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Abstract.—One of the most enduring evolutionary metaphors is Van Valen's (1973) Red Queen. According to this metaphor, as one species in a community adapts by becoming better able to acquire and defend resources, species with which it interacts are adversely affected. If those other species do not continuously adapt to compensate for this biotically caused deterioration, they will be driven to extinction. Continuous adaptation of all species in a community prevents any single species from gaining a long-term advantage; this amounts to the Red Queen running in place. We have critically examined the assumptions on which the Red Queen metaphor was founded. We argue that the Red Queen embodies three demonstrably false assumptions: (1) evolutionary adaptation is continuous; (2) organisms are important agents of extinction; and (3) evolution is a zero-sum process in which living things divide up an unchanging quantity of resources. Changes in the selective regime need not always elicit adaptation, because most organisms function adequately under many "suboptimal" conditions and often compensate by demonstrating adaptive flexibility. Likewise, ecosystems are organized in such a way that they tend to be robust and capable of absorbing invasions and extinctions, at least up to a point. With a simple evolutionary game involving three species, we show that Red Queen dynamics (continuous adaptation by all interacting species) apply in only a very small minority of possible outcomes. Importantly, cooperation and facilitation among species enable competitors to increase ecosystem productivity and therefore to enlarge the pool and turnover of resources. The Red Queen reigns only under a few unusual circumstances.

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Introduction

Van Valen (1973) chose the Red Queen metaphor in order to explain his observation that the probability of extinction of a given taxon is independent of the age (time since the origin) of that taxon. To him, the unvarying threat of extinction implies inexorable deterioration of the biotic environment brought about by the struggle of life itself. The Red Queen thus expresses the well-justified argument that most adaptive challenges faced by organisms arise from interactions among individuals for locally limited resources (Van Valen 1973, 1976, 1983; Vermeij 1982, 1987, 2004a). The idea has also been extensively applied to host-parasite relationships and to the evolution of sex (reviewed in Lively 2010).

While we strongly endorse the importance of organisms as selective agents, we question the validity and usefulness of the Red Queen framework for explaining the dynamics of evolution and extinction. Elaborating on earlier objections (Vermeij 1994; Roopnarine 2012), we argue that the Red Queen metaphor embodies three assumptions that are either demonstrably false or so often violated as to render the metaphor misleading. These assumptions are (1) evolutionary adaptation is continuous; (2) organisms are important agents of extinction; and (3) evolution is a zero-sum process in which living things divide up an unchanging quantity of resources. We also comment on the validity of the age-independent probability of extinction, on which Van Valen based the Red Queen metaphor. Instead we propose that most biotic interactions in communities lead to stabilizing selection and stasis. Stabilizing selection cements adaptive traits but does not result in phenotypic change representing improved capacities to obtain and keep resources.

Directional selection, which does lead to adaptive change, is an ephemeral process that requires the relatively rare combination of permissive conditions and the presence of abundant antagonistic interactions. In our view, the evolutionary turf over which the Red Queen reigns is so small that the Red Queen is best eased into retirement.

Invalid Assumptions

Adaptive Evolution is Continuous.—The Red Queen metaphor portrays species or populations as "running in place" to compensate adaptively for the continuously deteriorating biotic environment. There are, however, both theoretical and empirical arguments that cast doubt on continuity as the adaptive norm for evolution in the long run.

Although mutations occur frequently enough to be modeled as continuous, and adaptive change is often rapid and continuous on very short time scales, episodes of rapid adaptation are punctuated by much longer periods during which adaptive evolution at the level of the phenotype (physiology, morphology, and behavior) ceases. The fossil record provides overwhelming evidence for long-term adaptive stasis of species for periods of tens of thousands to millions of years (MacGillavry 1968; Eldredge and Gould 1972; Hunt 2007). Close inspection of purported cases of gradual (i.e., continuous) transformation from one species (or one phenotype) to another has revealed episodic speciation and intervening adaptive stability, as in the *Globorotalia tumida* clade of planktonic Foraminifera (Roopnarine 2001; Hull and Norris 2009).

The start-and-stop pattern of adaptive change calls into question the whole notion of a rate of evolution. A rate implies continuity of process. Its value depends strongly on the time interval over which it is measured, and true rates of evolution exist only if they are measured on per-generation time scales or at the scale of overlapping generations (instantaneous or intrinsic rates of evolution) (Gingerich 1983; Roopnarine 2003). If adaptive change is concentrated during certain short intervals, however, then combining those intervals with periods of stasis produces a meaningless average rate of change (Stanley

1979). Similar problems plague such other discontinuous phenomena as extinction and speciation, for which the concept of rate at short time scales is similarly misleading (Wiens 2011).

In their attempt to describe Red Queen dynamics, Stenseth and Maynard Smith (1984) applied adaptive landscapes and Maynard Smith's (1976) concept of lag load, the adaptive distance between a species and the ideal adaptive peak that the species in its contemporary environment would reach given sufficient time and consistent selection. The greater the load, the faster will be the rate of evolution of the species toward the peak; that is, as a species approaches the optimum, adaptive evolution slows. In this view, other species affect the height and position of the adaptive peak of any given species, and therefore tend to increase the lag load of that species. This circumstance sets up continuous adaptive accommodation of species to each other. The adaptive peak in this model is situated at a phenotypic extreme, a condition that species always approach but never reach.

Using a formulation informed by evolutionarily stable strategies, Rosenzweig and colleagues (1987) modified Stenseth and Maynard Smith's (1984) view by construing the adaptive peak as an optimal compromise that actually exists. In their view, species not only approach the adaptive peak through selection, but actually reach it; and once they do so, further adaptation ceases until an external circumstance affects the entire system. Selection continues to operate once the adaptive peak has been attained, but this selection is stabilizing, perpetuating the adaptive status quo rather than causing each species to evolve continuously as it chases the elusive adaptive peak in the fashion of the hapless Sisyphus of Greek mythology.

Besides the explicit assumption that a greater lag load translates into a high rate of evolution, a second implicit premise in Stenseth and Maynard Smith's (1984) model is that species are evolutionarily highly sensitive to variations in the adaptive landscape. In other words, a shift in position and height of an adaptive peak elicits a corresponding adaptive response. This assumption, like the notion of

the adaptive peak itself, flows from the perspective that species evolve toward some optimal adaptive state, and that evolution is an optimizing process (see Seger and Stubblefield 1996 for a summary of the optimality perspective in evolution). The assumption ignores the existence of negative genetic correlations among traits and the necessity of phenotypic trade-offs. If, however, adaptations are seen as adequate rather than optimal, then the possibility arises that adaptive sufficiency applies over a rather wide range of conditions. In this view, species at most times would be relatively insensitive to variations in the conditions of life, and would respond adaptively (that is, undergo directional selection) only under certain permissive circumstances (Vermeij 1987, 2004a). Their adaptations are always subject to improvement and can therefore never be "perfect," even in the formulation of Rosenzweig and colleagues (1987); but typically there may not be strong directional selection for improvement, either because constraints impose stability or because current adaptations suffice even if they do not attain the supposed optimum.

That adequacy rather than optimization is the evolutionary and adaptive norm is indicated by the high frequency of reports on species that perform better in terms of growth and fecundity in environments rarely occupied by these species than in the environments in which they evolved or still flourish. Dayton (1973) noted, for example, that mussels grow faster and reach much larger sizes in subtidal habitats, where they are rare, than in the intertidal zone, where the restricted activity of predators on adults enables them to form large aggregations. Geist (1978, 1983) observed that few large mammalian grazers reach their genetic potential of adult size because most live in areas where food is scarce enough to stunt growth. In the same vein, Huey and colleagues (2001) found that lizards of many species tend to have empty stomachs when found, indicating widespread hunger. Hermit crabs typically occupy shells that are too small for maximal fecundity (Bertness 1981). Clay-adapted tree species in Amazonian rain forests outcompete species specialized to nutrient-poor white-sand soils when grown in those sandy soils and when they are protected from herbivores; and trees specialized to grow in infertile sand do better on richer clay but do not naturally occur there because they are outcompeted by clay specialists (Fine et al. 2004). Species introduced by humans often become temporarily more abundant in their new homes than in their native habitats because they have left their natural enemies behind (Cornell and Hawkins 1993; Wolfe 2002; Mitchell and Power 2003; Torchin et al. 2003). The number of offspring in birds and mammals is often below the maximum observed for a species (Vercken et al. 2012), and frequently covaries with prevailing environmental circumstances (Risch et al. 1995). In all these examples and many more like them, enemies often exclude species from the environments where they would do best because of the ready availability of resources. Instead, these species get by in less favorable habitats or environments without evidence of continuous adaptive evolution or continuous optimization to varying environments. Adaptations work under a wide variety of circumstances, and are, by and large, not finely honed to any particular situations, which in any case are apt to be local and ephemeral.

Ecologists are acutely aware of the great variation that exists in most environments in time and space. Organisms often deal adaptively with such variation not by continuous genetic evolution, but by non-genetic mechanisms such as learning, adaptive morphological and behavioral plasticity, developmental epigenesis, and immune reactions to novel pathogens; that is, their adaptations are inducible and flexible. The widespread occurrence of inducible defenses, inducible variation in feeding structures, flexible trophic strategies, homeostatic mechanisms of internal physiology to counter external environmental fluctuation, and environmentally sensitive gene expression (Frank 1996; Agrawal 2001; Zangerl and Rutledge 1996; Poitrineau et al. 2004; Turner 2007; Mougi et al. 2011; Pyenson and Lindberg 2011) testifies to the robustness, flexibility, and broad applicability of adaptive states, and points to adequacy of function over a wide range of ecological circumstances.

Flexibility and generality offer a successful and common alternative to the Red Queen world of precision and continuous gene-based evolution.

As noted by Rosenzweig and colleagues (1987) and many others, the adaptive log-jam that prevents evolutionary improvement with respect to other species is enforced by pervasive functional trade-offs and by impediments related to activation energy. These constraints are lifted only when the total energy budget within which adaptive allocation among competing functions takes place is enlarged, or when energetically expensive adaptive states become more accessible as energetic hurdles are removed. These are the same conditions that in the human realm permit economic growth, conditions implying a relaxation of economic limitations (Vermeij 2004a). Such circumstances permissible enough to allow for adaptive improvement without undue compromise are likely to be rare. In the economic history of life, including that of our own species, energy-intensive adaptive improvements (such as endothermy, agriculture, exploitation of new fuel sources, rapid and long-distance transport, and defense) are concentrated in times and places with external triggers such as climatic warming and tectonically driven increases in resource availability (Vermeij 1995, 2004a; Vermeij and Leigh 2011). Living things have capitalized on these external releases of constraints by creating positive feedbacks between resource supply and demand. As a result, adaptive evolution is expected to be episodic, spurred by a combination of tectonic and climatic triggers and enhanced by biologically generated feedbacks between activity and resources (Vermeij 2004a; Vermeij and Leigh 2011).

Apparently accepting the predominance of stabilizing selection and the adaptive stasis of species, Venditti and colleagues (2010) proposed a version of the Red Queen in which speciation in a homogeneous clade occurs at a constant rate, in parallel with Van Valen's (1973) original conjecture that the probability of extinction does not change with a clade's age. This new claim implies that adaptive change is concentrated during or shortly after speciation events, whose frequency is controlled by external factors and by major genetic changes that cause reproductive isolation. However, paleontological studies of speciation in groups with an excellent fossil record, such as macroperforate planktonic Foraminifera, indicate that speciation is not constant, but instead is concentrated at certain times, often when a clade is still young (Ezard et al. 2011). Just as adaptation cannot be considered a continuous process, speciation and adaptive radiation occur in steps marked by rare opportunities for isolation and expansion (e.g., Martin and Wainwright 2013). Episodes of extinction likewise come in discrete time intervals, and the probability of extinction varies greatly among taxa, as does speciation (McCune 1982). In any case, extension of the Red Queen metaphor to speciation events seems to us unwarranted. The Red Queen was originally formulated in order to understand the dynamics of adaptation of species to each other (McCune 1982). Adaptive change may indeed often coincide with (or follow shortly after) speciation, but that link is not inherent in the Red Queen framework, and many instances of speciation have more to do with reproductive isolation than with adaptation to other species.

In general, these arguments point to a confusion of scale that has pervaded discussions of the Red Queen. Van Valen (1973) sought originally to explain a macroevolutionary phenomenon (stochastically constant extinction within an adaptive zone) by invoking a microevolutionary species-level explanation (continuous adaptive evolution within a lineage). Although subsequent revisions (Venditti et. al. 2010; Liow et al. 2011) admit macroevolutionary explanations for Van Valen's observation, a persuasive causal link between the purported pattern and microevolutionary or macroevolutionary explanation remains elusive, and indeed seems to us to be an illusion.

Recently Brockhurst (2011), in a comment on Morran et al. (2011), raised the question of whether the Red Queen would hold as pairwise coevolutionary systems are scaled up to include more ecologically realistic numbers of species interactions. The functional trade-offs of Rosenzweig et al. (1987) would

be added to the diversity of competitive interactions and other cooperative non-antagonistic interactions as agents of selection, as well as the diffuse and structured patterns of interactions known to exist in real biological communities (Roopnarine 2012). The effect of competing or potentially offsetting selective forces or agents has rarely been considered in the context of the Red Queen, yet in many cases could result in stabilizing selection in the same way that variable abiotic factors do. We demonstrate this with a simple evolutionary game in which players (species) are characterized by a single varying phenotypic trait, and the community is a configuration of interactions among the players. Players exert selection on each other in one of three modes: 0, +, and −. A 0 or null interaction denotes the absence of any interaction, while + and − selection cause opposite changes to another player's trait. The simplest non-trivial Red Queen system, beyond a pairwise coevolutionary system, is a three-player game with all interactions being either + or −. The game is initiated by altering the state of a single player, that is, increasing or decreasing its trait value, and then iterating all player responses in discrete time steps until a stable or fully predictable result is reached for all players. Traits are assumed to be unidimensional, and a change in player A causes a change in B, with the "direction" of change depending on whether the interaction is + or − (see Appendix). The strengths of interaction and selection are assumed to be uniform for all interactions.

Three results are possible for a species. First, the species is under continuous directional selection, with its trait forever changing in the same direction on the unidimensional scale (Fig. 1A). Adaptation or extinction is inevitable with these results and the rate of evolution is greater than zero. Second, the species' trait changes in alternating fashion, back and forth along the scale (Fig. 1B). Here, even though the instantaneous or per-iteration rate of evolution is greater than zero, the outcome is stabilizing selection. The long-term result is phenotypic stasis and an average evolutionary rate of zero. Third, a species' trait is subject to offsetting selection during each iteration, resulting in stabilizing selection and stasis or
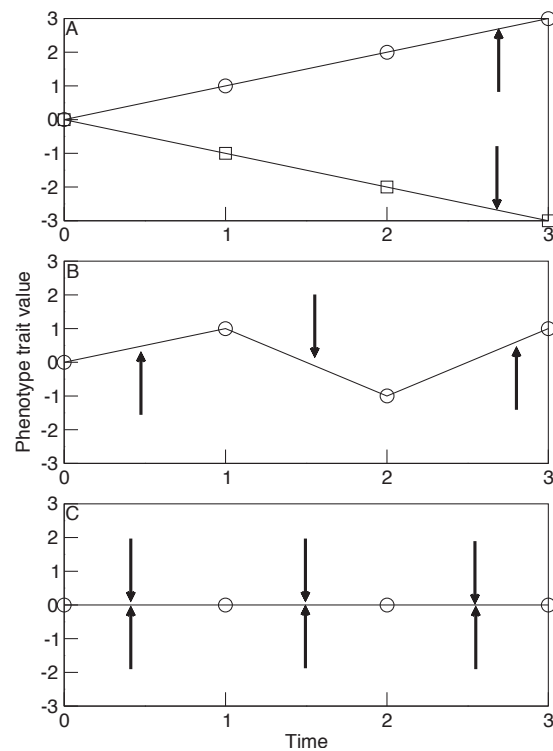

FIGURE 1. Three possible outcomes for a species involved in a three-species Red Queen game. Generations, or time, is represented on the x-axis, and the phenotypic dimension is represented on the y-axis. Net phenotypic change is shown by the plotted lines, with symbols indicating the state of the phenotype at the end of a discrete time step. Arrows show the net direction of selection during each interval. (A) Net directional change, or adaptation. Either trajectory would have evolutionary rates greater than zero. (B) Alternating or oscillating change, with no net adaptation and an average evolutionary rate of zero. (C) No net change, or stasis, caused by offsetting selection pressures during each iteration.

no phenotypic change or adaptation, and both instantaneous and average rates of evolution are zero (Fig. 1C). Of the 64 possible three-player games, only three (games 0, 45, and 58; see Appendix for explanation) yield directional selection for all three species and are therefore consistent with the Red Queen. Eight other games (7, 13, 16, 26, 32, 42, 55, and 61) result in directional evolution of the non-initiating species but stasis of the initiator. The remaining 53 games all result in alternating stabilizing selection or stasis for all species.

Morran and colleagues' (2011) experimental results are consistent with both the game and the Red Queen, but represent a small subset of

possible configurations of interactions. Mor-ran and colleagues exposed populations of the nematode *Caenorhabditis elegans* to the parasit-ic bacterium *Serratia marcescens*. *C. elegans* populations adapted by increasing the num-ber of males in the populations and hence the frequency of sexual (versus asexual) repro-duction. The experiment is consistent with game 58 if the trait under consideration is simply fitness, and the parasite interacts negatively with two other players, female and male *C. elegans*. The result is adaptive evolution of all the players, also consistent with Morran and colleagues' observation of adaptive coevolutionary responses of increas-ing sexual reproduction in *C. elegans* and increasing infectiousness of the parasite (Fig. 2A). Alternatively, if the initial change is an increase of resistance of either females or males of *C. elegans* to infection, the result is constantly increasing fitness in both sexes, and decreasing fitness of the parasite; this is game 45, and represents the second experiment of Morran et al. (2011), where less coevolved strains of *S. marcescens* were exposed to more highly coevolved and resistant *C. elegans* populations (Fig. 2B). The game, however, predicts that equally well-designed experi-ments consisting of most other patterns of interactions, such as two competing species and a common pathogen (for example, game 63), would not conform to the Red Queen (Fig. 2C). The expectation then is that less than 5% of three-species interactions in a community would be consistent with Red Queen dynam-ics, falsifying the assumption that biotic interactions lead inevitably to adaptation.

Organisms Are Important Agents of Extinc-tion.—The observation that led Van Valen (1973) to his Red Queen metaphor is the assertion that the probability of extinction of a taxon is independent of that taxon's age. This claim and its interpretation raise two questions. First, is Van Valen's empirical observation correct? Second, does adaptation by one species and the resulting environmental deterioration indeed often lead to the extinction of species that cannot adapt to the ensuing change?

Analyses of the excellent fossil record of planktonic Foraminifera of the last 65 million years have revealed a pattern of extinction
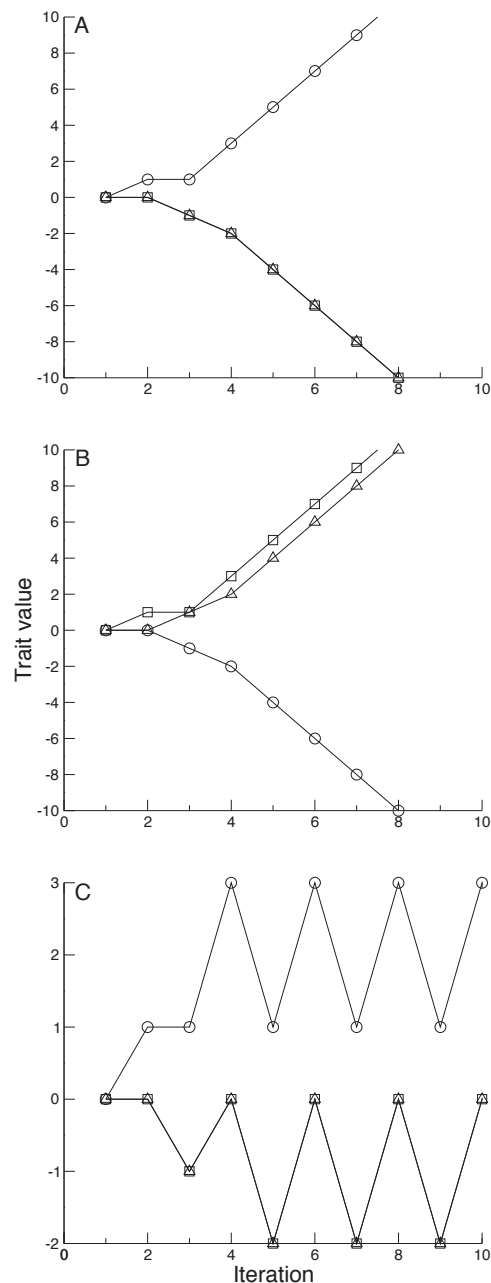

FIGURE 2. Phenotypic trajectories of players in a three-player Red Queen game under different rules of selective effects. (A) The *Caenorhabditis elegans–Serratia marcescens* game derived from the experiments of Morran et al. (2011). *Serratia marcescens* (circles) is the initially evolving species exhibiting continuous adaptation (increasing infectioness), whereas female and male *C. elegans* (squares and triangles respective-ly) exhibit constant adaptation. (B) Game representation of Morran et al.'s (2011) experiment involving less coevolved *S. marcescens*. Here the result is again constant adaptation of the parasite, and of female and male *C. elegans*. (C) An alternative Red Queen game where player A is again an infectious parasite, but players B and C are now competing species.

inconsistent with Van Valen's claim. After mass or other large-scale extinctions, many genera are short-lived, indicating that taxa early in their history have a higher probability of extinction than taxa do later (Doran et al. 2006; Ezard et al. 2011). The likelihood of extinction again rises later as taxa age (Pearson 1992). Patterns of extinction among invertebrate clades similarly reveal departures from a constant probability of extinction with taxon age (Finnegan et al. 2008). In contrast to the post-Cretaceous planktonic Foraminifera, genera of marine animals that persisted through the mass extinction events or that originated in their immediate aftermath have greater geological longevities than genera originating later in the same clades (Miller and Foote 2003). Whether this pattern holds at the species level is, however, doubtful. Nearly all molluscan species that have been described from the earliest Triassic and earliest Paleocene are confined to those short post-crisis intervals (Glibert 1973; Dockery 1986; Pacaud et al. 2000; Nützel and Schulbert 2005; Hautmann et al. 2011, 2013), a pattern that is more consistent with that seen in planktonic Foraminifera. This rapid turnover of species is symptomatic of highly unstable post-crisis ecosystems (Hansen 1988; Stanley 1990; Payne et al. 2004; Roopnarine et al. 2007).

Perhaps more importantly, vulnerability to extinction depends strongly on ecology and on adaptive syndrome. For example, the size increase that characterizes numerous mammalian clades is accompanied by an increase in vulnerability to extinction as indicated by shorter geological durations of large-bodied members of clades (Van Valen 1975; Van Valkenburgh et al. 2004). In particular, large-bodied top predators appear to have a particularly precarious tenure as compared to trophically lower-ranked predators (Van Valkenburgh et al. 2004). Large-bodied temperate marine molluscs in all parts of the world showed a higher vulnerability to extinction between the early Pliocene and the Recent than did smaller-bodied members of the same trophic guild (Vermeij 2012). If during their history clades occupy new ecological positions or change to new adaptive syndromes, the probability of extinction as averaged among ecologically diverse members is likely to change over time. The restriction to deep water seen among Cenozoic crinoids, brachiopods, glypheid lobsters, and numerous other clades relative to the broader (and often shallower) depth ranges of their more ancient counterparts is likely to have decreased vulnerability to extinction (Vermeij 1987). In short, a clade's adaptive and ecological heterogeneity affects the average probability of extinction of its members and may change over time, rendering that probability inconstant.

The role of organisms as agents of extinction has been widely assumed to be important (Wilson 1961; Ricklefs and Cox 1972; Van Valen 1973; Maynard Smith 1989; Davis 2003; Webb 2003) despite evidence that biotic causes of extinction have been demonstrated mainly for islands and in island-like habitats such as lakes. The most convincing cases come from human introductions of mainland species to oceanic islands and of freshwater species to lakes (Vermeij 2004b). Human-introduced species on continents and in the oceans rarely if ever cause extinctions of native species (Vermeij 2004b; Davis et al. 2011). When biotas from previously isolated regions exchange species as the dispersal barrier between them disappears, both biotas tend to become richer in species. If one of the biotas was previously continental, as in the case of South America before the Great American Interchange or Australia before connections with Southeast Asia were established, then a case can be made for mammals in the insular recipient region succumbing to extinction resulting from the influx of competitively superior species from the much larger donor biota (Vermeij 1991, 2004b, 2005).

A primary reason for the ineffectiveness of organisms as agents of extinction in most non-insular situations is the presence of refuges. The evolution or arrival of new predators, competitors, and pathogens often restricts the place and time of activity and viability of victim species and may indeed eliminate their victims from the most favorable parts of their former habitat; but in most cases, potential victims persist in refuges where their new enemies are absent or ineffective (Vermeij

2004b). Such restriction can in principle increase a species' chances of becoming extinct, but whether that chance is realized depends on how populations in refuges are affected by the various agencies (physical and biological) that cause extinction. Habitats where enemies are relatively ineffective, such as deep water, montane forests, and other marginal environments, also tend to be less productive and may generally be less susceptible to agencies of extinction linked to reductions in productivity. For example, the Phanerozoic record of many marine groups is characterized by a general retreat of shallow-water taxa to deep water, where they have persisted ever since, especially around the Eocene/Oligocene boundary when clades everywhere experienced high magnitudes of extinction because of major climatic and other abiotic events. An onshore-offshore shift in distribution has been a general feature throughout the Phanerozoic (Jablonski et al. 1983; Jablonski and Bottjer 1990).

Extinctions brought on by rare tectonic, climatic, or celestial events may alter interactions among species so much that these primary extinctions cause other species to disappear as well. Parasites and symbionts specialized to live with species that are vulnerable to physical calamities would be casualties if their hosts disappeared, but such collateral or secondary extinction would likely not spread beyond the specific association. Models of ecosystem disruption resulting from sharp reductions in productivity indicate that predatory species and their victims may face extinction because of destabilized predator-prey and competitive interactions (Roopnarine 2006; Roopnarine et al. 2007; Mitchell et al. 2012; Roopnarine and Angielczyk 2012). The trigger for such cascading collateral losses, however, is external to the system (Vermeij 2004b). The role of organisms in causing extinction therefore remains secondary and is often minor at best.

Van Valen (1973) assumed that extinction and adaptation are intimately linked processes. Although Stanley (1986) did not employ the Red Queen metaphor, he implicitly accepted this assumption by claiming that both extinction and speciation (and therefore by extension adaptation, which he associated with speciation) are promoted by the same conditions, especially small population size. The two opposing phenomena are therefore governed by the same circumstances (see also Allmon 1992, 2001). Moreover, the idea that extinction promotes subsequent speciation as newly emptied niches are being refilled is widespread among macroevolutionary paleobiologists (Sepkoski 1996). However, there is mounting evidence that the various processes governing adaptation and the comings and goings of clades operate independently. Kirchner (2002), for example, noted that extinctions tend to be clumped and global, whereas episodes of taxonomic origination are more dispersed and regional, as indeed are the recoveries from mass extinctions. The destruction of ecosystems by external causes is faster than the reconstruction and adaptive honing of ecological relationships, which involve feedbacks that gradually stabilize and increase resources (Kirchner 2002; Vermeij 2004a). Recent work by Peters et al. (2013) shows that the mechanisms and rates of extinction and speciation have been decoupled in Atlantic planktonic Foraminifera since at least the Cretaceous. Even in cases where taxon richness recovers quickly after a mass extinction, such as terrestrial communities in the wake of the end-Permian, communities may be unstable and do not exhibit patterns of interaction similar to the preceding communities (Irmis and Whiteside 2012; Roopnarine and Angielczyk 2012). Innovations that increase the scope and performance of adaptations in major clades typically come millions to tens of millions of years after mass extinctions, not immediately after those catastrophic events (Vermeij 2001, 2008, 2011; Kirchner and Weil 2000). Given that many ecosystems are undersaturated with respect to species, as demonstrated by increases in local species diversity when species arrive from elsewhere, there is no evidence for the claim by Van Valen (1973) and Liow et al. (2011) that extinction is linked to community saturation; extinction can occur whether the community is filled to capacity or not. In fact, the mutual enrichment of faunas during episodes of biotic interchange raises questions about the very notion

that communities are ever saturated (a state equated by Liow et al. [2011] with late-succession communities). The basic problem boils down to this: the circumstances of extinction are different from the circumstances of adaptation and species formation.

Critics might point to the incumbency effect, the resistance of well-established competitors to invasion or evolution by species with similar ecological roles, as evidence for community saturation and for a direct connection between speciation and prior extinction. The incumbency effect is real, but it has less to do with diversification than with adaptation. Would-be usurpers cannot dislodge established species because they are initially less well adapted to the role that the established species fills, and are unlikely to take over until the population of the established species is severely disrupted. Whether speciation (and diversification) occurs as species replace each other depends on opportunities for genetic isolation, which has no direct relationship to how well species are adapted.

That extinction through competition or predation might nevertheless be important could be inferred from some patterns of lineage accumulation in clades, but we suggest that such inferences and the analyses on which they are based are flawed. It has become common to use phylogenetic reconstructions of clades to plot the number of lineages within a clade as a function of time, where the origin of each lineage is estimated from methods based on the "molecular clock." A widespread but by no means universal pattern for post-Cretaceous clades is rapid net diversification (the rate at which lineages accumulate) followed by a slowing as diversity within the clade rises. This pattern is commonly cited in studies of phylogeny based on molecular sequences from living species (e.g., Ricklefs 2006; Rabosky 2009), but it has also been claimed on the basis of data from the fossil record (Krug et al. 2009; Rabosky 2009). Taken at face value, the decrease in diversification as the number of lineages within a clade rises implies that potential ancestors of new lineages are less likely to survive and therefore are more prone to rapid extinction than lineages appearing early in a clade's history. To Rabosky (2009) and many others,

this pattern implies that biotic agents prevent the establishment of many later lineages and therefore help bring about early extinction of would-be species arising in a clade of high diversity. Not only are there numerous exceptions to this pattern (Wiens 2011), but the plots from which the rates of diversification are estimated take into account only lineages with living representatives. At least in the cases where molecular phylogenies were used, extinct lineages were by necessity ignored. Furthermore, a slowing of diversification may simply reflect reduced opportunities for genetic isolation. Such opportunities depend both on geographic complexity and on the dispersibility of clade members. Fewer opportunities for isolation do not necessarily imply greater susceptibility of newly arising lineages to extinction.

The very large effect that the human species has had on species extinction over the past 50,000 years stands in obvious contrast to the generally small role of organisms as agents of extinction. Our unique role, made possible by unprecedented technology, should not be taken as the norm for extinction earlier in the geological record. Our culpability for causing widespread extinction therefore cannot be taken as theoretical justification for a Red Queen view of the world as general explanation or description of the phenomenon of extinction.

Evolution Is a Zero-Sum Game.—Undergirding the Red Queen framework is the assumption that evolutionary interactions occur against an ecological backdrop of a constant quantity of resources (Van Valen 1973; Finnegan et al. 2008; Liow et al. 2011). A gain by one species or individual therefore translates into a loss for others as members of an ecosystem compete for resources in this zero-sum world. Conversely, a loss by one species is used to advantage by other species, thus maintaining energy and community equilibrium in a version of compensatory dynamics (Liow et al. 2011). Evidence in support of compensatory dynamics as frequent or structuring processes in natural communities is, however, equivocal at best, with many situations involving similar, rather than different, responses among competing species to environmental perturbation (Houlahan et al. 2007; Gonzalez and Loreau 2009). Nevertheless, given two competing

species, it is entirely conceivable that adaptive or demographic gain by one species in response to a changed environment could have a negative effect on the other species. The species therefore co-vary negatively. There is a logical paradox, however, in such expectations of compensatory dynamics based on patterns of interaction. Three or more competing species cannot all be engaged in compensatory dynamics, since at least two competitors must always respond in the same manner to the third. Invoking suitably varying strengths of interaction or demographic parameters in order to produce compensatory dynamics under such circumstances amounts to special pleading for a hypothesis lacking in empirical support. The infrequency of compensation in even single communities speaks against the maintenance of a community equilibrium by community-wide zero-sum constraints (Fischer et al. 2001; Houlahan et al. 2007).

There is mounting evidence that the quantity and variety of resources rose during the course of life's history. Benton (1979) argued that the quantity has increased over time, and there is compelling geochemical evidence that the concentration of phosphate in seawater—a nutrient that globally limits marine primary productivity—increased by a factor of nearly seven from the early and middle Phanerozoic (Cambrian to Jurassic, 542 to 145 Ma) to the late Phanerozoic (Cretaceous to Recent, 145 Ma to the present) (Planavsky et al. 2010). Just before the Phanerozoic, increasing late Neoproterozoic concentrations of phosphate, which were apparently as high as Cretaceous to Recent values (Planavsky et al. 2010), coincide with major increases in oxygen levels, primary productivity, and adaptive radiation, culminating in the so-called "Cambrian explosion." During and after this initial stimulus, a 100-fold increase in chemical weathering of rocks on land by plants and their associated fungi, together with increasing bioturbation, greatly increased the availability of mineral nutrients both on land and in the sea (Moulton and Berner 1998; Bambach 1999; Beerling and Berner 2005; Knauth and Kennedy 2009). Together with many other lines of evidence indicating higher productivity over time, especially over the last 100 million years,

these arguments point to sharp stepwise increases in the stock of resources available to organisms (see also Vermeij 2011).

More important than the standing stock of resources are access to that stock and the productivity that the rate of turnover of resources can sustain. The mere existence of a resource does not mean that the resource will be put to use. For example, the vast reserves of coal and oil remained out of the reach of living things for hundreds of millions of years until humans invented the technology to extract these fuels and use them to perform the work that enabled humans to cement biological dominance over the planet. Resources provide the potential for doing biological work much as money provides the potential for doing human-economic work, but that potential is realized only when a combination of factors enables living things to apply resources toward the acquisition and defense of those resources. Besides technology, which itself requires a substantial energy investment, these factors include higher environmental or body temperatures, and release from (or dominance in) competition. Higher temperatures reduce the activation energy of the chemical reactions that underlie metabolism and synthesis; they increase the adaptive range of states attainable with a given level of technology. The faster resources are acquired and recycled, the greater is the power that those resources can provide and the greater are the productivity and the competitiveness of the system through which those resources flow. All mechanisms for increasing access to a stock of resources require an investment in material or energy in order to gain more energy; they are therefore inherently costly. This investment potentially increases a system's power and productivity and therefore increases the flow of resources, as long as those resources can be either replaced or recycled. In such a non-zero-sum system, the potential for adaptive improvement can be realized by many species, including species that compete with each other.

In addition to a fixed sum of resources, zero-sum scenarios assume that competition for those resources is perfect and constant. This underlies the effect of the biotic environ-

ment on species adaptation in the Red Queen. But zero-sum scenarios also assume that competitors have no common interests (Barash 2003), an assumption that is violated in at least two ways. First, intense competition among consumers for a diminished pool of resources, approaching a perfect zero-sum game, will lead to communities that are less robust against the cascades of collateral extinction mentioned earlier (Roopnarine 2012; Roopnarine and Angielczyk 2012). This was the situation of Early Triassic terrestrial communities in South Africa in the aftermath of the end-Permian mass extinction. Such communities, however, are unlikely to remain stable in their composition as selection drives them toward more robust groups of species and interactions and fewer extinctions. The "common interest" here is the overall resistance of the community to cascading extinctions. Hence the Red Queen state would be ephemeral (Roopnarine 2012). In contrast, enrichment of communities at the producer level tends to elicit positive responses in species at all trophic levels (Arditi and Ginzburg 2012), without destabilization, and contrary to the zero-sum expectation of competition for energy between trophic levels (Liow et al. 2011). Second, as in games of human interactions, it has been established that one strategy for moving beyond the constraints of zero-sum situations is cooperation among players. This amounts to mutually beneficial interspecific interactions in the natural world (Leigh 2010), and investment in common interests in the human world (Roopnarine 2013), rather than the exclusive antagonistic nature of interactions in the Red Queen's domain.

In the human economy, trade tends to increase productivity and wealth. This circumstance also applies to natural ecosystems. In part thanks to the activities of mobile animals, ecosystems often exchange nutrients (Polis et al. 1997). For example, birds feeding at sea ferry nutrients in the form of fish and guano to nesting sites on land, where these nitrogen-rich and phosphate-rich resources stimulate plant production and therefore chemical weathering. Animals burrowing into the seafloor bring up buried nutrients, which benefit both the burrowers themselves and organisms living on or above the seafloor (Thayer 1983; Lohrer et al. 2004). Ecosystems that once functioned more or less independently of each other thus become more mutually dependent and effectively larger, both in areal scale and in the stock of available resources. The increased speed and distance traveled by animals has, over the course of geological time, increased this large-scale ecological connectedness, and therefore allowed the stock of usable resources everywhere to increase (Vermeij 2004a; Vermeij and Leigh 2011).

In the long run, therefore, the biosphere as a whole and the most productive ecosystems in the biosphere can be portrayed as a non-zero-sum world. Episodic innovations in energy-intensive physiology, mutualistic symbiosis, photosynthetic capacity (Boyce et al. 2009; Boyce and Lee 2010; Brodribb and Feild 2010; Brodribb and McAdam 2011), and resource mining by burrowers and rooted land plants have progressively and permanently elevated resource constraints on adaptive responses by many species. Even species antagonistic to each other can adaptively improve at the same time in what amounts to a growing economy. These innovations were triggered by external economic stimuli, but through positive feedbacks between organisms and resources, the new partnerships and higher-performing species capitalized on those additional resources by enhancing productivity and consumption still further.

Concluding Remarks

We have argued here that the major assumptions underlying the Red Queen metaphor are either demonstrably false or applicable under very limited circumstances, making the Red Queen an unreliable guide to the dynamics of evolutionary adaptation. Rather than deposing the Red Queen outright, however, we must recognize that evolutionary dynamics vary according to circumstances, and ask under which of those circumstances the Red Queen can still reign.

Under which conditions is the Red Queen metaphor of species "running in place" to compensate for biotically caused environmen-

tal deterioration still applicable? We suggest that Red Queen dynamics can occur in the short term in episodes of strict coevolution, where two species such as a host and its parasite or a host and its mutualistic symbiont adapt to each other. Here the relevant adaptations are highly particular to the interaction. The metaphor may also apply for short time intervals to sexual selection, although in this case the adaptations and the dynamics involve members of only one species. In both cases, however, the Red Queen tires easily, and cannot run in place for long. As in other cases of more general adaptation, Red Queen dynamics quickly reach constraints that cause further adaptation to cease. Indeed, adaptations tailored to a highly specific interaction are just as subject to stasis as any other. Even if that were not the case, there is no reason to believe that short-term Red Queen dynamics increase the risk of extinction for the affected parties.

Like many other metaphors in science, the Red Queen, regardless of her faults and shortcomings, has played a constructive role in the development of ideas about adaptation and extinction. She has, however, outlived her usefulness as a general description of evolutionary dynamics. It is time to move on now that the assumptions and conclusions emanating from the Red Queen's reign have proven unsupportable.

Acknowledgments

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Appendix

The Red Queen Game.—All players or species affect all others evolutionarily in a Red Queen situation. The game here considers effects that are either positive (+) or negative (−) along a phenotypic trait dimension. A positive effect of player A on B means that if player A's trait evolves, then species B's trait will change in the same direction (that is, will either increase or decrease its quantitative value in accordance with change in A), and conversely for negative effects. A three-player game then consists of each player having two effects, one on each of the remaining two players. There are four possible pairs of effects, {++, −−, −+, +−}, and hence 4^3 ($=(2^2)^3$) or 64 possible games. All players' traits have an initial value of zero. The game is initiated by increasing the trait values of species A by one unit, updating the traits of players A, B, and C simultaneously in the second step according to the combination of effects selected for the game, and iterating the system until the evolutionary trajectory of each player has been fully determined. The ensuing game is governed by the following discrete and deterministic rules:

$$a(t+1) = a(t) + \Delta b(t) + \Delta c(t),$$

$$b(t+1) = b(t) + \Delta a(t) + \Delta c(t),$$

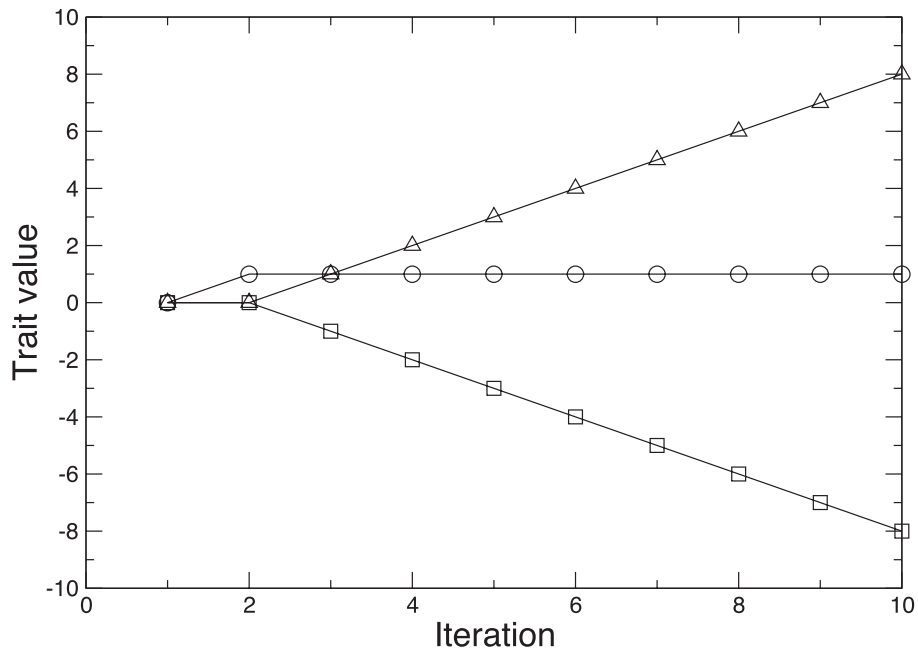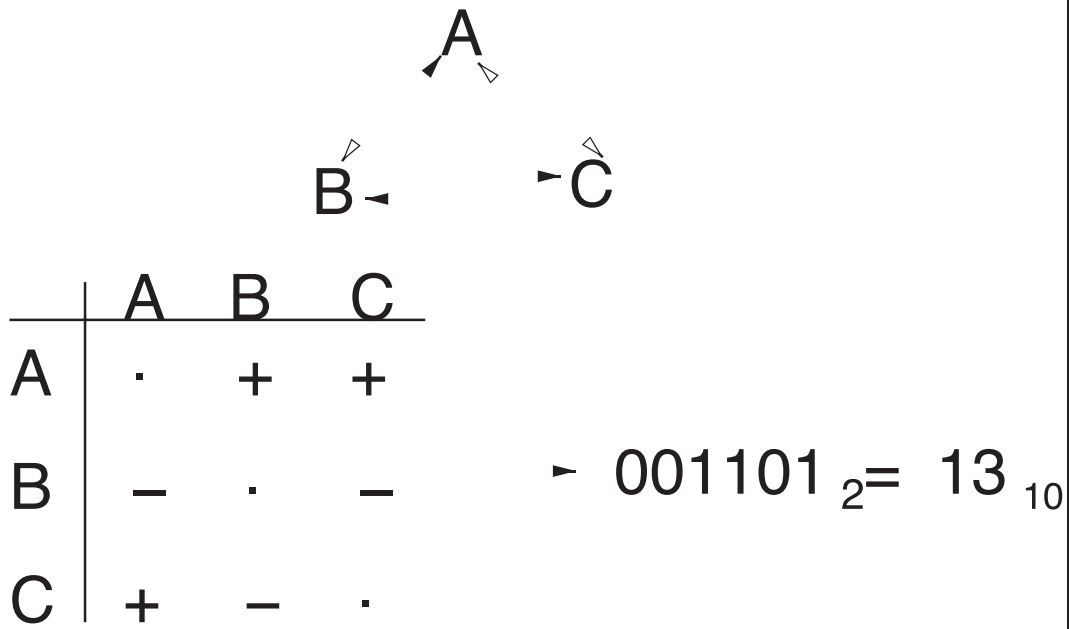|	A	B	C
A	·	+	+
B	−	·	−
C	+	−	·

$001101_2 = 13_{10}$

FIGURE A1. Graphic representation of a three-player Red Queen game. The upper network shows the effects of players A, B, and C on each other, where open arrows indicate positive (0) effects and filled arrows indicate negative (1) effects. This particular game is {++, −−, +−}. An alternative matrix representation is shown below. Writing the interactions as concatenated rows of binary symbols leads to the binary number 001101, which when converted to its decimal integer yields 13, the number of this game. The plot below illustrates the results of the game, with player A (circles) exhibiting stasis, B (squares) exhibiting a decreasing trait, and C (triangles) exhibiting an increasing trait.

TABLE A1. Sixty-four possible three-player Red Queen games, with rules and outcomes. Each game number is a base 10 representation of the rules when expressed as a binary string. Rules are read from left to right as effects of player A on B and C, B on A and C, and C on A and B. 0 represents + (positive effects), and 1 represents – (negative effects). Results show the long-term deterministic outcomes for A, B, and C as a concatenated string, with characters indicating the following: a, adaptation (increasing or decreasing trait value); o, oscillating trait value; and s, stasis.

Game number	Rules	Results
0	000000	aaa
1	000001	sss
2	000010	soo
3	000011	ooo
4	000100	sss
5	000101	ooo
6	000110	ooo
7	000111	saa
8	001000	soo
9	001001	ooo
10	001010	ooo
11	001011	ooo
12	001100	ooo
13	001101	saa
14	001110	ooo
15	001111	ooo
16	010000	saa
17	010001	ooo
18	010010	soo
19	010011	ooo
20	010100	ooo
21	010101	soo
22	010110	sss
23	010111	ooo
24	011000	ooo
25	011001	ooo
26	011010	saa
27	011011	ooo
28	011100	ooo
29	011101	ooo
30	011110	ooo
31	011111	soo
32	100000	saa
33	100001	ooo
34	100010	ooo
35	100011	ooo
36	100100	ooo
37	100101	soo
38	100110	ooo
39	100111	ooo
40	101000	ooo
41	101001	sss
42	101010	saa
43	101011	ooo
44	101100	sss
45	101101	aaa
46	101110	ooo
47	101111	soo
48	110000	ooo
49	110001	ooo
50	110010	soo
51	110011	ooo
52	110100	ooo
53	110101	ooo

TABLE A1. Continued.

Game number	Rules	Results
54	110110	ooo
55	110111	saa
56	111000	soo
57	111001	ooo
58	111010	aaa
59	111011	sss
60	111100	ooo
61	111101	saa
62	111110	sss
63	111111	ooo

$$c(t+1) = c(t) + \Delta a(t) + \Delta b(t),$$

where

$$\Delta a(t) = 0 \text{ if } |a(t) - a(t-1)| = 0,$$

else

$$\Delta a(t) = 1 \text{ if } a(t) > a(t-1),$$

else

$$\Delta a(t) = -1 \text{ if } a(t) < a(t-1),$$

with t being the iterative step. Full determination requires five or fewer iterative steps (Fig. A1).

Examination of the 64 possible games shows that there are three possible evolutionary trajectories for a player: Evolution can be directional (trait always increases or always decreases in value), oscillating between trait increase and decrease, or fully static with no trait change. A full list of all games, with outcomes for each species, is given in Table A1. Game numbers are derived as follows: Designate positive effects as 0 and negative effects as 1. Then the effects of players A, B, and C on each other may be written sequentially and uniquely as a binary string, which, when converted to base 10, yields a unique base 10 designation for the game as used in the main text (Fig. A1).