ECOLOGY LETTERS cnrs WILEY

The enrichment paradox in adaptive radiations: Emergence of predators hinders diversification in resource rich environments

P. Catalina Chaparro-Pedraza[1,2,3] ⓘ | Gregory Roth[4] | Ole Seehausen[1,2]

[1]Aquatic Ecology and Evolution, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland

[2]Department of Fish Ecology and Evolution, Swiss Federal Institute of Aquatic Science and Technology (EAWAG), Kastanienbaum, Switzerland

[3]Department Systems Analysis, Integrated Assessment and Modelling, Swiss Federal Institute of Aquatic Science and Technology (EAWAG), Dübendorf, Switzerland

[4]Friedrich Miescher Institute for Biomedical Research, Basel, Switzerland

Correspondence
P. Catalina Chaparro-Pedraza, Überlandstrasse 133, 8600 Dübendorf, Zürich, Switzerland.
Email: Catalina.Chaparro@eawag.ch

Funding information
H2020 European Research Council, Grant/Award Number: 898687; Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: 31003A163338

Editor: Kristen Ruegg

Abstract

Adaptive radiations are known for rapid niche diversification in response to ecological opportunity. While most resources usually exist prior to adaptive radiation, novel niches associated with novel resources can be created as a clade diversifies. For example, in African lake cichlid radiations some species prey upon other species of the clade (intraclade consumers). Using a trait-based eco-evolutionary model, we investigate the evolution of intraclade consumers in adaptive radiations and the effect of this novel trophic interaction on the diversification process of the radiating clade. We find that the evolutionary emergence of intraclade consumers halts the diversification processes of other ecomorphs as a result of increased top-down control of density. Because high productivity enables earlier evolution of intraclade consumers, highly productive environments come to harbour less species-rich radiations than comparable radiations in less productive environments. Our results reveal how macroevolutionary and community patterns can emerge from ecological and microevolutionary processes.

KEYWORDS
adaptive radiation, community assembly, diversification, ecological opportunity, evolutionary branching, frequency-dependent selection, macroevolution, trophic interaction

INTRODUCTION

The extraordinary diversity of life on Earth has emerged through a variety of biological processes. One of these is adaptive radiation, which is thought to have given rise to much of this diversity (Simpson, 1953). Adaptive radiations are known for rapid diversification of a single ancestral species into an array of species exploiting a variety of ecological niches (Schluter, 2000). Most classical examples document occurrence of adaptive radiations on islands, in lakes, and on mountaintops, or after mass extinction events. This suggests that the availability of relatively unoccupied ecological niches, known as ecological opportunity, is required for an adaptive radiation to occur (Stroud & Losos, 2016).

Most niches, or rather the resources that form them, usually exist prior to the arrival of the ancestral species and are filled as the colonist population begins to diversify into a clade. Traditional theory predicts that over the course of a radiation, the rate of diversification slows down because vacant or underutilised ecological niches become increasingly scarce (Gavrilets & Vose, 2005; Harmon et al., 2003; McPeek, 2008; Pimm, 1979; Rosenzweig, 1978; Stroud & Losos, 2016). However, an alternative possibility is that novel niches emerge as a clade diversifies (Harmon, 2019; Martin & Richards, 2019). This scenario is likely to occur when new trophic levels emerge through the evolution of predator-prey interactions within the radiation (intraclade consumer). Indeed, species that feed upon other members of the

clade have been observed in various adaptive radiations: the African Lake cichlid radiations (Seehausen, 2006), the Bahamas *Cyprinodon* pupfish radiations (Martin & Wainwright, 2011), the Lake Baikal amphipods radiation (Naumenko, 2017). Trophic diversification by the evolution of a higher trophic level has been proposed as a source of additional ecological niches that allows diversification of the radiating clade beyond the niches built on resources that existed prior to the radiation (Losos & Mahler, 2010; Seehausen, 2015; Stroud & Losos, 2016). However, predation can alter prey diversification by reducing prey population size and thus the strength of resource competition (Meyer & Kassen, 2007). Hence, whether the evolution of a new trophic level that feeds on other members of the radiation promotes or reduces diversification and ensuing diversity in an adaptive radiation is not clear. The theory that links ecological and evolutionary processes on the micro-scale with macro-evolutionary patterns is needed to tackle this question (Harmon et al., 2019).

While a large body of theory has investigated how a clade diversifies and fills up niches based on resources that existed prior to the emergence of the radiation (Dieckmann & Doebeli, 1999; Doebeli, 1996, 2011; Gavrilets & Vose, 2005; Ito & Dieckmann, 2007; Kondrashov & Kondrashov, 1999), there have been few attempts to understand how novel niches emerge over the course of a radiation and how such emergent niches are filled up by the radiating clade (Brännström et al., 2011; Ingram et al., 2009; Loeuille & Loreau, 2005). The few existing examples assume a single food resource, despite this being exceedingly rare in adaptive radiations that typically involve diversification to exploit a variety of different dietary resources (Losos & Gavrilets, 2009; Martin & Richards, 2019).

The aim of this study was to gain insight into how intraclade consumers evolve as a clade diversifies to exploit a wide diversity of resources, and how the addition of this new trophic level in turn affects the diversification process of the radiating clade. Specifically, we examine the effects of diversity of preexisting resources and of productivity on the eco-evolutionary dynamics of adaptive radiations using a model that combines a Lotka-Volterra model for the ecological dynamics and the adaptive dynamics framework for the evolutionary dynamics. In the model, an ecological trait that determines resource use can evolve in response to natural selection. The fitness landscape is dynamical: individual fitness increases with food availability and decreases with vulnerability to intraclade consumers, and these quantities are altered by the density of individuals of the radiating clade and their resource use. Our model thus incorporates the feedback between ecology and evolution that is required to unravel how the diversification process of a radiating clade gives rise to novel ecological opportunity, and how the evolution of these new ecological interactions in turn affects the diversification process of the radiating clade.

MODEL DESCRIPTION AND ANALYSIS

We formulate an eco-evolutionary model of a radiating clade, and use a combination of analytical and numerical techniques to examine in this model the ecological conditions promoting the evolutionary emergence of an intraclade consumer, and the effect of the novel ecological interaction on the further diversification process. Additionally, to evaluate the generality of our results in sexually reproducing populations, we investigate the evolution of assortative mating using an individual-based model.

Ecological dynamics

We consider n food resources to exist prior to the arrival of the radiating clade (preexisting resources, $i = 1, \ldots, n$) with density R_i, and m emerging ecomorphs ($j = 1, \ldots, m$) with density N_j. We associate a feeding niche trait η to each ecomorph in the radiating clade.

We assume that there exists an optimal trait value θ_i to consume each preexisting resource and an optimal trait value θ_c to feed upon other members of the radiating clade (e.g. morphology of specialised zooplanktivores, algivores, etc. vs. of specialised fish eaters in the cichlid radiations). We consider these optimal traits to be ordered along the feeding niche trait axis (i.e. $\theta_c < \theta_1 < \ldots < \theta_n$) and equally distant from one another by a distance D (deviations from this assumption are investigated in Supporting Information S4). The attack rate of an individual with feeding niche trait η on the ith preexisting resource, $a_i(\eta)$, equals the maximum attack rate A when its feeding niche trait η equals θ_i, and decreases in a Gaussian manner as η moves away from θ_i, that is $a_i(\eta) = A \exp\left[-(\eta - \theta_i)^2 / (2\tau^2)\right]$. In this expression, τ determines the width of the Gaussian function and hence, when it is small, an ecomorph must be highly specialised to successfully attack the resource i. The attack rate of an individual with feeding niche trait η on other individuals of the radiating clade, $a_c(\eta)$, is similarly defined: $a_c(\eta) = A \exp\left[-(\eta - \theta_c)^2 / (2\tau^2)\right]$. We refer to ecomorphs that feed upon other members of the clade as intraclade consumers, a broader term to comprise ecological interactions of predation and parasitism. Although the evolution of piscivory often requires the evolution of a larger body size than the prey, in cichlid radiations, many consumer species and their prey have similar body size, because they feed upon eggs or larvae of their prey (Seehausen, 1996, 2015). We do not consider therefore the evolution of body size in this model.

Assuming linear functional responses, the fitness of the jth ecomorph equals

$$W\left(\eta_j\right) = \varepsilon \left[\underbrace{\sum_{i=1}^{n} a_i\left(\eta_j\right) R_i}_{\text{Ingestion of preexisting food resources}} + \underbrace{\sum_{\substack{k=1 \\ k \neq j}}^{m} a_c\left(\eta_j\right) \lambda N_k}_{\text{Ingestion of other ecomorphs}} - \underbrace{\sum_{\substack{k=1 \\ k \neq j}}^{m} a_c\left(\eta_k\right) \lambda N_k - \delta}_{\text{Mortality due to ingestion by other ecomorphs}} \right], \quad (1)$$

where ε is the efficiency with which food is converted to biomass and δ is the intrinsic mortality rate. In addition, because all biomass in the radiating clade may not be available for intraclade consumers, we introduce the parameter λ that determines the fraction of biomass that can be consumed by intraclade consumers. For instance, in the cichlid radiations, some predators specialise on preying on the eggs or young of other species while the adults are out of reach. For simplicity, we exclude the possibility of cannibalism (deviations from this assumption are investigated in Supporting Information S7).

Then, the ecological dynamics of the system follow:

$$\frac{dN_j}{dt} = N_j W\left(\eta_j\right), \quad (2a)$$

$$\frac{dR_i}{dt} = \rho\left(R_{i\,max} - R_i\right) - \sum_{j=1}^{m} a_i\left(\eta_j\right) R_i N_j, \quad (2b)$$

where ρ and $R_{i\,max}$ are the renewal rate and the carrying capacity of the ith preexisting resource respectively.

The total productivity of the habitat is the sum of the carrying capacities of preexisting resources $P = \sum_i R_{i\,max}$. We assume $R_{i\,max}$ to be equal for all preexisting resources, hence $R_{i\,max} = P/n$. However, deviations from this assumption are investigated in Supporting Information S4.

Evolutionary dynamics

We consider the evolution of m ecomorphs with trait values $\eta = \left(\eta_1, \ldots, \eta_m\right)$ through gradual adaptation when natural selection is directional and diversification when it is disruptive. We use the adaptive dynamics framework (Dieckmann et al., 2004; Geritz et al., 1998), which assumes that evolution occurs via small, infrequent mutational steps, and thus that the system reaches the ecological equilibrium in between two mutations. Under this assumption, the rate of change in the feeding niche trait of the jth ecomorph population can be approximated by the canonical equation (Dieckmann & Law, 1996):

$$\frac{d\eta_j}{dt} = \frac{1}{2}\mu\sigma^2 N_j^*\left(\eta_j\right) \left.\frac{\partial W\left(\eta_j', \eta\right)}{\partial \eta_j'}\right|_{\eta_j' = \eta_j}. \quad (3)$$

In this expression, μ is the mutation rate per birth event, σ^2 is the variance of the mutational phenotypic effect, $N_j^*\left(\eta_j\right)$ is the density of the jth resident ecomorph at ecological equilibrium, and $\left.\frac{\partial W\left(\eta_j', \eta\right)}{\partial \eta_j'}\right|_{\eta_j' = \eta_j}$ is the selection gradient.

Diversification occurs through a process of evolutionary branching, whereby a population evolves to a point where it undergoes disruptive selection and splits up into two phenotypically diverging lineages (Dieckmann et al., 2004; Geritz & Kisdi, 2000) (see Supporting Information S2).

Model analysis

We investigate the conditions that enable initial diversification, by analytically studying the behavior of the system in the simplest case: when one population colonises an environment with two different food resources (Supporting Information S3). In addition, we use numerical simulations to study how habitat productivity and diversity of preexisting resources affect the evolution of intraclade consumers and their effect on the further diversification process. To do so, we simulate adaptive radiations when intraclade consumers cannot evolve (i.e. the consumer niche θ_c is too far away along the trait axis from any optimal trait θ_i for consuming preexisting resources) and when they can evolve (the consumer niche θ_c is close to the optimal trait value θ_1). Throughout the simulation, we follow the number of ecomorphs, their feeding niche trait and their densities as well as the densities of resources, which we use to calculate the fitness landscape experienced by a mutant. We use as a reference radiations in which intraclade consumers cannot

evolve and compare the temporal dynamics (Figures 1–3; Figures S2 and S3) and the resulting diversity (Figure 4; Figures S4 and S5) of these reference radiations to radiations in which intraclade consumers can evolve (a detailed description is in Supporting Information S1).

Additionally, we implement an individual-based model with sexual reproduction based on the ecological dynamics of the model described above. We assume the feeding niche trait and a mating trait to be quantitative traits. Mating probabilities depend on the mating trait as in Dieckmann and Doebeli (1999). The individual-based model incorporates demographic stochasticity, cannibalistic interactions and the evolution of reproductive isolation via assortative mating (a detailed description can be found in Supporting Information S1).

RESULTS

Conditions that enable diversification

A population experiences disruptive selection when intermediate phenotypes have a fitness disadvantage compared with more extreme phenotypes, in other words, when the mean phenotype resides at a local minimum of the fitness landscape. Disruptive selection has a diversifying effect when the local fitness minimum is an attractor of the evolutionary dynamics, namely, when the mean trait of the population moves towards this trait value (Rueffler et al., 2006).

Our analytical investigation of the fitness landscape of a population colonising an environment with two different food resources reveals the conditions for diversification:

- Condition 1: The condition such that the mean phenotype of the population at equilibrium corresponds to a local fitness minimum:

$$D > 2\tau. \tag{4}$$

Therefore, when the distance between the optimal trait values to feed on preexisting resources D is too small relative to the degree of diet generalisation, disruptive selection does not occur. In other words, the more generalist an ecomorph is, the greater must be the distance between the optimal trait values for feeding on preexisting resources for disruptive selection to occur.

- Condition 2: The condition such that this equilibrium, where the population experiences disruptive selection, is an attractor of the evolutionary dynamics:

$$D < 2\sqrt{2\tau^2 W_0\left(\frac{\varepsilon AP}{2\delta}\right)}, \tag{5}$$

where $W_0(\varepsilon AP/\delta)$ increases with increasing ε, A, and P, and decreases with increasing δ. This implies that there exists a maximum distance between the optima to feed on preexisting resources D that enables the trait of the population to be attracted to the point where selection becomes disruptive. This maximum distance increases with increasing productivity and decreasing mortality.

The derivation of Expressions (4) and (5) can be found in Supporting Information S3.

For the numerical simulations, we adopt a value of D that, given other parameter values (Table S1), enables the evolutionary equilibrium where the population experiences disruptive selection to be a global attractor at intermediate and high productivities (Figure S1).

Intraclade consumer evolution halts diversification in adaptive radiations

Numerical simulations show that in the absence of intraclade consumers, a clade diversifies to occupy all available niches (i.e. to use all preexisting resources) in the environment colonised by the ancestral population. Hereafter, we refer as intraclade consumer to any ecomorph with a trait that enables a higher attack rate on other members of the clade than on any of the preexisting resources. After colonisation of the environment, the ancestral population evolves towards the trait value in between the optimum to feed on resource 1 and the optimum to feed on resource 2 (in between θ_1 and θ_2 in Figure 1a, therefore condition 2 is met). At this point, the population experiences disruptive selection (therefore condition 1 is met) due to density-dependent resource depletion and undergoes a diversification event (time 500 in Figure 1a). After diversification, the traits of the two resulting populations diverge. One of the populations evolves towards the trait value that is optimal to feed on resource 1, whereas the other evolves towards the trait value in between the optima to feed on resources 2 and 3. The first population now experiences balancing selection. The second population, in contrast, experiences disruptive selection again, resulting in a new diversification event. This alternation between adaptation through directional selection and diversification through disruptive selection is repeated until all preexisting resources are fully utilised by the radiating clade.

When we allow the evolution of intraclade consumers (i.e. a consumer niche trait exists in the neighborhood of traits optimal for feeding upon preexisting resources), similar dynamics drive the radiation in the early phase. Although the fitness of a consumer feeding upon other members of the clade is positive since very early (Figure 1d), intraclade consumers do not evolve until much later. This is because in the early stages of the radiation there is a region of negative fitness between the optima to feed on resource 1 (θ_1) and to feed
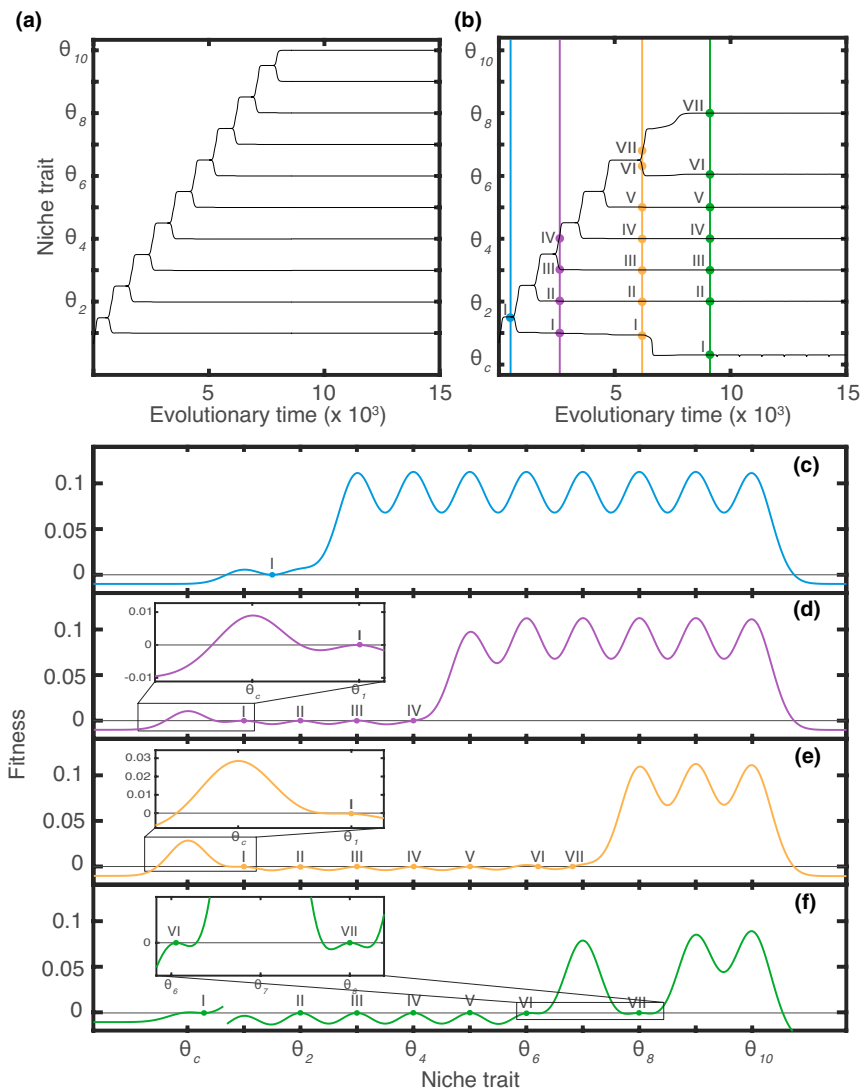
FIGURE 1 Evolutionary dynamics of a clade when (a) an intraclade consumer cannot evolve ($\theta_c = -10$), and (b) when it can evolve ($\theta_c = 0$). Black lines represent the niche trait value of the ecomorph populations of the radiating clade. Optimal trait values to feed on preexisting resources (θ_i) and on other members of the clade (θ_c) are indicated by the ticks on the vertical axis. (c–f) Fitness landscape at four different time points of the adaptive radiation when an intraclade consumer can evolve (indicated by the vertical color lines in panel (b)). Dots show the position of the existing ecomorph populations on the trait axis. In (d), ecomorph IV, which is in the expansion front of the radiation, has a trait equal to θ_4 and experiences a positive selection gradient. In (e), ecomorphs VI and VII experience negative and positive selection gradient, respectively. For all other ecomorphs using preexisting resources, the selection gradient is zero. Fitness is zero at the trait value that is occupied by an ecomorph population because the population is in its demographic equilibrium. The discontinuity in (f) is a consequence of the fact that the intraclade consumer does not experience predation mortality, while all other ecomorphs experience this mortality exerted by the consumer (see Equation 1). Productivity equals 10 g/L. Other parameter values as in Table S1. Analogous to panels (c–f), the fitness landscape of an adaptive radiation when an intraclade consumer cannot evolve can be found in Figure S2

on other members of the radiation (θ_c) (zoomed region in Figure 1d). As the radiation progresses, the trait and niche expansion increase the total biomass in the radiating clade, raising the food available for a consumer and thus the fitness associated with this phenotype (e.g. a consumer with a trait equal to θ_c has a higher fitness at time 6120—Figure 1e—than at time 2600—Figure 1d). The region of negative fitness between these optima eventually disappears, and the intraclade consumer emerges through character displacement from one of the earliest evolved ecomorphs (ecomorph that initially had

a trait equal to θ_1 evolves to have a trait closer to θ_c at time 6600 in Figure 1b).

The evolution of this intraclade consumer has an unexpected effect on the radiation: diversification is halted and several niches remain unoccupied (Figure 1b). After the evolution of the intraclade consumer, directional selection does no longer drive the trait of the ecomorph at the ecological expansion front of the radiation towards trait values in between the optima to feed on two different resources. Instead, this ecomorph evolves towards an optimum to feed on one resource (θ_8 in Figure 1b). Further
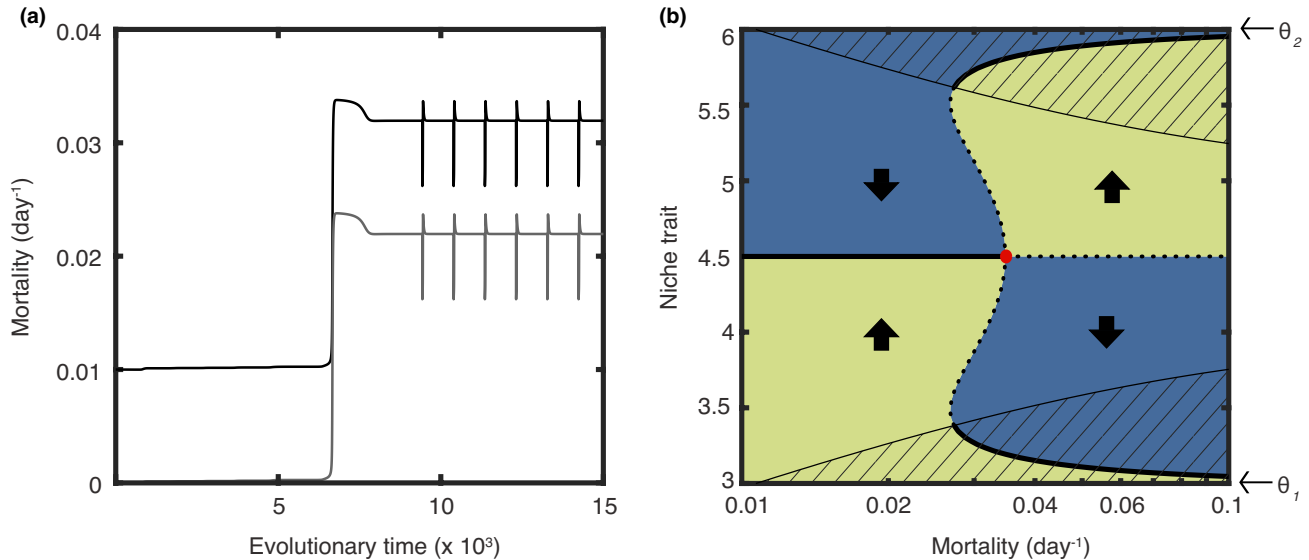
FIGURE 2 (a) Total mortality (black line) and mortality due to ingestion by other ecomorphs (grey line) experienced by ecomorphs specialized to feed on preexisting resources in Figure 1b. Mortality increases when an intraclade consumer evolves (at time 6120 in Figure 1b). Parameter values as in Figure 1b. (b) Fitness landscape of a population colonizing an environment with two different resources as a function of mortality. Diversification occurs only at low values of mortality because the mean trait of the population evolves towards the evolutionary equilibrium that corresponds to a fitness minimum, that is, where the mean trait equals 4.5 (arrows indicate the direction of selection). On the contrary, when mortality is high, the population evolves toward the vicinity of either of the optimal traits to feed on the preexisting resources, that is, in the neighborhood of either θ_1 or θ_2, depending on the initial trait value of the population. These trait values correspond to local fitness maxima, therefore once the population evolves to either one of them, diversification does not occur. Background color indicates the selection gradient (yellow when positive and blue when negative). Evolutionary equilibria are indicated by thick black lines (solid when they are attractors and dotted when they are repellors of the evolutionary dynamics). Evolutionary equilibria in the hatched regions are fitness maxima, whereas outside these regions are fitness minima. The carrying capacity of the resources is equivalent to the carrying capacity of each resource in Figure 1 to allow comparison ($R_{1\,max} = R_{2\,max} = 1$ g/L). $\theta_1 = 3$, $\theta_2 = 6$. Other parameter values as in Table S1

diversification does not occur because all ecomorphs feeding on preexisting resources experience balancing selection (their trait value resides at a local maximum of the fitness landscape, Figure 1f). Further analyses indicate that this halt in diversification may not depend on the fraction of biomass that can be consumed by intraclade consumers, λ (Figure S3).

Additionally, the evolution of the intraclade consumer from the ecomorph that used resource 1 in the early stages of the radiation through character displacement results in the niche to feed on resource 1 remaining unoccupied. As a consequence, four niches, that in the absence of intraclade consumers would have become occupied by the radiating clade, remain unoccupied (i.e. trait values θ_1, θ_7, θ_9 and θ_{10}). The final diversity of the clade is, therefore, lower when an intraclade consumer evolves than when it does not evolve (7 vs. 10 ecomorphs). Evolutionary cycles in the intraclade consumer population can occur (Supporting Information S5). A delayed evolution of the intraclade consumer, for instance, due to large separation in the trait space between the trait that is optimal for a consumer niche and the trait of the ancestral population, reduces the negative effect on the final diversity of the clade (Supporting Information S6, Figure S4).

Individual-based model simulations confirm that the evolution of intraclade consumers has a negative effect

on the final diversity of the clade. Additionally, they show that assortative mating does evolve and reduce gene flow in sexually reproducing populations, enabling speciation (see Supporting Information S7, Figure S5).

High mortality prevents diversification

The cause of the stalling of the diversification process and the resulting muted diversity is the increase in mortality imposed by the intraclade consumer (Figure 2a). Predation mortality reduces the density of ecomorphs feeding on preexisting resources, resulting in weak food resource competition and thus frequency-independent selection. Conversely, when mortality is low, ecomorph populations have a high density and experience strong competition for food resources, resulting in frequency-dependent selection.

We examine how mortality alters the fitness landscape in the simplest case, in which one population colonises an environment with two different food resources (Figure 2b). This analysis reveals that the trait value in between the optima for feeding on the resources (trait value of 4.5), which is a local fitness minimum, is an attractor of the evolutionary dynamics only when mortality is low and thus competition is strong. In contrast, when mortality is high, the population evolves away from this
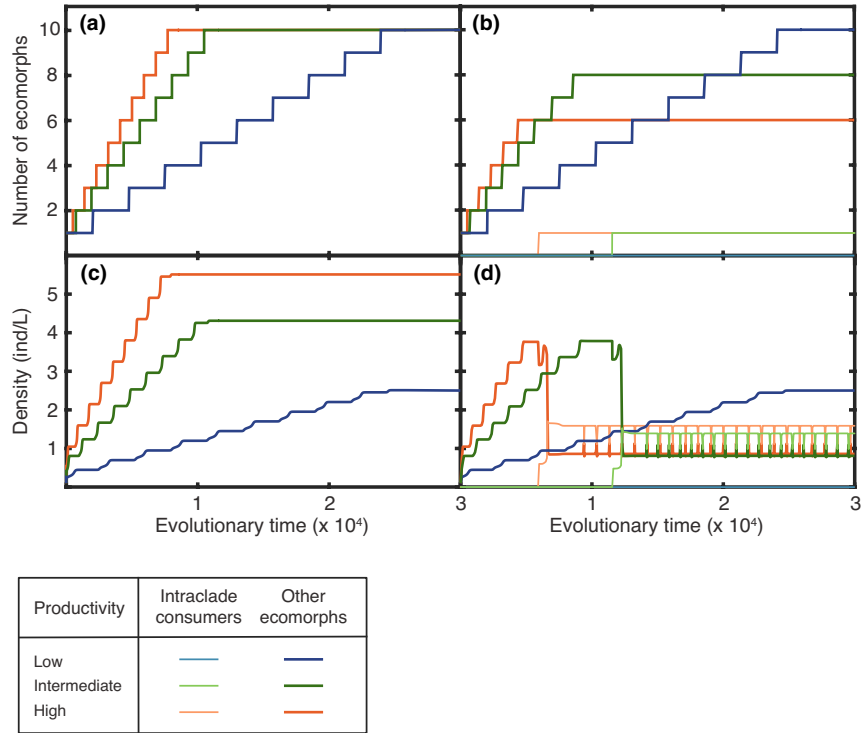
FIGURE 3 (a, b) Diversity and (c, d) individual density of ecomorphs for three different levels of productivity when (a), (c) a consumer cannot evolve ($\theta_c = -10$), and when (b), (d) it can evolve ($\theta_c = 0$). Low productivity prevents the evolution of intraclade consumers (light blue line). In contrast, intraclade consumers evolve at intermediate (light green line) and high productivities (light orange line). Productivity equals 5, 8 and 10 g/L when its level is low, intermediate, and high, respectively. In all simulations, the ancestral population encounters 10 preexisting resources ($n = 10$). Other parameter values as in Table S1

trait value and towards the proximity of one of the two optima (either trait value of 3 or 6 in Figure 2b). Because a population with a trait equal to either optimum does not experience disruptive selection, it does not diversify. In other words, there exists a threshold of maximum mortality that enables the population to evolve towards the trait value where selection is disruptive, and it equals:

$$\delta = \frac{4\tau^2 \varepsilon A P}{D^2} \exp\left(\frac{-D^2}{8\tau^2}\right). \tag{6}$$

This threshold (red dot in Figure 2b) results of solving δ from Equation (5) and depends on the degree of specialisation required to successfully attack a preexisting resource τ, the assimilation efficiency ε, the maximum attack rate A, the total productivity P, and the distance between the trait optima for feeding on the resources D. Interestingly, as productivity increases, the threshold increases.

High productivity reduces diversity in radiations with intraclade consumers

In the absence of intraclade consumers, the diversification rate increases with system-wide productivity. A clade diversifies and fills up niches faster when productivity is higher (Figure 3a). Likewise, individual density increases faster when productivity is higher (Figure 3c).

When we allow the evolution of intraclade consumers (i.e. a consumer niche trait exists in the neighborhood of optimal traits to feed upon preexisting resources), intraclade consumers only evolve at intermediate and high productivities. An intraclade consumer evolves only after the clade has already diversified into eight different ecomorphs feeding on preexisting resources when productivity is intermediate, but already after the clade has diversified into six different ecomorphs feeding on preexisting resources when productivity is high. This is because the prey density for an intraclade consumer (i.e. the total density of all populations of ecomorphs that feed upon preexisting resources) increases faster following each diversification event when productivity is high than when it is intermediate (orange vs. dark green line in Figure 3d). In a more productive system, each niche supports a larger population, and fewer occupied niches are sufficient to reach the total prey density where the emergence of an intraclade consumer is possible. When productivity is low, on the other hand, the radiation never reaches this critical level of prey density and intraclade consumers cannot evolve (dark blue line in Figure 3d).

Because fewer ecomorphs feeding on preexisting resources are required for the evolution of an intraclade consumer when productivity is high and because its emergence halts the diversification process, the final diversity of the clade is lower when productivity is higher. In fact, when productivity is high, the clade diversifies
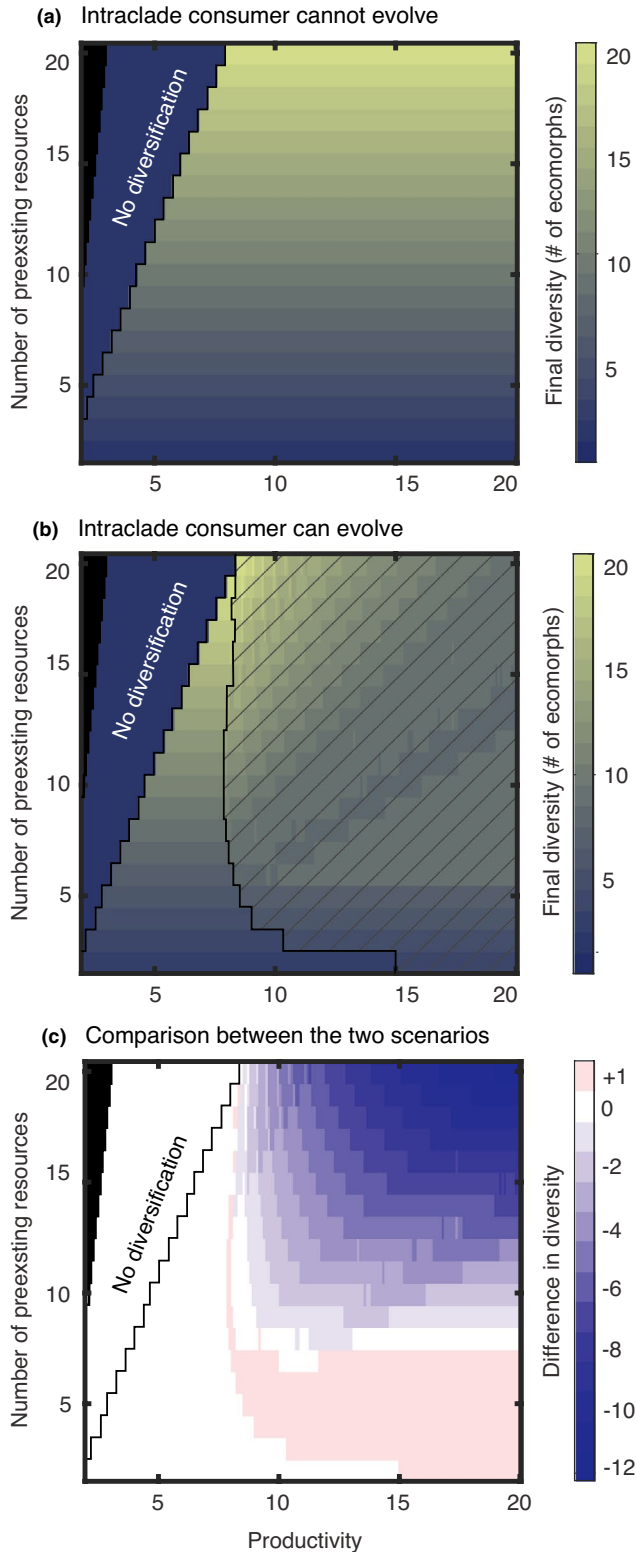
FIGURE 4 (a) Effects of productivity and diversity of preexisting resources on the final diversity of the clade when (a) a consumer cannot evolve ($\theta_c = -10$), and when (b) it can evolve ($\theta_c = 0$). (c) Difference in the final diversity of the clade between the two scenarios (i.e. number of ecomorphs when a consumer can evolve—number of ecomorphs when a consumer cannot evolve). In the top left black region, the ancestral population cannot persist. In the hatched region (in panel b), intraclade consumers evolve. Notice that the minimum number of preexisting resources in the vertical axis is 2. Parameter values as in Table S1

into seven different ecomorphs; whereas, when productivity is intermediate, it diversifies into nine different ecomorphs (Figure 3). Interestingly, although increased productivity increases the threshold of maximum mortality that still permits diversification (Equation 6), it also enables an early emergence of an intraclade consumer, which causes an early rise in mortality. The net effect of high productivity is the reduction in diversity as a consequence of an earlier increase in mortality.

Diversity hinders rather than begets diversity when intraclade consumers evolve

At very low productivity, a population colonising a new environment cannot persist, especially when the low productivity is partitioned into several resources (black regions in Figure 4). A small increase in productivity enables persistence of this population, however, diversification cannot occur (dark blue region in Figure 4a,b). Higher productivity is required to enable diversification. In the absence of intraclade consumers, the clade diversifies to use all the preexisting resources (Figure 4a).

When we allow the evolution of intraclade consumers (i.e. a consumer niche trait exists in the neighbourhood of traits optimal for feeding upon preexisting resources), they do emerge only at intermediate and high productivity levels (hatched region in Figure 4b). The evolution of intraclade consumers enhances richness in the radiating clade when the diversity of preexisting resources is low, but it reduces richness when the resource diversity is high (Figure 4c). This is because when the diversity of preexisting resources is low, productivity is partitioned among few resources, hence, each niche supports a large population and thus the increase in clade biomass following each diversification event occurs in large steps. Low diversity of preexisting resources thus implies that all or nearly all preexisting resources need to be utilised to reach the prey density at which the emergence of intraclade consumers occur. Conversely, consumers may emerge before all of the resources become utilised if there is a high diversity of preexisting resources. As a consequence of the early emergence of intraclade consumers and the associated halt of diversification, several niches can remain unoccupied. When the diversity of preexisting resources is high, the evolution of intraclade consumers therefore reduces the clade richness compared to the expected richness in the absence of consumers. This negative effect grows with increasing productivity (top right corner in Figure 4c). Qualitatively, this result is robust to varying distances between the trait optima for feeding on different resources (Figure S6), and an uneven partitioning of productivity among the preexisting resources (Figure S7).

In summary, novel niches for intraclade consumers that emerge as a clade diversifies enhance diversity in adaptive radiations only when the diversity of preexisting

niches is limited. Paradoxically, in environments harbouring a wide diversity of preexisting resources, the evolution of intraclade consumers hinders rather than begets diversity in adaptive radiations, and this effect is most apparent in highly productive environments.

DISCUSSION

The evolution of novel trophic interactions within adaptive radiations has been proposed as a mechanism whereby additional niche space may be generated by the adaptive radiation process, potentially promoting further diversification and larger diversity (Harmon et al., 2019). In line with this hypothesis, our results suggest that diversification eventually enables the transition towards a higher trophic level and associated trophic interactions from within the radiation. However, we find that the evolution of this novel trophic level, once emerged, stymies further diversification. As a result, the clade may not expand across the entire niche spectrum that it could potentially use, and its ensuing diversity may fall behind expectations in the absence of the novel trophic interaction. We furthermore show that this impact on the resulting diversity is more negative with increasing productivity and diversity of preexisting resources. This is because increased mortality imposed by consumers halts the diversification process, and consumers can evolve earlier in the radiation when productivity is higher.

This negative impact of consumers on the diversity of a radiating clade is not specific to consumers evolving within the radiation. Previous theoretical (Abrams et al., 2008) and empirical studies investigating the impact of consumers when they do not evolve within the radiation have also demonstrated this negative effect. The addition of consumers as an experimental treatment in an adaptive radiation occasionally enhanced diversification but only when the diversity of resources was limited. In situations with a wide diversity of resources, the presence of predators slowed diversification (Benmayor et al., 2008; Kassen, 2009). Observations in natural systems reveal a similar pattern; among the African Great Lakes, those with native top predators harbour less diverse cichlid radiations than otherwise comparable lakes that lack top predators (Jackson, 1961; Seehausen, 2007; Wagner et al., 2012).

The magnitude of the negative effect of consumers on the diversity of a radiating clade may be affected by diverse factors. A delayed emergence of a consumer due to large separation in the trait space between the trait of the ancestral population and the optimum trait to feed on other members of the radiation can reduce this magnitude (Supporting Information S6). Likewise, high variation in the productivity of preexisting resources, and high variation in the distance in the trait space between optima to feed on different resources can reduce the effect (Supporting Information S4). Additionally,

the degree of specialisation of the consumers may have an effect. In our model, we consider the evolution of a consumer that can prey upon all other members of the radiation. However, consumers may specialise on feeding upon subsets of ecomorphs. Such specialisation may lead to further diversification of the intraclade consumer in a similar manner that specialisation on preexisting resources leads to diversification among non-predator ecomorphs. Although one could expect that this mechanism increases diversity, previous theoretical studies on co-radiating prey and predator lineages showed that the conditions enhancing diversity are very limited (Pontarp & Petchey, 2018). Different from our study, they considered independent prey and predator lineages. Hence, further research is needed to understand the effect of specialised predators evolving within the radiation on the further diversification process.

The evolutionary history of the radiating lineage may also affect the magnitude of the effect that an intraclade consumer has on the final diversity. It is reasonable to speculate that new predator species emerging within a clade of older predators may be more efficient than novel predators arising in lineages that are ancestrally non-predators. As a consequence, the first would have a stronger negative effect on further diversification within the own lineage. Consistent with this prediction, radiations of Nile perch, a lineage of specialised piscivorous predators, have occurred in several of the African Great lakes but in no case exceeded four species (Brodersen et al., 2018). This contrasts with the cichlid radiations in the same lakes (from non-predatory ancestors), which have resulted in hundreds of species (Brodersen et al., 2018).

Our model, like most diversification models of adaptive radiations, relies on resource competition among similar phenotypes as mechanism for diversification. However, diversification can also occur when prey populations adapt in different ways to avoid consumption by a common predator (Brown & Vincent, 1992; Landi et al., 2013; Ripa et al., 2009). Thus, one could expect increased diversity when both mechanisms operate. However, using a model in which the predators do not evolve within the radiation, Pontarp and Petchey showed that the combination of both mechanisms often results in less diverse radiations than comparable radiations that lack top predators (Pontarp & Petchey, 2018). The predictions of this model and ours are supported by experimental laboratory studies and empirical data from nature that suggest that competition is the strongest driver of diversification at least in some adaptive radiations (Losos & Mahler, 2010).

A recurrent pattern in diversification models based on adaptive dynamics is niche subdivision and weakened disruptive selection after each diversification event, which results in decelerating diversification rate as the radiation progresses (Dieckmann & Doebeli, 1999; Doebeli et al., 2005; Polechová & Barton, 2005). This pattern contrasts

with empirical observations of accelerating or continuous speciation rates during some rapid radiations (Martin & Richards, 2019). In contrast to previous theoretical studies, we do not model competition for a continuous pre-existing resource but for a variety of discrete resources, similar to observations of adaptive radiations in which intraclade consumers have evolved (Losos & Gavrilets, 2009; Martin & Richards, 2019). As a consequence of this difference, we do not see a decelerating rate of diversification as the radiation progresses and fills up ecological niches, but a continuous diversification rate as hypothesised in African cichlid radiations (Harmon et al., 2019). An extension of our model implementing a diversity of discrete and continuous resource axes in many dimensions may result in varying diversification rates in different lineages of the clade, which might contribute to further reconcile theory and empirical observations.

We investigate the environmental conditions that enable diversification and the emergence of intraclade consumers through evolution on a single trait axis that determines the diet niche. Following adaptive dynamics (Dieckmann & Law, 1996), phenotypic changes are driven by gradual evolution in the direction of the fitness gradient. Therefore, deep fitness valleys in the one-dimensional trait space cannot be crossed. However, in the real world the trait space is multi-dimensional. While the existence of multiple traits may hinder diversification due to tradeoffs among traits that stimies niche specialisation, it may also facilitate diversification because niches separated by fitness valleys along one trait dimension may be connected through ridges on other trait axes (Seehausen, 2015). Hence, the existence of multiple trait axes may hinder or facilitate diversification of both ecomorphs using preexisting resources and intraclade consumers. Another possibility that may enable the crossing of fitness valleys is non-gradual evolution (Kagawa & Takimoto, 2018). For instance, introgressed variation was essential for the evolution of intraclade consumers in the Bahamas *Cyprinodon* pupfish radiation (Richards & Martin, 2017) and in the haplochromine cichlid radiations in African Great Lakes (McGee, 2020). Future research is needed to understand whether non-gradual evolution in a high dimensional phenotype space facilitates or hinders diversification in adaptive radiations when intraclade consumers can evolve.

Does diversity beget diversity? Evolutionary biologists have been asking this question for a long time (Emerson & Kolm, 2005; Martin & Richards, 2019; Palmer & Maurer, 1997; Whittaker, 1972). Our findings shed new light on this debate when the mechanism involves the evolution of predators and suggest that the answer may be system-specific. We find support for the idea that additional niche space, resulting in a novel trophic level, may be generated as the radiation progresses. However, this expansion of the niche space involving the evolution of intraclade consumers may enhance diversity in adaptive radiations only when ecological opportunity

at the onset was modest. Counterintuitively, it hinders diversity when ecological opportunity is extensive. In the latter case, a portion of the niche space remains unoccupied, perhaps creating opportunity for other clades that colonise to occupy those niches and coexist in the same environment. The niche space expansion through the emergence of intraclade consumers in a radiation may therefore be one of the factors that determine the phylogenetic structure of local communities. Future research is required to understand how multiple clades diversifying interact, especially when novel trophic interactions emerge as radiations progress.

Ecological interactions have long been thought to be critical in microevolution and macroevolution (Harmon et al., 2019). In turn, evolutionary processes in general and adaptive radiation in particular can have major ecological effects (Losos & Mahler, 2010). By incorporating the feedback between ecology and evolution, we provide a quantitative link between the concept of ecological opportunity, eco-evolutionary processes, and adaptive radiations. Our results recover the strong influence that ecological interactions and microevolutionary processes have on each other, and reveal a mechanistic link to macroevolutionary patterns that can result from the interactions of these processes. This highlights the need to synthesise ecological and evolutionary approaches in the study of community assembly and evolutionary diversification.

AUTHOR CONTRIBUTIONS
P. Catalina Chaparro-Pedraza and Ole Seehausen conceived the idea. P. Catalina Chaparro-Pedraza and Gregory Roth analyzed the model. P. Catalina Chaparro-Pedraza led the writing of the manuscript, and Ole Seehausen and Gregory Roth critically revised and contributed to later versions. All authors gave final approval of the manuscript to be published.

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13955.

DATA AVAILABILITY STATEMENT
No new data were collected and used for this study. Computer code associated to this article is available in https://doi.org/10.5281/zenodo.5597900.

ORCID
P. Catalina Chaparro-Pedraza https://orcid.org/0000-0001-9801-3878

REFERENCES

Abrams, P.A., Rueffler, C. & Kim, G. (2008) Determinants of the strength of disruptive and/or divergent selection arising from resource competition. *Evolution*, 62, 1571–1586.

Benmayor, R., Buckling, A., Bonsall, M.B., Brockhurst, M.A. & Hodgson, D.J. (2008) The interactive effects of parasites, disturbance, and productivity on experimental adaptive radiations. *Evolution*, 62, 467–477.

Brännström, Å., Loeuille, N., Loreau, M. & Dieckmann, U. (2011) Emergence and maintenance of biodiversity in an evolutionary food-web model. *Theoretical Ecology*, 4, 467–478.

Brodersen, J., Post, D.M. & Seehausen, O. (2018) Upward adaptive radiation cascades: predator diversification induced by prey diversification. *Trends in Ecology & Evolution*, 33, 59–70.

Brown, J.S. & Vincent, T.L. (1992) Organization of predator-prey communities as an evolutionary game. *Evolution*, 46, 1269.

Dieckmann, U. & Doebeli, M. (1999) On the origin of species by sympatric speciation. *Nature*, 400, 354–357.

Dieckmann, U., Doebeli, M., Metz, J.A.J. & Tautz, D. (2004) *Adaptive speciation. Adaptive speciation. (Cambridge studies in adaptive dynamics)*. Cambridge University Press. https://doi.org/10.1017/CBO9781139342179

Dieckmann, U. & Law, R. (1996) The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology*, 34, 579–612.

Doebeli, M. (1996) A quantitative genetic competition models for sympatric speciation. *Journal of Evolutionary Biology*, 9, 893–909.

Doebeli, M. (2011) *Adaptive diversification*. Princeton Monographs. https://doi.org/10.23943/princeton/9780691128931.001.0001

Doebeli, M., Dieckmann, U., Metz, J.A.J. & Tautz, D. (2005) What we have also learned: adaptive speciation is theoretically plausible. *Evolution*, 59, 691.

Emerson, B.C. & Kolm, N. (2005) Species diversity can drive speciation. *Nature*, 434, 1015–1017.

Gavrilets, S. & Vose, A. (2005) Dynamic patterns of adaptive radiation. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 18040–18045.

Geritz, S.A.H. & Kisdi, E. (2000) Adaptive dynamics in diploid, sexual populations and the evolution of reproductive isolation. *Proceedings of the Royal Society B-Biological Sciences*, 267, 1671–1678.

Geritz, S.A.H., Kisdi, E., Meszena, G. & Metz, J.A.J. (1998) Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12, 35–57.

Harmon, L.J. et al. (2019) Detecting the macroevolutionary signal of species interactions. *Journal of Evolutionary Biology*, 32, 769–782.

Harmon, L.J., Schulte, J.A., Larson, A. & Losos, J.B. (2003) Tempo and mode of evolutionary radiation in iguanian lizards. *Science*, 301, 961–964.

Ingram, T., Harmon, L.J. & Shurin, J.B. (2009) Niche evolution, trophic structure, and species turnover in model food webs. *The American Naturalist*, 174, 56–67.

Ito, H.C. & Dieckmann, U. (2007) A new mechanism for recurrent adaptive radiations. *The American Naturalist*, 170, E96–E111.

Jackson, P.B.N. (1961) The impact of predation, especially by the tiger-fish (*Hydrocyon vittatus* cast.) on African freshwater fishes. *Proceedings Zoological Society of London*, 136, 603–622.

Kagawa, K. & Takimoto, G. (2018) Hybridization can promote adaptive radiation by means of transgressive segregation. *Ecology Letters*, 21, 264–274.

Kassen, R. (2009) Toward a general theory of adaptive radiation. *Annals of the New York Academy of Sciences*, 1168, 3–22.

Kondrashov, A.S. & Kondrashov, F.A. (1999) Interactions among quantitative traits in the course of sympatric speciation. *Nature*, 400, 351–354.

Landi, P., Dercole, F. & Rinaldi, S. (2013) Branching scenarios in eco-evolutionary prey-predator models. *SIAM Journal on Applied Mathematics*, 73, 1634–1658.

Loeuille, N. & Loreau, M. (2005) Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 5761–5766.

Losos, J.B. & Gavrilets, S. (2009) Adaptive radiation: contrasting theory with data. *Science*, 323, 732–738.

Losos, J.B. & Mahler, D.L. (2010) Adaptive radiation: the interaction of ecological opportunity, adaptation, and speciation. In: Bell, M.A., Futuyma, D.J., Eanes, W.F. & Levinton, J.S. (Eds.) *Evolution since Darwin: the first 150 years.* Oxford: Oxford University Press, pp. 381–420.

Martin, C.H. & Richards, E.J. (2019) The paradox behind the pattern of rapid adaptive radiation: how can the speciation process sustain itself through an early Burst? *Annual Review of Ecology Evolution and Systematics*, 50, 569–593.

Martin, C.H. & Wainwright, P.C. (2011) Trophic novelty is linked to exceptional rates of morphological diversification in two adaptive radiations of cyprinodon pupfish. *Evolution*, 65, 2197–2212.

McGee, M.D., Borstein, S.R., Meier, J.I., Marques, D.A., Mwaiko, S., Taabu, A. et al. (2020) The ecological and genomic basis of explosive adaptive radiation. *Nature*, 586, 75–79.

McPeek, M.A. (2008) The ecological dynamics of clade diversification and community assembly. *The American Naturalist*, 172, E270–E284.

Meyer, J.R. & Kassen, R. (2007) The effects of competition and predation on diversification in a model adaptive radiation. *Nature*, 446, 432–435.

Naumenko, S.A., Logacheva, M.D., Popova, N.V., Klepikova, A.V., Penin, A.A. & Bazykin, G.A. et al. (2017) Transcriptome-based phylogeny of endemic Lake Baikal amphipod species flock: fast speciation accompanied by frequent episodes of positive selection. *Molecular Ecology*, 26, 536–553.

Palmer, M.W. & Maurer, T.A. (1997) Does diversity beget diversity? A case study of crops and weeds. *Journal of Vegetation Science*, 8, 235–240.

Pimm, S.L. (1979) Sympatric speciation: a simulation model. *Biological Journal of the Linnean Society*, 11, 131–139.

Polechová, J. & Barton, N.H. (2005) Speciation through competition: a critical review. *Evolution*, 59, 1194–1210.

Pontarp, M. & Petchey, O.L. (2018) Ecological opportunity and predator-prey interactions: linking eco-evolutionary processes and diversification in adaptive radiations. *Proceedings of the Royal Society B-Biological Sciences*, 285.

Richards, E.J. & Martin, C.H. (2017) Adaptive introgression from distant Caribbean islands contributed to the diversification of a microendemic adaptive radiation of trophic specialist pupfishes. *PLoS Genetics*, 13.

Ripa, J., Storlind, L., Lundberg, P. & Brown, J.S. (2009) Niche co-evolution in consumer-resource communities. *Evolutionary Ecology Research*, 11, 305–323.

Rosenzweig, M.L. (1978) Competitive speciation. *Biological Journal of the Linnean Society*, 10, 275–289.

Rueffler, C., Van Dooren, T.J.M., Leimar, O. & Abrams, P.A. (2006) Disruptive selection and then what? *Trends in Ecology & Evolution*, 21, 238–245.

Schluter, D. (2000) *The ecology of adaptive radiation*. Oxford: OUP.

Seehausen, O. (1996) *Lake Victoria rock cichlids: taxonomy, ecology and distribution*. Leiden: Verduyn Cichlids.

Seehausen, O. (2006) African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society B-Biological Sciences*, 273, 1987–1998.

Seehausen, O. (2007) Evolution and ecological theory: chance, historical contingency and ecological determinism jointly determine the rate of adaptive radiation. *Heredity*, 99, 361–363.

Seehausen, O. (2015) Process and pattern in cichlid radiations - inferences for understanding unusually high rates of evolutionary diversification. *New Phytologist*, 207, 304–312.

Simpson, G. (1953) *The major features of evolution*. New York, NY: Columbia University Press.

Stroud, J.T. & Losos, J.B. (2016) Ecological opportunity and adaptive radiation. *Annual Review of Ecology Evolution and Systematics*, 47, 507–532.

Wagner, C.E., Harmon, L.J. & Seehausen, O. (2012) Ecological opportunity and sexual selection together predict adaptive radiation. *Nature*, 487, 366–369.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon*, 21(2-3), 213–251. https://doi.org/10.2307/1218190

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.