al.*, 2002; Schluter, 2009; Mahler *et al.*, 2013). For example the evolution of *Anolis* lizards have repeatedly been shown to evolve in a predictable manner, where independently evolved island communities are strikingly similar in the composition of ecological traits (Losos *et al.*, 1997; Losos *et al.*, 1998; Mahler *et al.*, 2013). Theoretical research suggests this diversification can arise due to advantages from specialising on one or two resource types that allows coexistence of multiple specialised species (MacArthur and Levins, 1967) and selects for multiple species specialising in particular resources (Dieckmann and Doebeli, 1999; Doebeli and Ispolatov, 2010). Despite this predictability, however, there are multiple possible configurations of *Anolis* communities. For example an island might contain species with different sizes, large and small, or a few medium-sized species, each with intraspecific variation (Munoz *et al.*, 2014). Either configuration might be stable (Sherratt *et al.*, 2015), but which configuration occurs on a given island might be unpredictable. This type of situation, in which there are two configurations both of which are stable, can be shown in ecological models such as Lotka–Volterra competition models (Law and Morton, 1993). Furthermore, numerous studies have shown that natural communities can exist in one of two alternative states (Scheffer *et al.*, 1997; Ackerly, 2003; Scheffer and Carpenter,

2003; Staver *et al.*, 2011), suggesting that the ecological community assembly process may depend on stochastic events that determine which state emerges. Theoretical studies also find that evolutionary models of competition can lead to alternative stable states under certain circumstances (Geritz *et al.*, 1999; Kremer and Klausmeier, 2017).

Just as evolution caused by competition is thought to drive diversification in single trophic-level systems (Dieckmann and Doebeli, 1999), coevolutionary arms races between consumers and their resources in systems with two trophic levels have long been thought to drive diversification in ecological communities (Darwin, 1859; Ehrlich and Raven, 1964). One potential mechanism driving diversification of multiple trophic levels is trait matching, in which consumer traits must match up with traits of their resource to allow successful consumption (Brown and Vincent, 1992; Loeuille and Loreau, 2005; Ripa *et al.*, 2009; Yoder and Nuismer, 2010). Examples of matching traits are habitat preferences that align with a particular food source, and sensitivity to the kairomones emitted by a particular resource species that allows resource location. Trait matching promotes diversification through niche separation in a manner similar to competitive communities, where specialist consumers each adopt specific trait values associated with particular resource species (Brown and Vincent, 1992; Loeuille and Loreau, 2005; Ripa *et al.*, 2009; Yoder and Nuismer, 2010).

In contrast to trait matching, consumer–resource interactions are often governed by the consumer’s ability to

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overcome a prey's defensive traits, such as a consumer's need to pierce the resource species' physical defences (Toju *et al.*, 2011), a herbivore's ability to digest or sequester a certain amount of plant toxins (Kursar *et al.*, 2009), or a predatory fish needing a large enough gape to consume prey of a particular size (Palkovacs and Post, 2009). These examples do not involve trait matching, because there is a monotonic relationship between the expression of a trait (e.g. size of a prey or gape of a predator) and the ability of a resource species to escape a consumer, or a consumer species to eat a resource. In contrast, for trait matching there is an intermediate optimal trait value for resource and consumer species that depends on the trait value of consumer and resource species respectively. In models for single consumer and single resource traits that do not assume trait matching and hence do not impose niche separation, arms races inhibit rather than promote diversification (Yoder and Nuismer, 2010). Thus, although specialised trait matching might be common for some specific types of consumer–resource interactions (such as between specialist parasites and their hosts), this type of specialisation is unlikely to be the sole generator of the morphological and physiological diversity in consumer and resource species observed in nature.

Evidence of arms race coevolution influencing trait divergence has emerged from field data (Bagchi *et al.*, 2014; Condon *et al.*, 2014), phylogenetic analyses (Janz *et al.*, 2006; McKenna *et al.*, 2009) and observation of community coevolution in the laboratory (Fukami *et al.*, 2007; Herron and Doebeli, 2013a; Betts *et al.*, 2018). This body of empirical evidence contrasts current evolutionary theory suggesting limited potential for consumer–resource co-evolution to drive diversification (Yoder and Nuismer, 2010). The composition of ecological communities in nature depends on whether different species are able to reach and occupy fitness peaks that represent different phenotypic niches (Martin and Wainwright, 2013). The complicated nature of these fitness landscapes and the evolutionary processes responding to them may allow evolutionary arms races to lead to alternative stable communities. Indeed, fossil records suggest communities evolving during glacial or interglacial periods represent alternative states, with different community types occurring in similar environmental conditions (Rodríguez, 2006). Furthermore, some plant defences show no phylogenetic signal in plant traits, such that evolutionarily related plant species are not more likely to be defended against the same herbivores (Kursar *et al.*, 2009). This absence of phylogenetic structure suggests that evolution driven by plant–herbivore arms races can occur rapidly, leaving no signal of evolutionary history. However, current theory does not explain how evolutionary arms races lead to this type of diversification of resources and consumers, much less alternative stable communities.

Here, we use a simple consumer–resource model to evaluate the potential for arms races to promote diversification when resources and consumers have multiple traits for defence and offense, in the absence of specialised trait matching. Traits governing the arms race may describe, for example plant secondary compounds that provide monotonically increasing protection against insect herbivores or increasing running speeds that monotonically increasing a prey's ability to escape

a predator. Arms-race models containing single generalised (non-matching) traits are expected to promote sweeping, directional evolution leading to convergence of each trophic level (Yoder and Nuismer, 2010). However, empirical studies suggest arms races comprising more traits should lead to diversification (Kursar *et al.*, 2009; Betts *et al.*, 2018). There are also theoretical results suggesting that multidimensional antagonistic traits with trade-offs may behave as matching traits, which in turn can lead to disruptive selection in single consumer–single resource models (Yamamichi *et al.*, 2019). However, we are not aware of any model that has explored the potential for coevolutionary arms races to generate diverse multi-species communities that are both evolutionarily and ecologically stable.

In our model, the traits between resource and consumer are paired, so that increasing the resource trait value (e.g. particular plant secondary compounds) can be overcome by increasing the value of a trait in the consumer (e.g. herbivore detoxification of that compound); these traits, however, increase (for consumers) or decrease (for resources) the strength of consumer–resource interactions monotonically, so there is no trait matching. The costs of increased investment in a trait are exacted through some other component of fitness. For example increased investment in secondary compounds might decrease possible investment in photosynthesis (Halitschke *et al.*, 2011; Züst and Agrawal, 2017), or investment in running speed could increase metabolic costs and hence lower reserves for reproduction (Lovegrove, 2001). In the model, the costs of investing in arms-race traits occur as decreases in the population growth rate of the species independently from consumer–resource interactions (Northfield and Ives, 2013; Züst and Agrawal, 2017). For both resources and consumers, there can be non-additive trade-offs between arms-race traits (parameters η_R and η_C); if there are positive trade-offs for two traits (η_R or $\eta_C > 0$), increasing investment in both traits together will decrease the population growth rate (independent of the consumer–resource interaction) more than the average decrease in the same investment in both traits separately. This may occur, for example if it is particularly costly for an animal to become both strong and fast to improve both fight and flight responses (Lovegrove, 2001). We also consider negative trade-offs ($\eta_R < 0$, $\eta_C < 0$) to describe scenarios where investing in one trait facilitates investing in a second. We modelled trait evolution using two methods. First, we used an adaptive dynamics-type of individual clone-based approach that simulates growth of asexually reproducing organisms. Second, we used a quantitative genetics approach that is more analytically tractable. In the models, there is no environmental gradient, so that all adaptive peaks are generated intrinsically by the consumer–resource interactions.

MODEL DESCRIPTION

The model is designed to ask whether coevolutionary arms races can generate multiple peaks in the adaptive landscapes of resource and consumer species, and hence generate species diversity. The model considers only selective forces generating diversification (Schluter, 2000; Gavrillets and Losos, 2009;

Yoder and Nuismer, 2010), rather than also the speciation process, although densities as well as trait values are included. The specific functional forms for equations were selected to ensure the possibility that maximum fitness is achieved at intermediate trait values. This requires population dynamic equations in which population growth rates are concave functions of trait values for both resources and consumers.

We assume that the consumer attack rate for consumer j on resource i is determined by the $1 \times k$ vectors of k defensive traits V_i , and k offensive traits U_j . To ensure that resource and consumer traits scale the same way in the attack rate, we assume increasing values of the consumer offensive trait decrease the attack rate. Thus, higher offensive trait values imply reduced consumer ability to overcome the resource defence. We assume all elements of V_i and $U_j \geq 0$. Given population densities of x_i for resource i ($i = 1, \dots, n$) and y_j for consumer j ($j = 1, \dots, p$), the per capita population growth rate of resource 1 is

$$F_1 = \exp\left(r_1 \left[1 - A(V_1) \sum_{i=1}^n x_i - \sum_{j=1}^p B(V_1, U_j) y_j\right]\right) \quad (1)$$

where r_1 is the intrinsic rate of increase. The attack rate of consumer j on resource i , $B(V_i, U_j)$, is given by $\beta e^{-V_i^* (U_j^t)^2}$, where each element of V_i and U_j is squared, $*$ is vector multiplication and t represents transpose. This squared, multiplicative term makes the population growth rate of resource and consumer concave with respect to trait values, with $B(V_i, U_j)$ declining with increases in each element of V_i and U_j . The costs to resources of investing in defensive traits occur through decreases in the population growth rate, scaled by the total density of the resources; $A(V_i) = a + f V_i^* C^* (V_i)^t$, where a defines the baseline competition coefficient, and f represents the cost of defensive traits. (A similar model in which $A(V_i)$ is not scaled by densities $\sum_{i=1}^n x_i$ in eqn 1 gives qualitatively similar results.) C is a $k \times k$ matrix with diagonal elements equal to one, and off-diagonal elements equal to η_R that gives the non-additive trade-offs among traits on their costs. When η_R is positive, investing in multiple traits V_i that decrease the attack rate $B(V_i, U_j)$ causes a greater decrease in fitness than the sum of the decreases caused by investing in each trait separately.

The per capita population growth rate of consumer 1 is

$$G_1 = \exp\left(c \sum_{i=1}^n B(V_i, U_1) x_i - M(U_1)\right). \quad (2)$$

The consumer experiences a cost of increasing its attack rates through increased mortality; specifically, $M(U_j) = m + g (U_j^* D^* (U_j)^t)$, where g governs the consumer's cost of offence, and D is a $k \times k$ matrix with diagonal elements equal to one and off-diagonal elements equal to $-\eta_C$. When η_C is positive, investing in multiple traits U_i that increase the attack rate $B(V_i, U_j)$ causes a greater decrease in fitness than the sum of the decreases caused by investing in each trait separately. The parameters c and m represent the conversion rate of resources consumed to consumers produced, and consumer mortality rate respectively.

For the analyses, we first evaluated the clone-based implementation of the model. This model was initiated with single resource and consumer clones, and each iteration each clone gave rise to a daughter clone with probability μ by selecting

trait values from normal distributions with means given by the mother's trait values and standard deviation σ . We then analysed the same model using a quantitative genetics approach that allows mathematical tools for finding alternative stable states. For the quantitative genetics approach, we refer to clones as species, because we start with a predetermined number of them and analyse how they diverge via evolution. We started with 20 species of resource and consumer, and simulated dynamics for 10^6 time steps, after which we randomly perturbed the trait value of a species using normal distributions with means equal to the mother species trait values and standard deviations allowing daughter species to 'jump' to different alternative states. Finally, to evaluate the effects of major disruptions in community evolution, we combined two alternative communities that emerged from the clone-based communities into a single community and allowed the community to evolve for a further 10^7 time steps. Detailed descriptions of models for evolutionary trait change, model analyses and the mathematical genesis of alternative states are presented in Appendix S1.

RESULTS

The individual clone-based and quantitative genetics approaches gave similar results but expose complementary information about the diversification process. Therefore, we present results from both, starting with the simple case of two arms-race traits and then extending to three. Using the clone-based approach in which there are positive resource costs ($\eta_R > 0$) and negative consumer costs ($\eta_C < 0$), the resources evolved to three groups of phenotypically similar clones which, for clarity, we will refer to as species (Fig. 1). Two resource species expressed a high level of one trait and zero for the other trait (black and red), whereas a third species expressed both traits at moderately high levels (blue). The two resulting consumer species had alternative high and low expressions of their two traits (Fig. 1).

To investigate the mathematical processes underlying the evolution of multiple species, we used a quantitative genetics approach (Abrams, 2001). For the same model and parameters as the clone-based example (Fig. 1) and two traits, the quantitative genetics approach identifies a set of four alternative states, with a fifth state (all resources and all consumers the same) being an unstable saddle point (Fig. 2). The resources showed a pattern of one trait high and the other zero, (+0) or (0+), or both traits intermediate (++) , with the possibility of all three resource species coexisting (Fig. S1). The all-or-nothing expression of some resource traits is a consequence of the positive costs ($\eta_R > 0$); when there are negative costs for the consumers ($\eta_C > 0$), some consumer traits show similar all-or-nothing expression. The existence of alternative states requires two or more traits, however, because when there is a single trait, we observed no species trait divergence (Fig. S2).

Diversification reflects the adaptive landscapes experienced by consumers and resources (Fig. 2). The adaptive landscape for one trophic level depends on the trait values and species abundances in the other trophic level, rather than an environmental gradient. The interaction between landscapes can lead

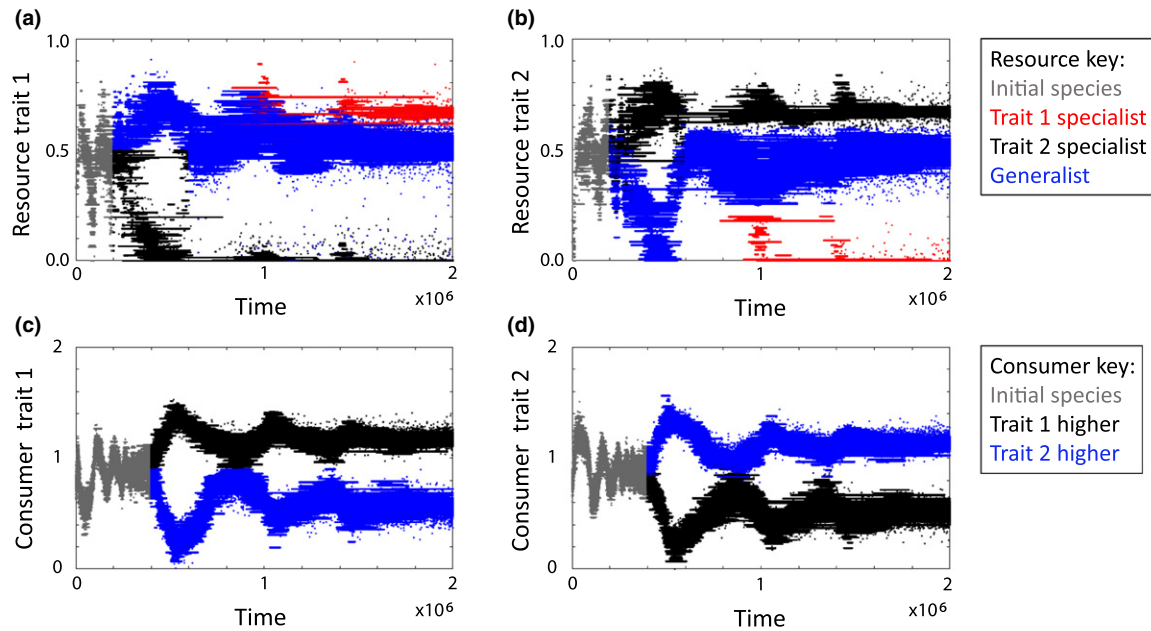


Figure 1 Clone-based model for two resource and consumer traits in a single community for 2×10^6 model iterations. Each point at a given time represents an individual clone that has the same phenotype (trait values), and a clone is assumed to terminate when its density drops below 0.0001. To identify the traits across the same groups of resource clones, after 0.2×10^6 iterations clones with final values of trait 1 (trait 2) < 0.2 are coloured black (red) after trait divergence, and the remaining clones are coloured blue; a similar approach is used for consumer traits using a trait value threshold of 0.9 after 0.4×10^6 iterations. Resource traits diverged before consumer traits, and therefore the change in colour occurs earlier resources (a and b) than consumers (c and d). Parameter values are $r = 0.05$, $a = 2$, $f = 0.1$, $\beta = 0.05$, $c = 1$, $m = 0.01$, $g = 0.01$, $\eta_R = 0.1$ and $\eta_C = -0.1$. The probability of mutation is $\mu = 0.01$, and the standard deviation of mutations is $\sigma = 0.05$; this mutation distance is large enough to allow mutant clones to jump far enough to potentially find alternative optima.

to many more outcomes when three traits exist (Table 1). There were seven possible types of resource species with qualitatively different traits: (+++), (++0), (+0+), (0++), (+00), (0+0) and (00+), with (000) never occurring. Consumers generally expressed intermediate trait values which depended on the resource community composition. There were many alternative communities; we found 42 different communities for a single parameter set (Table S1), with the largest communities containing six resource and six consumer species (Table 1).

Community assembly depends not only on coevolution but also on historical contingencies (Comes and Kadereit, 1998; Fukami *et al.*, 2007). To investigate this for our coevolving communities, we used the clone-based model to simulate two isolated communities and then combined them together to create a third (Fig. 3). The initial two communities differed, with both containing two resource and two consumer species. When they were combined, new resource and consumer species evolved that were not contained in the initial two communities. This type of pattern is expected due to the multiple alternative states of the model; the combining of the two initial communities represented a large perturbation, leading to convergence to a different community optimum.

While large perturbations such as combining communities are likely to cause changes in alternative states, smaller perturbations may also cause switching, and if the alternative states are not strongly stable, the evolutionary dynamics may generate a continuous drift among states. For example for weaker trade-offs than we considered in previous examples (e.g.

$\eta_R = 0.05$ and $\eta_C = -0.05$), consumers show evolutionary patterns that seem to migrate continuously but slowly among alternative states: at any point in time there is a consumer community with discrete trait clusters, yet the clusters change, branch and merge through time (Fig. 4). Even though alternative states are not stable enough to permanently capture the evolutionary dynamics, they nonetheless promote genetic and phenotypic diversity in the consumer guild.

In the simulations described earlier, we assumed there was a positive trade-off cost between resource traits ($\eta_R = 0.1$) and a negative trade-off cost between consumer traits ($\eta_C = -0.1$). When considering both positive and negative trade-off costs, positive trade-offs for resources ($\eta_R > 0$) are necessary for multiple communities to be stable (Table 1A). However, the situation for consumers is more complicated. For multiple stable states, trade-offs for consumers (η_C) can be either positive or negative (Table 1A). Furthermore, even when there are negative trade-off costs for resources, it is still possible for multiple consumer species to evolve, even though there is only one stable community state (Table 1B). Therefore, at least in this model, consumers do not rigidly specialise in traits. For strong trade-offs in consumer and resource traits, the system becomes evolutionarily unstable (Table 1), leading to complex trait dynamics with no stationary states (Fig. S3). Larger numbers of traits relative to the number of species can encourage non-stationary equilibria such as evolutionary limit cycles (Fig. S4). The mathematical genesis of the multiple states involves a pair of neutrally stable structures each

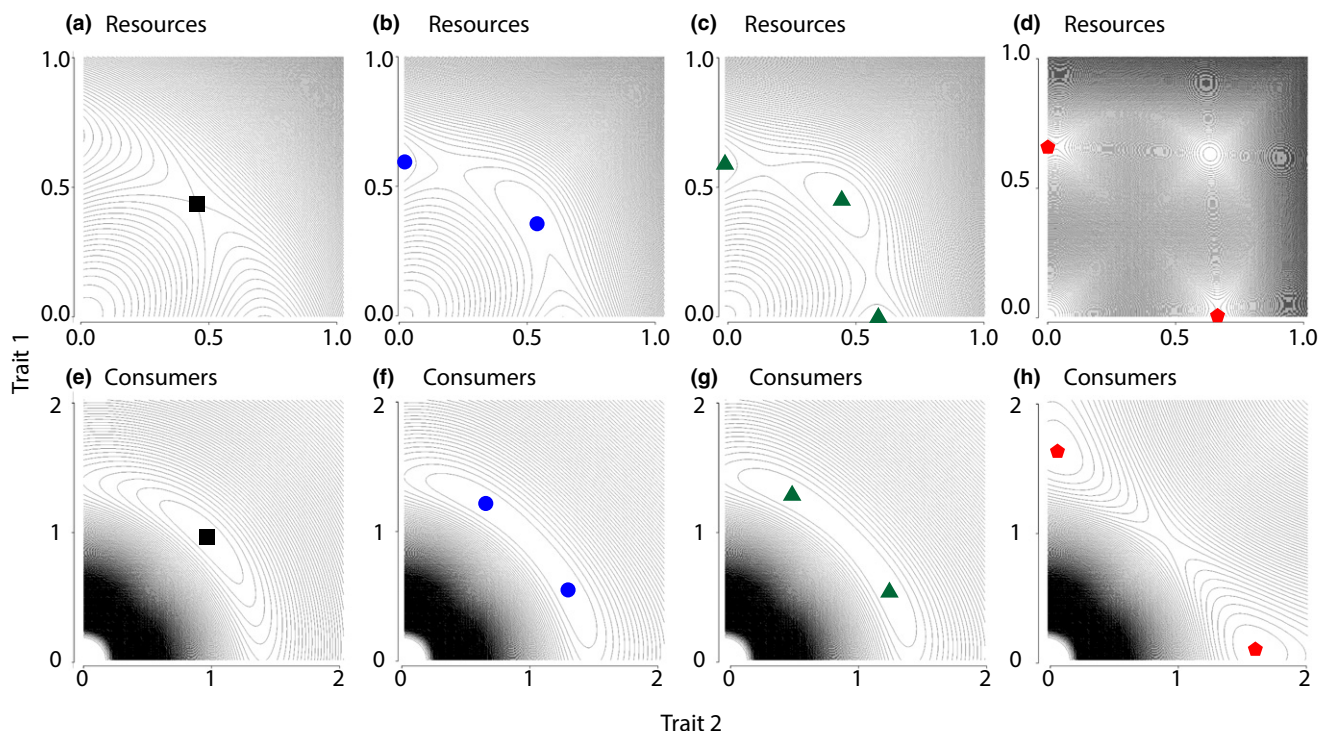


Figure 2 Fitness landscapes given by quantitative genetics dynamics for two resource (a, b, c and d) and consumer (e, f, g and h) traits in a single community. Each column of panels represents the resources (top row) and consumers (bottom row) from a particular community. Three locally stable equilibria are shown, two with two resource and two consumer species (b, d, f, h; blue circles and red pentagons), and one with three resource and two consumer species (c and g; green triangles). There is also an unstable equilibrium with one resource and consumer species (a and e; black squares), and an additional stable equilibrium (not shown here) is the reflection of the two-resource, two-consumer equilibrium shown with blue circles (bandf). Parameter values are the same as in Figure 1: $r = 0.05$, $a = 2$, $f = 0.1$, $\beta = 0.05$, $c = 1$, $m = 0.01$, $g = 0.01$, $\eta_R = 0.1$ and $\eta_C = -0.1$. Genetic variance was set to 0.05 for both resources and consumers.

allowing an infinite number of resource or consumer trait combinations when costs to both are additive ($\eta_R = \eta_C = 0$); stable states are generated as additivity is lost (Appendix S1, Figs S5 and S6).

DISCUSSION

Although there is a long-held view that coevolutionary arms races can generate species diversity (Ehrlich and Raven, 1964), theoretical models including only single traits show that diversification requires trait matching in which consumer species must phenotypically match an intermediate trait value of the resource to maximise consumption (Yoder and Nuismer, 2010). Similarly, in our models without trait matching, we found that coevolutionary arms races including a single consumer and a single resource trait do not promote diversification (Fig. S2). In contrast, our model can contain multiple generalised offensive and defensive traits which are under directional selection. When there are trade-offs among these traits, co-evolution between resources and consumers leads to diversification of resources and consumers ‘easily’, in the sense that numerous evolutionarily stable combinations of resource and consumer traits emerge under a wide range of model parameter values.

In their seminal paper, Ehrlich and Raven (1964) proposed a stepwise process where the presence of caterpillars may drive

the evolution of novel plant defences, which in turn drives caterpillar/butterfly diversification as a subset of these species adapt to the new defences. In this manner, the authors suggested that arms races can lead to paired consumer–resource interactions within ecological communities. Each speciation event in this speciation cascade can be considered as a form of trait-matching in which multiple antagonistic traits coupled with trade-offs leads to consumers that match the weaknesses in the resources’ defences (Yamamichi *et al.*, 2019). We have taken a community eco-evolutionary approach to this problem, asking what suites of resource and consumer species might evolve, and also whether the resulting communities are evolutionarily and ecologically stable. The possibilities for alternative stable configurations of resource–consumer communities are large: with three resource and consumer traits, we catalogued 42 different stable communities made up of resources and consumers with distinct but stable traits. This shows the possibility of extensive diversification driven by arms races. We further show that when trade-offs are strong, highly unstable population dynamics can emerge similar to findings of Doebeli and Ispolatov (2014), who observed chaotic dynamics in coevolutionary competition models when trait space has many traits.

Our results suggest that trade-offs associated with multiple traits can transcend trophic levels: trade-offs among resource traits can influence the diversity of the consumer guild and

Table 1 The case of three resource and consumer traits governing their strength of interactions can give rise to a large number of alternative stable communities

(A) Stable community states

		η_C						
		-0.3	-0.2	-0.1	0	0.1	0.2	0.3
η_R	-0.3	1	1	1	n	1	1	1
	-0.2	1	1	1	n	1	1	1
	-0.1	1	1	1	n	1	1	1
	0	1	n	n	n	n	n	u
	0.1	u	30	42	8	1	1	1
	0.2	u	31	33	9	1	2	8
	0.3	u	u	23	u	5	4	7

(B) Maximum number of resource species (trait states)

		η_C						
		-0.3	-0.2	-0.1	0	0.1	0.2	0.3
η_R	-0.3	1	1	1	n	1	1	1
	-0.2	1	1	1	n	1	1	1
	-0.1	1	1	1	n	1	1	1
	0	1	n	n	n	n	n	u
	0.1	u	6	6	3	1	1	1
	0.2	u	6	6	4	3	3	3
	0.3	u	u	6	u	3	3	4

(C) Maximum number of consumer species (trait states)

		η_C						
		-0.3	-0.2	-0.1	0	0.1	0.2	0.3
η_R	-0.3	1	1	1	n	3	3	3
	-0.2	1	1	1	n	3	3	3
	-0.1	1	1	1	n	3	3	3
	0	u	n	n	n	n	n	3
	0.1	u	6	6	7	1	3	3
	0.2	u	6	6	4	3	3	3
	0.3	u	6	6	u	3	3	3

Positive values of η_R and η_C represent positive trade-off costs for resources and consumers, respectively, whereas negative values represent negative trade-off costs. For different levels of η_R and η_C , we performed 200 simulation trials using the quantitative genetics model (e.g. Fig. 2) in which new species were added with random initial trait values (Appendix S1). We tallied the number of distinct stable communities at the end of the 200 simulations, and the numbers of resource and consumer species they contained, where species are defined by qualitatively distinct patterns in trait values. (A) The total number of alternative stable states at can be large when $\eta_R > 0$ and $\eta_C < 0$. Communities designated 'n' were neutral states with no local fitness peaks, and communities designated 'u' included at least one non-stationary (e.g. cyclic) evolutionary state. The maximum numbers of (B) resource and (C) consumer species found in stable community states implies that large communities can be generated when $\eta_R > 0$ and $\eta_C < 0$. Parameter values are as follows: $r = 0.05$, $a = 2$, $f = 0.1$, $\beta = 0.05$, $c = 1$, $m = 0.01$, $g = 0.01$

vice versa. Positive costs associated with resource traits ($\eta_R > 0$) were required for resource diversification (a stable community containing more than one resource species) (Table 1B). Consumer diversification, however, was contingent on trade-offs in both trophic levels. Specifically, negative costs among consumer traits ($\eta_C < 0$) only stimulated consumer diversification when resource trade-offs were positive ($\eta_R > 0$);

when $\eta_C < 0$ and $\eta_R < 0$, no consumer diversification occurred (Table 1C). Given that diversification of both trophic levels is driven by interactions between them, and that evolution of this interaction depends upon traits in both trophic levels, it is not surprising that trade-offs in one trophic level affect diversification in the other. A population's evolutionary constraints have long been known to influence the dynamics of other trophic levels (Pimentel, 1968), and recent experimental research suggests that manipulation of one trophic level can alter the fitness landscape and diversification of another (Betts *et al.*, 2018). Nonetheless, our model is a reminder that species diversity driven by coevolution requires understanding the factors influencing the evolution of coevolutionarily coupled species (Northfield and Ives, 2013).

Traits and trade-offs

The easy diversification in our models is promoted by positive resource trade-off costs associated with investing in multiple traits, as found for models describing diversification in single trophic levels (Doebeli and Ispolatov, 2010). Empirical evidence suggests that multiple trait types govern arms races that promote diversification (Agrawal *et al.*, 2009), but a remaining question is what types of cost correlations (i.e. positive or negative trade-off costs) exist for multiple traits associated with such arms races (Agrawal *et al.*, 2010). These correlations are difficult to describe in nature (Agrawal *et al.*, 2010), but our results suggest that quantifying these interactive costs may be critical to understanding the effects of arms races on diversification.

To translate our theoretical results into biological expectations, we must consider in more detail what traits and trade-offs occur. A key attribute of the model is that traits act on the strength of interactions between trophic levels: resource traits defend against consumers and consumer traits overcome these defences. This coupling between resource and consumer traits in the model implies that different traits must have qualitatively different effects on resource–consumer interactions. For example the ratio of tibia to femur, and the ratio of fast-twitch to slow-twitch muscles, are biologically distinct, yet they both likely affect resource–consumer interactions in a similar way: they affect running speed. Therefore, from the perspective of our model, they might be subsumed within a single trait.

The model is built around the assumption that each resource species and each consumer species has multiple traits. In real communities, resource species might show few defensive traits targeting a limited number of consumer species, and consumer species similarly might have traits that target a limited range of resources. Does the observation from real communities that resource and consumer species each shows a limited number of arms-race traits imply that the model is of limited application to real communities? No. To justify this answer, we must separate model assumptions from model outcomes. The model assumes every species that emerges during the diversification process has the potential to show multiple traits, but this potential is generally not realised. For example across the 42 alternative communities produced in the model (with $\eta_R = 0.1$, $\eta_C = -0.1$, Table S1), 54% of the resource

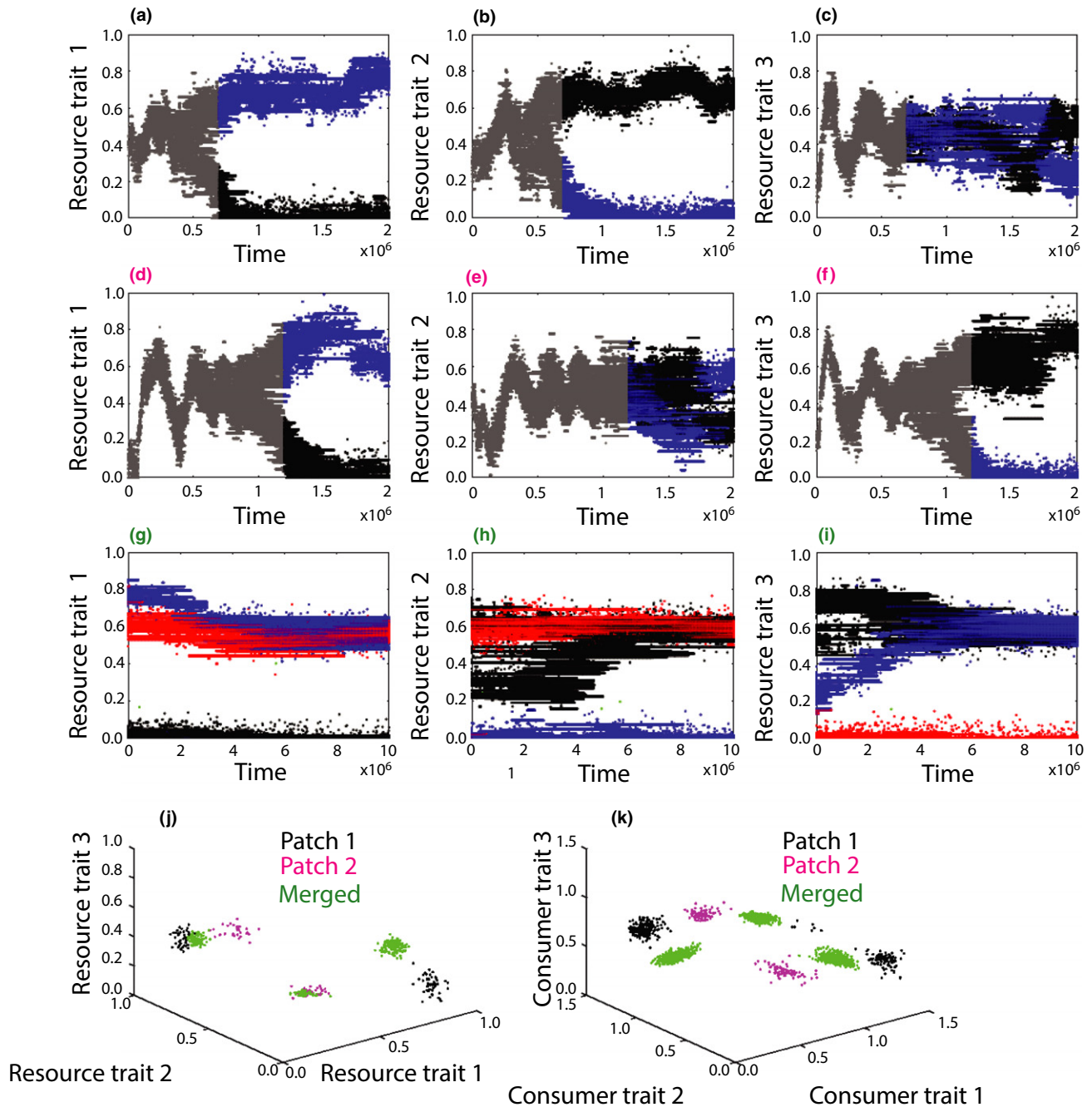


Figure 3 Clone-based model for three resources and three consumer traits. The first two rows of three panels on the top (a–f) give the dynamics of resource trait 1 (a) or 2 (b) in two separated communities for 2×10^6 model iterations, showing that they evolve towards different equilibria. To identify the traits across the same species, after 0.7×10^6 and 1.2×10^6 iterations for communities 1 and 2, clones with final values of traits less than 0.2 are coloured black or blue. The third row of three panels (g–i) shows the evolution of the joint community generated by adding together the final communities presented in panels a–f, starting at model iteration $2 \times 10^6 + 1$. Clones with final values of traits less than 0.2 are coloured black, blue, or red after trait divergence. The three-dimensional panels at the bottom of the figure (j and k) give the trait values at the final iteration for the two separate communities (black and magenta) and the combined community (green). The colours of the panel labels for the trajectories (a–i) correspond with the colours of that simulation's final trait values depicted in panels j and k. Parameter values are the same as Figures 1 and 2: $r = 0.05$, $a = 2$, $f = 0.1$, $\beta = 0.05$, $c = 1$, $m = 0.01$, $g = 0.01$, $\eta_R = 0.1$ and $\eta_C = -0.1$. The probability of mutation is $\mu = 0.01$, and the standard deviation of mutations is $\sigma = 0.05$.

species exhibited one dominant defensive trait, 46% exhibited two, none exhibited all three defensive traits. Therefore, the high specialisation that is an outcome of the model does not imply that each resource species itself is expected to show multiple defensive strategies.

These arguments imply that consumer–resource diversification as generated in our model would lead to communities in nature in which species may differ in whether or not they exhibit distinctly different traits or strategies for engaging in consumer–resource interactions. The suite of arms-race traits

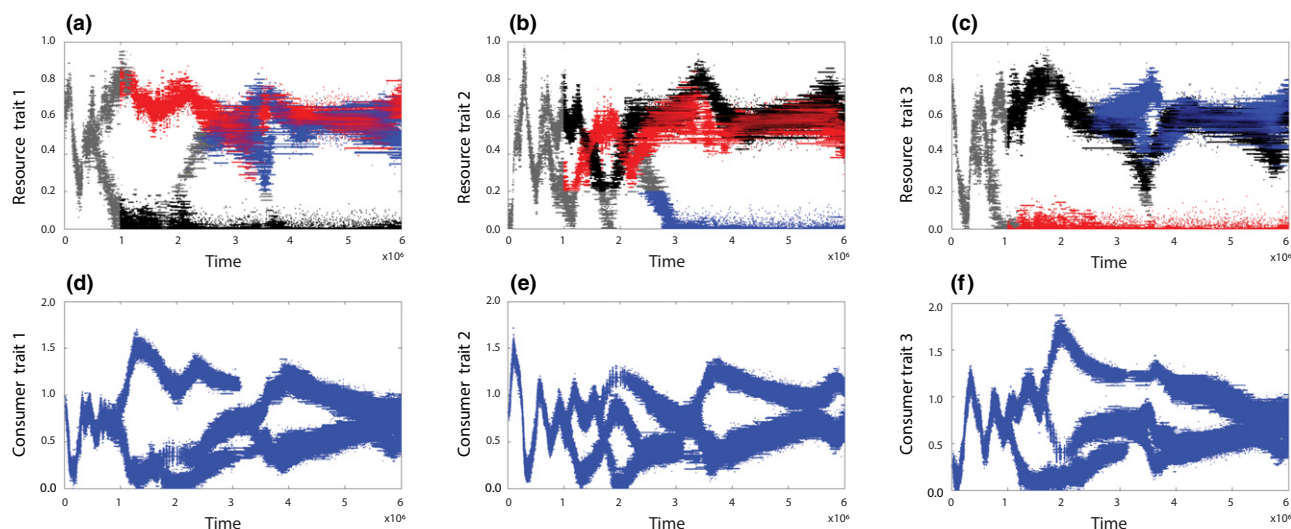


Figure 4 Clone-based model for three resource and consumer traits in a single community for 6×10^6 model iterations switching between alternative stable states. Values represent trait 1 (a,d), trait 2 (b,e) or trait 3 (c,f) for resources (a,b,c) or consumers (d,e,f). Each point at a given time represents an individual clone that has the same phenotype (trait values), and a clone is assumed to terminate when its density drops below 0.0001. To identify the traits across the same groups of resource clones, after 1×10^6 iterations clones with values of trait 1 less than 0.2 and values of traits 2 and 3 greater than 0.2 are colored black; blue and red dots correspond to clones similarly dominated by low values of traits 2 and 3, respectively. Parameter values are $r = 0.05$, $a = 2$, $f = 0.1$, $\beta = 0.05$, $c = 1$, $m = 0.01$, $g = 0.01$, $\eta_R = 0.05$ and $\eta_C = -0.05$. The probability of mutation is $\mu = 0.01$, and the standard deviation of mutations is $\sigma = 0.05$; this mutation distance is large enough to allow mutant clones to jump far enough to potentially find alternative optima

includes not just the traits exhibited by one species, but instead the collection of traits expressed by all species in the same guild. Evidence for arms-race coevolution driving consumer–resource diversification might therefore only be apparent after reconstructing their evolutionary history [e.g. by evaluating the fossil record (Herron and Doebeli, 2013b)], making it possible to determine the total collection of arms-race traits that species could potentially exhibit, even though no single species exhibits all traits.

Alternative states

Our model easily generates large numbers of alternative locally stable communities. This shows not only that diversification can be extensive, but also that even though there are a finite number of possible resulting communities, which community evolves is difficult to predict. These theoretical results align with the variability in bacterium–phage communities that diversified in laboratory colonies (Betts *et al.*, 2018), and variation in community composition across islands (Cowie, 1995; Losos *et al.*, 1998) or bodies of water (Taylor and McPhail, 2000; Langerhans *et al.*, 2007) with similar environmental conditions.

In ecological community assembly models, the potential for alternative states is common; for example in a simple model of competition, 75% of communities assembled from 12 species exhibited alternative states (Ives and Carpenter, 2007). Therefore, given that coevolution in the model can lead to resource and consumer species diversification, it might be expected that the diversification comes in the form of alternative states. Nonetheless, the large number of alternative states did surprise us. We expected either fewer communities with few species, or fewer communities with many species, but what we found was communities with both few and many

species as alternative states. Roughgarden (1979) posed the question of whether, for multispecies communities at a stable ecological equilibrium, coevolution will lead to instability and species loss. This question approaches diversification from the opposite direction from the one we took; we asked how coevolution leads to diversification from the bottom up. Roughgarden's answer was yes, although the analysis did not investigate the number of possible paths to species extinction. Other models also show that coevolution can lead to alternative stable states (Edwards *et al.*, 2018). For example in an evolutionary diversification model of competitors along a fluctuating gradient (temperature), Kremer and Klausmeier (2017) demonstrate alternative states at some amplitudes of the environmental fluctuations corresponding to transitions in species packing. They show that as the fluctuation amplitude increases relative to the fixed width of species' tolerance, more species can co-occur, and between amplitudes giving purely n and purely $(n + 1)$ -species communities, there are amplitudes that can give either n - or $(n + 1)$ -species communities as alternative states. We do not know, however, of previous models that give the rampant evolutionarily and ecologically alternative states of the model we investigated.

Many of the alternative states produced in our model are 'permutation' states: for example for the model with two possible arms-race traits, one alternative community had a resource that expressed trait 1 and not trait 2, and another alternative community contained the mirrored consumer species expressing trait 2 but not trait 1. From a mathematical perspective, the existence of both alternative states is expected, because the traits are symmetric. This does not mean, however, that the alternative communities are ecologically trivial. Even though two traits might have the same effects on fitness benefits and costs (as they do in the model), they might

nonetheless create physiological, morphological and ecological differences between resource species. Therefore, 'permutation' mathematical alternative states might be bona fide ecological alternative states.

How often would we expect alternative evolutionary states driven by resource–consumer interactions to be visible in nature? The obvious place to look is islands that represent repeated evolutionary experiments that might exhibit alternative outcomes. Detailed, long-term studies on islands have demonstrated alternative evolutionary states in lizard and snail communities (Cowie, 1995; Munoz *et al.*, 2014), but in these cases, the driving coevolutionary forces are likely competitive. In mainland communities, alternative states might be seen in the temporal replacement of alternative communities, either due to random evolutionary or ecological events through time (Fig. 4) or due to the removal of barriers between two distinct communities leading to the creation of a third (Fig. 3). Reconstructing temporal changes in coevolving communities, however, will likely be difficult and require extensive historical information such as a good fossil record. Finally, the coevolutionary forces driving alternative states might not lead to alternative states due to mixing in space of geographically separated populations or mixing through time of evolving communities; there could be a geographical mosaic of coevolution (Thompson, 2005) that in the absence of mixing would lead to alternative states, yet these alternative states never form completely. In this case, we suspect the same forces that drive isolated systems to alternative states will lead to the maintenance of genetic diversity for arms-race traits in both resource and consumer species. If there were potential for only a single coevolutionarily stable state, then spatial and/or temporal variability would likely lead to trait fixation. Instead, if there were the potential for alternative coevolutionarily stable states, spatial and temporal heterogeneity would maintain phenotypic diversity within resource and consumer populations even if true alternative communities could not evolve. Most of the alternative states we identified are only locally stable. Therefore, our model shows this type of maintenance of variation in consumers when 'mutant' offspring clones are sufficiently different from parent clones that there is repeated jumping among alternative states (Fig. 4).

Our findings help explain empirical studies showing that community assembly and diversification are contingent upon the historical community context (Schluter, 2009; Losos, 2010; Fukami, 2015). While our model is necessarily a simplified caricature of reality, it provides a mechanism for the idea that coevolutionary arms races are a widespread source of diversification. Furthermore, it provides a framework for understanding the interplay between arms races, diversification, determinism and historical contingency.

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AUTHORS' CONTRIBUTIONS

TDN and ARI conceived the study and all authors developed and analysed the models. TDN wrote the first draft of the article, with revisions by all authors.

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DATA AVAILABILITY STATEMENT

Matlab code for the clone-based model and R code to simulate our quantitative genetics model are available in Dryad (<https://doi.org/10.5061/dryad.s1rn8pk4f>).

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