Evolutionary Ecology Research, 2016, **17**: 757–770

Replacement and displacement driven by innovations, competition, and extinctions

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ABSTRACT

Background: A key innovation may allow one group of species to radiate and replace another, but the role of competition and background extinctions for the replacement process is vigorously debated and unclear.

Questions: Is a minimum competitive advantage necessary to initiate replacement? Are background extinctions of the incumbent species necessary? What speciation and extinction dynamics characterize the replacement process and how do they differ from radiation into an empty niche space?

Model features: We used a classic eco-evolutionary model describing asexual species competing for resources distributed along a single niche axis. Successive evolutionary branching generated an adaptively radiating community. Evolutionary innovation was introduced as an increased carrying capacity. Externally driven extinctions were also added.

Mathematical methods: The model was studied using individual-based simulations. We monitored the radiation of the new group into the niche space of the original group and recorded the time to near-complete (90%) and complete (100%) replacement, along with rates of extinction and speciation of new and old groups.

Results and conclusions: We demonstrate that replacement may occur by the radiation of a competitively superior group. Increasing the competitive advantage shortened replacement times, but there was no particular threshold advantage. Origination rates in new groups were comparable to extinction rates of the original groups, keeping the total number of species approximately constant – tentatively a result of niche widths and overall available niche space in the underlying model being unaffected by these innovations. Extra background extinctions speeded up the process, consistent with observed patterns in the fossil record that replacement is sped up during mass extinctions, but an increased extinction rate also introduced uncertainty and a higher risk of global extinction of the superior group.

The replacement process was mainly driven by evolutionary competitive exclusion. The old, inferior type had an elevated rate of extinction matched by an increased speciation rate of the superior type. Incumbency also played a role, but we found little support for a strict incumbent replacement scenario, where replacement is driven entirely by background extinctions of the old group and opportunistic speciations of the new group.

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Compared with adaptive radiation into an empty niche space, replacement was slow and relict species from the original group could linger in marginal and previously unexploited niche space that provided a niche refuge and prevented complete replacement. Similar patterns are also found in the fossil record.

Keywords: adaptive radiation, competition, extinction, incumbent replacement, key innovation, macroevolution, relict species.

INTRODUCTION

Evolution sometimes takes major steps. Key innovations appear that change the rules, break constraints, and enable new types of species to diversify (Simpson, 1953; Rosenzweig and McCord, 1991). Heard and Hauser (1995) identify three types of key innovations of relevance for evolutionary diversification: (*i*) those that represent new adaptive zones, (*ii*) those that increase fitness, and (*iii*) those that increase the potential for specialization. Innovations of type *ii* imply a competitive advantage and can lead to a replacement of the ancestral type, a process that has been observed several times in the fossil record. An example is Stanley and Newman's (1980) description of the replacement of chthamaloid barnacles by the closely related balanoids. Balanoid barnacles have a tubiferous wall structure that allows for more rapid growth and leads to competitive exclusion of chthamaloids except in the uppermost intertidal and other marginal habitats (Stanley and Newman, 1980). Rosenzweig and McCord (1991) studied the replacement of straight-necked turtles (Amphichelydia) by turtles that could flex their necks and hide it under the shell. Amphichelydians were replaced several times in different biota by groups that could flex their heads either sideways or vertically, which probably gave an advantage in terms of a reduced predation risk (Rosenzweig and McCord, 1991).

The process of replacement is akin to that of an adaptive radiation (which may follow a type *i* innovation). A single ancestral species radiates into a suite of ecological niches. However, the niches are not empty; instead, they are occupied by fully adapted, close relatives of the new clade. Each niche requires its special adaptations, and it is unclear how a new type can outcompete an incumbent niche-occupant before acquiring those special adaptations. Rosenzweig and McCord (1991) argued that replacement processes are mainly driven by background extinction events. New types can only claim new niche space when it is empty, following random extinctions of the old type. Only then does the competitive advantage of the key innovation become operative, letting new types win the competition for the vacant spot. Rosenzweig and McCord found support for this *incumbent replacement* scenario in the fossil record of the replacement of amphichelydian turtles by cryptodiran turtles in western North America. The extinction rate of amphichelydians was comparable to that of cryptodirans, whereas the speciation rate of cryptodirans was higher than that of its predecessor. These observations are consistent with incumbent replacement, but not with a replacement process where the old type is directly driven to extinction by competition from the new type. It has also been noted that replacements often are associated with mass extinctions (Benton, 1987; Rosenzweig and McCord, 1991), which is in line with the incumbent replacement scenario. In the same vein, Gilinsky and Bambach (1987) note that extinction rates are relatively stable in the fossil record, compared with origination rates, and argue that incumbency can buffer old taxa against replacement.

Replacements as described above are probably common in the evolutionary history of life on Earth, but have received only modest theoretical attention. Mathematical models have been developed to study how variation in extinction and speciation rates across clades may explain patterns of turnover in the fossil record (e.g. Raup, 1981). Sepkoski (1996) modelled the replacement process with species-level Lotka-Volterra competition equations. Other theoretical studies (based on community assembly) have explored how interactive communities such as food webs may recover from mass extinctions (e.g. Solé *et al.*, 2002) and how the evolution of food web structure is affected by repeated random extinctions (e.g. Hironaga and Yamamura, 2010). However, the eco-evolutionary process in which one group of species equipped with a key innovation replaces an ancestral similar group lacking this adaptation has not been studied explicitly. Here we set out to make a first modelling attempt of this presumably important evolutionary process. First, what conditions are necessary and sufficient for a replacement process to get started? Is there a 'threshold advantage', below which the innovation is not a *key* innovation and never goes beyond the boundaries of a single species? Second, how important are background extinction events? Are they essential or do they merely accelerate the process? Third, we are interested in the species dynamics of the process. Is the replacement always gradual, such that the old species are replaced one by one, or can the process be more catastrophic?

THE MODEL

We used a well-studied, eco-evolutionary model of a competitive community with Lotka-Volterra style interactions (Roughgarden, 1972; Christiansen and Loeschke, 1980). In this model, a single ancestral species can diversify through repeated competitive speciations (Rosenzweig, 1978; Dieckmann and Doebeli, 1999) into a community of co-existing species. There is a single evolving trait, x, which maps onto a continuous, Gaussian, distribution of resources, such that an intermediate trait value, $x = 0$, corresponds to the maximal amount of resources. Competition between individuals depends on their distance from one another in trait space, with similar phenotypes competing the most.

For the purpose of our study, we modified the original model in two ways. First, we incorporated key innovations in the form of a fitness advantage (increased carrying capacity) for one randomly selected species, which then potentially could diversify into a whole new clade thus replacing the old one. Second, we incorporated externally driven, neutral extinctions.

Our model is driven by individual births and deaths. A time-step in the model is equal to the generation time of the evolving organism. Mutations, natural selection, and drift generate microevolution (gradual changes of extant species) but also macroevolution (speciations, extinctions, adaptive radiations, and replacement processes). We can thus use the model to interpret patterns across time-scales – how macroevolution can be driven by microevolution that ultimately is driven by ecological interactions.

Eco-evolutionary model

In each generation, each individual (asexually) produces a Poisson distributed number of offspring with a mean given by

$$G(x', \mathbf{x}) = 1 + r\left(1 - \frac{\Sigma_i \alpha(x', x_i)}{K(x')}\right), \qquad (1)$$

where x' is the trait value of the focal individual and $\mathbf{x}$ is a vector with elements x_i corresponding to the trait value of individual i in the population. The parameter r is the intrinsic growth rate, $\alpha(x', x_i)$ is the competition from individual i on the focal individual, and the sum is across all individuals in the community. $K(x')$ is the carrying capacity given by the resources available to the focal individual. The function $K(x)$ represents the resource distribution and is of Gaussian shape with a maximum K_0 at $x = 0$:

$$K(x) = K_0 \exp\left(-\frac{x^2}{2\sigma_K^2}\right). \tag{2}$$

Finally, the competition kernel $\alpha(x_1, x_2)$ expresses how much the presence of an individual with $x = x_2$ decreases the expected reproduction of an individual with $x = x_1$ according to

$$\alpha(x_1, x_2) = \exp\left(-\frac{(x_1 - x_2)^2}{2\sigma_\alpha^2}\right). \tag{3}$$

Competition is symmetric ($\alpha(x_1, x_2) = \alpha(x_2, x_1)$) and decays with distance in trait space. The niche width parameter σ_α sets the rate of decay, where a large σ_α corresponds to a large niche width and strong competition.

The offspring of all individuals constitute the next generation and the parent generation is discarded. Each offspring inherits its parent's x-value, but will with probability P_μ mutate to an x-value drawn from a normal distribution with a mean given by the parent's x and a standard deviation σ_μ.

Species definition, speciations, and extinctions

Simulation of this model will, as long as mutations are not too large or frequent (see Champagnat *et al.*, 2006), produce gradually evolving *clusters* in trait space (see also Leimar *et al.*, 2008). We identify such clusters as *species*, even though reproduction is entirely clonal. In our simulations, we defined a cluster as a set of individuals with common descent and a maximal distance of 0.1 to the nearest within-cluster neighbour in trait space. Cluster identity was for this purpose modelled as an inherited trait. At each sampling time (every 1000 generations), each cluster was checked for gaps in the distribution of phenotypes. If a gap larger than 0.1 was detected, the cluster was split into two new clusters and a speciation event was recorded. Each individual in the two new clusters was assigned the corresponding cluster identity, which was then inherited by its offspring. If a cluster of the previous sample had no members in the current one, we recorded that as an extinction event. Recorded extinction events are marked with black squares in Fig. 1. Note that some small ‘stubs’ are not marked, since they were never registered as species according to the definition above. A smaller maximal gap distance than 0.1 would repeatedly record such short-lived clusters as species, although they would rarely show up in the corresponding hypothetical fossil record. We therefore kept the higher value of 0.1, acknowledging that there is an element of arbitrariness here.

Speciation mechanism

New species came about through competitive speciation, or more precisely *evolutionary branching* at evolutionary branching points (Geritz *et al.*, 1998). An evolutionary branching point is an attractor of the gradual, directional evolution of a species, but is also a point in trait space where the species is subject to disruptive selection. A branching point in one dimension also assures that nearby morphs or clusters can co-exist on opposite sides of it. A single cluster (or species) will therefore evolve to a branching point and subsequently diversify into two separating clusters – a speciation event. In our model, the intermediate trait value $x = 0$ is an evolutionary branching point of a single evolving species as long as $\sigma_\alpha < \sigma_K$. A single ancestral species will thus split into two, but the two new species will once again end up at evolutionary branching points and split again. This process of repeated evolutionary branchings gradually built up competitive communities in our simulations. The total number of species levelled off as the species densities became small enough for demographic stochasticity to halt the speciation process (Johansson and Ripa, 2006; Claessen *et al.*, 2007; Pontarp *et al.*, 2012). New species were still produced, but were only ephemeral. The community thus reached a steady state of relatively constant species diversity (Pontarp *et al.*, 2012) (see also Fig. 1).

Extinction mechanisms

Extinctions occurred throughout the evolutionary process as soon as a cluster lost its last individual due to demographic stochasticity. This could be an entirely stochastic event, but could also be driven by competitive exclusion by one or more nearby species in trait space. Another reason may be a species being driven to the edge of the resource distribution, where the carrying capacity was too low for long-term persistence. In addition, we added an external extinction mechanism: with probability P_e per generation per cluster, a cluster would go extinct by simple elimination of all its individuals. This additional extinction mechanism allowed us to adjust the background extinction rate by altering the parameter P_e. The underlying biological mechanism may be extinctions driven by species-specific epidemics or sudden collapses of the corresponding part of the resource distribution.

Innovation

We introduced a key innovation in the simulations at generation 2×10^6, when the initial adaptive radiation was completed and the community had reached a steady state. This key innovation was modelled as a new type with a slightly higher value of K_0 (eq. 2), which made it slightly less sensitive to competition (eq. 1) and gave it an overall competitive advantage to the ancestral type. We define the *innovation size* I as the relative increase in K_0, such that $I = 0.1$ means a 10% increase in K_0. The new type was introduced by substituting a randomly chosen individual of the evolved community with 100 individuals of the new type, but with the same x-value as the chosen individual (the number 100 is quite arbitrary, but chosen high enough to prevent immediate extinction due to demographic stochasticity). The new type evolved just like the old type, except that all offspring inherited the elevated value of K_0.

Time to replacement

The new type introduced as a key innovation normally replaced much of the community, but one or two relict species at the margin of the resource distribution could linger for a very long time. We define the *time to replacement*, T_R, as the number of generations from introduction of the new innovation to the first sampled generation when 90% of the whole community consisted of the new type (see Fig. 1a). If replacement was still incomplete at the end of a simulation, we recorded the maximal possible time to replacement (see Simulations below). If the new type went extinct, the replacement was regarded as having failed and no time to replacement was recorded.

Extinction and speciation rates

We measured extinction and speciation rates in three different ways. (*i*) Background rates of the old, ancestral type were measured during the period 1.5×10^6 to 2×10^6 generations. In this time interval, the community has reached a steady state and the innovation has not yet appeared (see Fig. 1). Extinction and speciation rates of the (*ii*) old type and (*iii*) new type were measured from the appearance of the innovation until the community consisted of 90% of individuals of the new type, or until the new type went globally extinct, whichever came first. Each rate was estimated as the total number of events divided by the total number of 'cluster-samples', i.e. the sum of the number of clusters present in each sample, which was then divided by the number of generations between samples. In this way, we standardized the unit of each rate to events per cluster per generation.

Simulations

Simulations were run in C++ , but all analyses and plotting were performed in Matlab R2014b (The Mathworks, MA, USA). The entire community was sampled every 1000th generation for analysis and plotting. Simulations with $I = 0.03$ or 0.05 were run for 1.2×10^7 generations, allowing for a maximal replacement time of 10^7 generations. All other simulations were stopped after 7×10^6 generations, which constrained the maximal T_R to 5×10^6 generations. This last constraint had very little effect on the results, since the replacement process was usually complete much sooner (see below). Simulations with $P_e = 0$ and 2×10^{-6} were replicated 50 times and those with $P_e = 5 \times 10^{-6}$ were replicated 100 times. An extra set of simulations with $I = 0$, $P_e = 5 \times 10^{-6}$ were replicated 10^4 times (due to the low probability of a replacement).

RESULTS

Figure 1a shows a typical simulation with a key innovation ($I = 0.05$) introduced in generation 2 x 10^6 (black vertical line). The clusters we define as species are easily identified. As can be seen, the adaptive radiation of the ancestral type (grey) is fast compared with the replacement process following the key innovation. The old type functions as an evolutionary hurdle that delays the adaptive radiation of the new type (black).

The replacement is quite smooth. Roughly, one species at a time is replaced such that the total number of species is kept more or less constant. This pattern was consistent for all investigated parameter values.

The dashed vertical line in Fig. 1a indicates the generation where for the first time 90% or more of the individuals stem from the new type, which is the basis for our calculation of replacement time, T_R (Fig 1a). Note the long-term persistence of the old type species at the margins of trait space. These species have low densities but occupy unattractive regions of trait space, regions that were only partly occupied before the innovation event. This

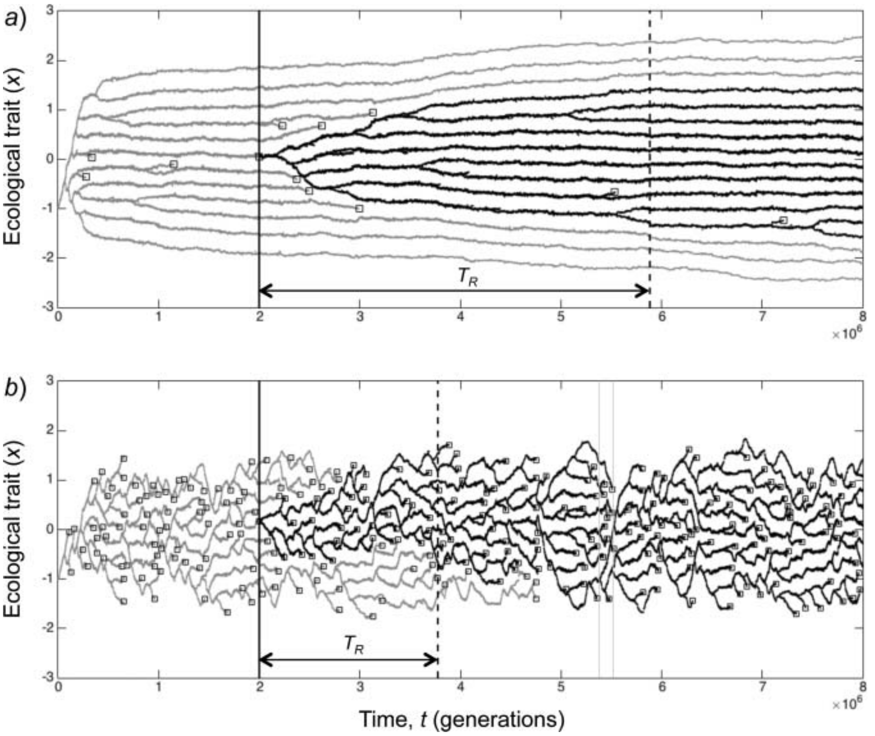

Fig. 1. Two sample simulations, one with no external extinctions (*a*: $P_e = 0$), and the other with a high background extinction rate (*b*: $P_e = 5 \times 10^{-6}$). Each dot represents at least 100 individuals with the same ecological trait (y-axis) at a given point in time (x-axis). Dots representing the ancestral type are coloured grey, and those of the new type, introduced at $t = 2 \times 10^6$, are coloured black. The squares indicate extinctions as identified by the clustering algorithm described in the text. The black, vertical, solid line indicates the time of introduction and the black, vertical, dashed line the time at which 90% of all individuals were of the new type. The difference between the two time-points is our definition of time to replacement, T_R. The two grey vertical lines in panel (*b*) indicate the beginning (left line) and 100% completion (right line) of a neutral replacement of the new type. Parameter values: $I = 0.05$, $K_0 = 10^4$, $r = 0.25$, $\sigma_K = 1$, $\sigma_\alpha = 0.2$, $\sigma_\mu = 0.01$.

displacement thus protects them from competitive exclusion by the new type. Such relict species often persisted until the end of our simulations (this simulation lasted until generation 1.2×10^7, but is truncated in the figure).

Figure 1b shows a sample simulation with additional, externally driven, extinctions ($P_e = 5 \times 10^{-6}$). The parameter values are otherwise the same as in Fig. 1a. The steady-state community before the innovation now has a much higher turnover of species – the extra extinctions lead to new speciations and the community as a whole is more evolutionarily labile. This high turnover also accelerates the replacement process and prevents long-term persistence of relict species. The two grey extra lines to the right indicate a neutral, random replacement. A single lineage of the new type rapidly takes over 100% of the community.

Figure 2a shows mean time to 90% replacement as a function of innovation size I, for different values of P_e. As expected, the replacement process is faster if the competitive

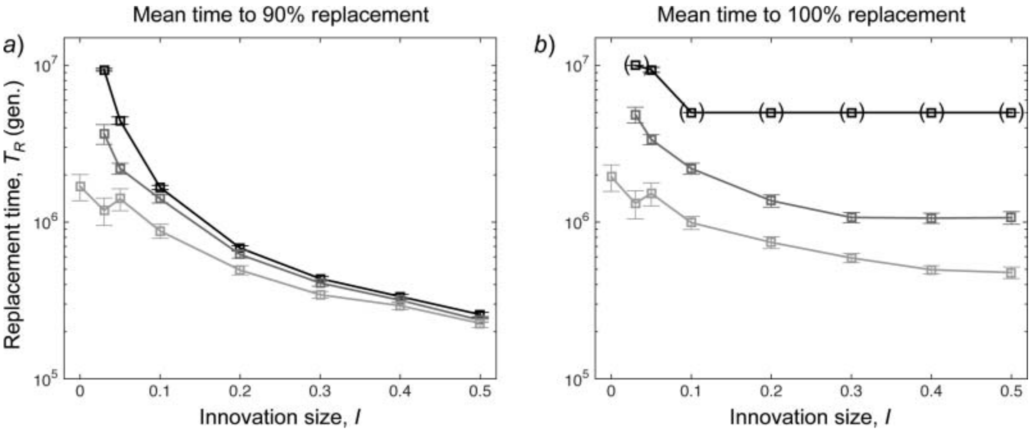

Fig. 2. Mean time to 90% (*a*) and 100% (*b*) replacement, plotted against innovation size, *I*. The error bars indicate standard errors. Cases when no replacement was complete by the end of the simulation are indicated by parentheses. The different shades of grey represent different values of the external extinction rate; $P_e = 0$ (black), $P_e = 2 \times 10^{-6}$ (dark grey), and $P_e = 5 \times 10^{-6}$ (light grey). Note the extra data point for $I = 0$, $P_e = 5 \times 10^{-6}$. All other parameter values are as in Fig. 1.

advantage of the new type, *I*, is larger. The replacement is also faster if the background extinction rate is higher. Background extinctions have a particularly strong influence on recorded replacement times at low values of *I*. Do note, however, that the risk of global extinction of the new type also is higher for low values of *I* (see evolutionary-ecology.com/data/2975Appendix.pdf, Fig. A1). We discuss this in more detail below.

The effect of lingering relict species can be seen in Fig. 2b, which shows the mean time to 100% replacement. Without externally driven extinctions (i.e. when $P_e = 0$), the species belonging to the old type often survived until the end of simulations (the black line in Fig. 2b follows closely the maximal simulation time). A high extinction rate, on the other hand, rapidly eliminated the marginal species and the mean time to 100% replacement was not much different from that to 90% replacement (compare the light grey lines in Fig. 2a and 2b), except at high values of *I*. The last marginal species are not primarily eliminated by competitive exclusion, but by random extinction. The competitive advantage is thus less important, even though it plays a role in the marginalization process itself.

Figure 3 depicts the measured speciation and extinction rates. The horizontal dashed line in each panel indicates the background level for the steady-state community before the time of the innovation. The major deviations from the background levels consist of an elevated speciation rate of the new type (Fig. 3a,b) and an elevated extinction rate of the old type (Fig. 3c,d). Both of these effects can be associated with the successive divergence of the new, superior type and competitive exclusion of the old, inferior type. The relative increase of the extinction rate (Fig. 3c,d) and the speciation rate (Fig. 3a,b) are of similar magnitude, which means the two effects are equally important. They also seem to be additive. The new type speciation rate in Fig. 3b is well predicted by adding the corresponding speciation rate in Fig, 3a to the background rate from Fig 3b (grey line, Fig. 3b). The same conclusion applies to the old type extinction rate (grey line, Fig. 3c). A third notable deviation from the background rates is a reduction of the old type speciation rate

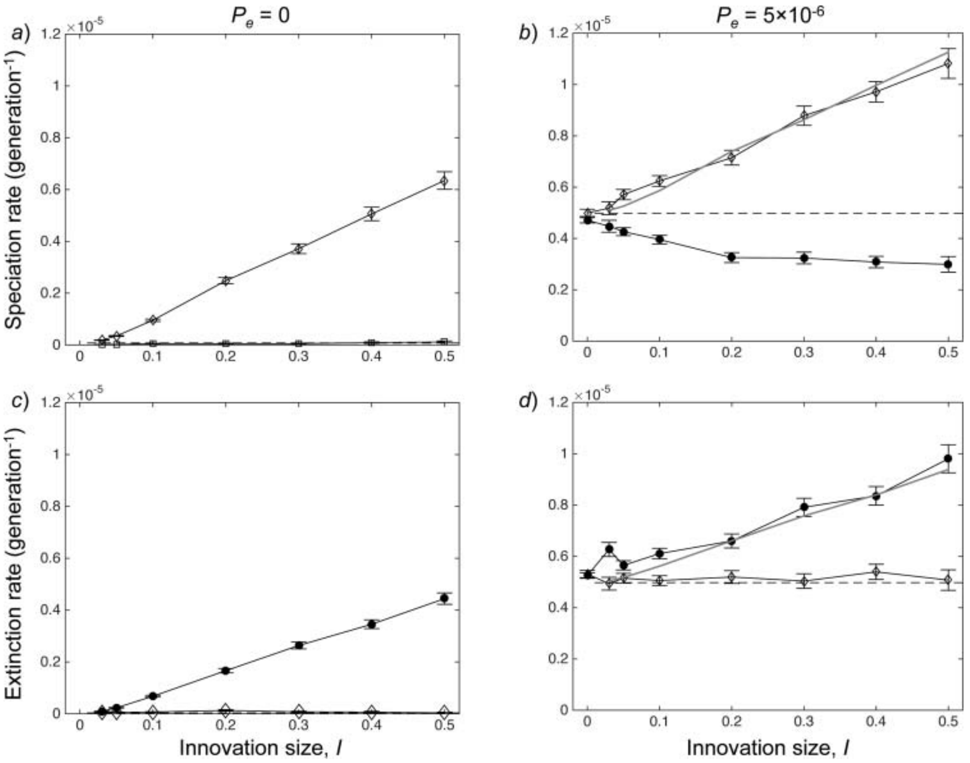

Fig. 3. Speciation rates (*a*, *b*) and extinction rates (*c*, *d*) of the ancestral (solid circles) and new (diamonds) types plotted against innovation size, *I*. The error bars indicate standard errors. The rates were measured from the introduction of the new type until 90% replacement or the new type went extinct, whichever came first. The background rates, measured before the time of introduction, are indicated with horizontal dashed lines in each panel: (*a*, *c*) $P_e = 0$; (*b*, *d*) $P_e = 5 \times 10^{-6}$. The solid grey lines in (*b*) and (*d*) indicate the corresponding rate in *a*, *c* added to the new background rate. Other parameter values are as in Fig. 1.

at high background extinction rates (Fig. 3b). This reduction is stronger at higher values of *I* and can be attributed to competition from the new type to fill niches emptied by the extra extinctions.

Not all innovation events resulted in replacement. In some simulations, the new, superior type went extinct due to demographic stochasticity or an external extinction event before it had time to diversify (2975Appendix). The probability of such ‘innovation failures’ was higher if the new type had only a marginal advantage (i.e. for low values of *I*). The probability of failure was also higher if the external extinction rate, P_e, was high. At extreme values ($I = 0.03$, $P_e = 5 \times 10^{-6}$), only 15 out of 59 innovation events resulted in a completed replacement (the ancestral type went extinct before the innovation time in 41 out of the 100 simulations). The extra simulations with neutral innovations ($I = 0$) yielded a low replacement probability of 0.37%. At *I*-values above 0.1, the replacement success rate was consistently above 50% and often close to 100% (2975Appendix).

DISCUSSION

Here, we have investigated theoretically a replacement process driven by competitive superiority. Our model is individual-based, which makes a number of species-level properties – population size, rates of adaptation, speciation, and extinction – truly emergent from lower-level processes (with the single exception of the external extinction events). That being said, we have simplified many potentially important aspects of reality to keep the model transparent and to facilitate interpretation of the results. The model lacks spatial structure, genetic recombination, multidimensional phenotypes, trophic interactions, and variable environments, to name a few. However, this is our first attempt to model replacement scenarios by letting macroevolution be driven almost entirely by microevolution. Moreover, we can relate our results to existing data and we have identified unexpected mechanisms, which is all very encouraging for future work.

No threshold innovation size

We found no critical advantage of an innovation (our parameter I) below which replacement will not take place. A very small competitive advantage may be lost due to stochastic extinctions or the replacement may take a very long time (Fig. 2), but there is no sudden transition in extinction probability or time to replacement. In fact, we found a low probability of replacement even without a competitive advantage, driven by stochastic extinctions and compensatory speciations. Whether an innovation is 'key' or not is thus, from this perspective, quite arbitrary.

Smooth replacement

The replacement process in our simulations was relatively smooth in the sense that species were replaced one by one while the total number of species remained approximately constant. The pattern of a gradual decrease of species of the old group and associated gradual increase of species in the new group corresponds to the so-called double-wedge scenario described by Benton (1987). This outcome may be attributed to the relatively simple eco-evolutionary scenario we have considered here. Interaction strength declines strongly along the (single) niche axis and therefore the extinction of a species and its replacement by a slightly fitter one has relatively little influence on fitness and selection for species further away in niche space. Thereby replacement of single species may proceed without affecting the whole community.

Replacement processes can be more complex in other types of communities. Extinctions, driven by competition or by chance, may trigger secondary extinctions. Removal of so-called keystone species may cause extinction cascades in food webs (Paine, 1966; Borrvall *et al.*, 2000; Solé and Montoya, 2001). Secondary extinctions may also occur on a microevolutionary time-scale. In such cases, species removal triggers evolutionary adjustments in the remaining community during which additional species go extinct (Bronstein *et al.*, 2004; Johansson and Dieckmann, 2009). Furthermore, the radiation of the invading species group may be more complicated than in our scenario. Successful invasion or divergence may, for example, require the presence of mutualistic partner species or co-evolution among pairs or groups of closely interacting species. In general, replacement processes can thus be far less gradual than predicted here, also in the absence of external environmental changes. Instead of species being replaced one by one, species of the old group may disappear in catastrophic extinction cascades that are not immediately balanced by speciation of the new group. An interesting avenue for future research, therefore, is to analyse replacement dynamics in various types of communities, not least to explore the conditions for when replacement processes are gradual, as we found here, and when they are not.

Mass extinctions accelerate replacement

Background extinctions accelerate the replacement process in our model, especially following only moderately advantageous innovations (low values of *I*; Fig. 2). It follows that periods of elevated extinction rates, such as mass extinctions, should be associated with substantial advancements in the replacement of an old type by a new one. This prediction is well supported in the data (Benton, 1987; Rosenzweig and McCord, 1991; Roy, 1996). A tentative conclusion from our simulations is that replacement before or after a mass extinction may be so slow that it is hard to detect in data sets, whereas the mass extinction itself may bring about substantial, detectable, changes in the relative occurrence of the two groups. It may thus appear that the mass extinction was the main driver or even cause of the replacement, even though the underlying mechanism was competition. Benton (1987) points at the importance of mass extinctions for several documented replacements and questions the role of competition. Our results confirm the importance of mass extinctions but do not rule out the possible role of competition. Hausdorf (2001) argues that many examples from the fossil record are analysed at an inappropriate taxonomic level (genera or above) to detect the effects of competition. Rather, such effects are visible at the species level or below (including spatial distribution).

Another conclusion from our simulations is that the main mechanism underlying the accelerated replacement during mass extinctions may be nothing but an observation bias. If a mass extinction strikes blindly among the extant taxa, specious groups are less likely to be completely eradicated. A new group carrying a key innovation may have a high risk of global extinction *unless* it quickly increases in diversity. If we only observe such successful groups, the result is a biased rate of replacement.

Evolutionary competitive exclusion and incumbency

The incumbent replacement scenario requires that an old type species is replaced by a new type species only after a random (background) extinction event. This scenario was observed by Rosenzweig and McCord (1991) and Roy (1996) and also described by Gilinsky and Bambach (1987). Incumbent replacement can be characterized by an equal extinction rate of all types, but an elevated speciation rate of the new type. We find an elevated speciation rate of the new, superior type, but also an increased extinction rate of the old type (Fig. 3), pointing to a scenario more like competitive exclusion through gradual evolution and niche takeover. That being said, the difference between the two evolving clades is consistently larger in the speciation rates than the extinction rates, especially when we add extra background extinctions (Fig. 3b,d). That last result points to some role of incumbency, although we cannot confirm incumbent replacement *sensu stricto*. Certain model features may explain why a strict incumbent replacement scenario is not observed in our simulations. We have, for instance, a continuous resource landscape that allows a species to gradually shift its phenotype and make way for a superior competitor. A model with more discrete niches may be more dependent on incumbency, but that is mere speculation. The presence of a superior competitor, even if it is not adapted to the same niche, can decrease the equilibrium density and/or range of an inferior type such that it is more easily driven to extinction by other factors – a scenario described by Stanley and Newman (1980).

Sepkoski (1996) pointed out that evolutionary replacement even by a single species is an inherently different process than ecological competitive exclusion. The time-scales and underlying mechanisms are different, although competition plays a central part in both. The process of 'evolutionary competitive exclusion', where the two species co-exist initially, requires the gradual evolution of the superior species and/or the inferior species such that the inferior one eventually goes extinct due to strong competition from the superior species. In our simulations, we see a mixture of evolutionary competitive exclusion and incumbency, but more work is needed to determine under what circumstances one process or the other is more important.

Relict species in marginal niche refuges

Our finding of long-lived, marginalized, relict species also has several supporting examples from the fossil record. Contemporary chthamaloid barnacles have been displaced by banaloids to the upper intertidal, really deep waters, or highly disjoint, disseminated distributions (Stanley and Newman, 1980). Semislugs of the group Vitrinidae are partly replaced by closely related slugs (Boettgerillidae, Limacidae, and Agriolimaciadae) in Europe and Asia. Where semislugs and slugs co-occur, the semislugs are marginalized to cold seasons (winter) or high altitudes (Hausdorf, 2001). On the Macaronesian islands (Azores, Madeira, and Canary Islands), on the other hand, slugs are absent (except very recent invasions) and the semislugs are active the whole year and occur predominately at low altitudes (Hausdorf, 2001). According to our results, a species or group of species can be 'pushed' into marginal niche space by a superior competitor. Such marginal niches may then act as refuges for an ancestral type, otherwise outcompeted by the derived, superior type. The marginal niches are relatively evolutionarily unattractive and are therefore more easily monopolized by the incumbent old type (cf. Rosenzweig and McCord, 1991; De Meester *et al.*, 2002; Urban and De Meester, 2009; Ripa, in prep.). Admittedly, the marginal refuge effect described here is quite hypothetical. Further theoretical and empirical work is necessary to establish its plausibility, to describe better the underlying mechanisms, and to assess its importance in natural systems. For instance, we hypothesize that central European semislugs were not active during winter before the appearance of slugs, but we know of no data to confirm or reject this hypothesis.

Final words

Here, we have connected competitive superiority at the individual level on an ecological time-scale to patterns of species dynamics at the macroevolutionary scale, something that is not captured by standard species-level models (e.g. Raup, 1981; Sepkoski, 1996). Our results show the possible importance of the background extinction rate for the pace of observed replacement processes, and how relict species may linger for long times in marginal regions of trait space. We hope our study will stimulate further theoretical work on the importance of eco-evolutionary feedbacks on the macroevolutionary scale. So far, we have merely scratched the surface.

ACKNOWLEDGEMENTS

We thank Per Lundberg, Mike Rosenzweig, Doug Morris, and all the other participants of the Tucson workshop for interesting discussions and constructive suggestions. In particular, we thank Doug Morris and Kalle Parvinen for helpful comments on an earlier version of the manuscript. We also thank the Swedish Research Council (VR) for financial support.

REFERENCES

Benton, M.J. 1987. Progress and competition in macroevolution. *Biol. Rev.*, **62**: 305–338.

Borrvall, C., Ebenman, B. and Jonsson, T. 2000. Biodiversity lessens the risk of cascading extinction in model food webs. *Ecol. Lett.*, **3**: 131–136.

Bronstein, J.L., Dieckmann, U. and Ferrière, R. 2004. Coevolutionary dynamics and the conservation of mutualisms. In *Evolutionary Conservation Biology* (R. Ferrière, U. Dieckmann and D. Couvet, eds.), pp. 305–326. Cambridge: Cambridge University Press.

Champagnat, N., Ferrière, R. and Méléard, S. 2006. Unifying evolutionary dynamics: from individual stochastic processes to macroscopic models. *Theor. Pop. Biol.*, **69**: 297–321.

Christiansen, F.B. and Loeschke, V. 1980. Evolution and intraspecific exploitative competition I. One-locus theory for small additive gene effects. *Theor. Pop. Biol.*, **18**: 297–313.

Claessen, D., Andersson, J., Persson, L. and de Roos, A.M. 2007. Delayed evolutionary branching in small populations. *Evol. Ecol. Res.*, **9**: 51–69.

De Meester, L., Gómez, A., Okamura, B. and Schwenk, K. 2002. The Monopolization Hypothesis and the dispersal–gene flow paradox in aquatic organisms. *Acta Oecol.*, **23**: 121–135.

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

Geritz, S.A.H., Kisdi, É., Meszéna, G. and Metz, J.A.J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, **12**: 35–57.

Gilinsky, N.L. and Bambach, R.K. 1987. Asymmetrical patterns of origination and extinction in higher taxa. *Paleobiology*, **13**: 427–445.

Hausdorf, B. 2001. Macroevolution in progress: competition between semislugs and slugs resulting in ecological displacement and ecological release. *Biol. J. Linn. Soc.*, **74**: 387–395.

Heard, S.B. and Hauser, D.L. 1995. Key evolutionary innovations and their ecological mechanisms. *Hist. Biol.*, **10**: 151–173.

Hironaga, R. and Yamamura, N. 2010. Effects of extinction on food web structures on an evolutionary time scale. *J. Theor. Biol.*, **263**: 161–168.

Johansson, J. and Dieckmann, U. 2009. Evolutionary responses of communities to extinctions. *Evol. Ecol. Res.*, **11**: 561–588.

Johansson, J. and Ripa, J. 2006. Will sympatric speciation fail due to stochastic competitive exclusion? *Am. Nat.*, **168**: 572–578.

Leimar, O., Doebeli, M. and Dieckmann, U. 2008. Evolution of phenotypic clusters through competition and local adaptation along an environmental gradient. *Evolution*, **62**: 807–822.

Paine, R. 1966. Food web complexity and species diversity. *Am. Nat.*, **100**: 65–75.

Pontarp, M., Ripa, J. and Lundberg, P. 2012. On the origin of phylogenetic structure in competitive metacommunities. *Evol. Ecol. Res.*, **14**: 269–284.

Raup, D.M. 1981. Extinction: bad genes or bad luck? *Acta Geol. Hisp.*, **16**: 25–33.

Ripa, J. in prep. On niche conservatism, niche monopolization and the mechanics of adaptive trait evolution.

Rosenzweig, M.L. 1978. Competitive speciation. *Biol. J. Linn. Soc.*, **10**: 275–289.

Rosenzweig, M.L. and McCord, R.D. 1991. Incumbent replacement: evidence for long-term evolutionary progress. *Paleobiology*, **17**: 202–213.

Roughgarden, J. 1972. Evolution of niche width. *Am. Nat.*, **106**: 683–718.

Roy, K. 1996. The roles of mass extinction and biotic interaction in large-scale replacements: a reexamination using the fossil record of stromboidean gastropods. *Paleobiology*, **22**: 436–452.

Sepkoski, J.J., Jr. 1996. Competition in macroevolution: the double wedge revisited. In *Evolutionary Paleobiology* (D. Jablonski, D.H. Erwin and J.H. Lipps, eds.), pp. 221–255. Chicago, IL: University of Chicago Press.

Simpson, G.G. 1953. *The Major Features of Evolution*. New York: Columbia University Press.

Solé, R.V. and Montoya, J.M. 2001. Complexity and fragility in ecological networks. *Proc. R. Soc. Lond. B: Biol. Sci.*, **268**: 2039–2045.

Solé, R.V., Montoya, J.M. and Erwin, D.H. 2002. Recovery after mass extinction: evolutionary assembly in large-scale biosphere dynamics. *Phil. Trans. R. Soc. Lond. B: Biol. Sci.*, **357**: 697–707.

Stanley, S.M. and Newman, W.A. 1980. Competitive exclusion in evolutionary time: the case of the acorn barnacles. *Paleobiology*, **6**: 173–183.

Urban, M.C. and De Meester, L. 2009. Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. *Proc. R. Soc. Lond. B: Biol. Sci.*, **276**: 4129–4138.