

Review

The sixth mass coextinction: are most endangered species parasites and mutualists?

Robert R. Dunn¹, Nyeema C. Harris¹, Robert K. Colwell²,
Lian Pin Koh³ and Navjot S. Sodhi^{4,5,*}

¹Department of Biology, North Carolina State University, Raleigh, NC 27607, USA

²Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043, USA

³Institute of Terrestrial Ecosystems, ETH Zürich, CHN G74.2, Universitätstrasse 16, 8092 Zürich, Switzerland

⁴Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Republic of Singapore

⁵Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

The effects of species declines and extinction on biotic interactions remain poorly understood. The loss of a species is expected to result in the loss of other species that depend on it (coextinction), leading to cascading effects across trophic levels. Such effects are likely to be most severe in mutualistic and parasitic interactions. Indeed, models suggest that coextinction may be the most common form of biodiversity loss. Paradoxically, few historical or contemporary coextinction events have actually been recorded. We review the current knowledge of coextinction by: (i) considering plausible explanations for the discrepancy between predicted and observed coextinction rates; (ii) exploring the potential consequences of coextinctions; (iii) discussing the interactions and synergies between coextinction and other drivers of species loss, particularly climate change; and (iv) suggesting the way forward for understanding the phenomenon of coextinction, which may well be the most insidious threat to global biodiversity.

Keywords: mass extinction; coextinction; chains of extinction; secondary extinctions; climate change; emerging diseases

1. INTRODUCTION

Even as the number of extinct and endangered species grows, our understanding of the dynamics and causes of extinction remains incomplete (Brook *et al.* 2008). Debate remains active, with regard to both the most important drivers of extinction and the magnitude of extinction rates (Laurance 2007). Diamond (1989) suggested that there were four main drivers of extinction, which he likened to the four horsemen of the apocalypse. The first three of these—habitat loss, species invasion and overkill—have been relatively well studied. The fourth horseman—cascades of extinctions or coextinctions—has until recently been essentially ignored and is rarely even mentioned in studies of extinction rates (e.g. Pimm & Raven 2000). Coextinction refers to the loss of one species as a result of the extinction of a species it depends on (see data S1, electronic supplementary material) and models suggest that coextinction should be the most common form of species loss (Koh *et al.* 2004; Dunn *in press*).

In an effort to understand whether coextinction is common but ignored, or ignored because it is uncommon, we begin by reviewing models and empirical

examples of coextinction. We then highlight what we need to know about coextinction in order to understand its frequency of occurrence and consequences for biodiversity. Finally, we identify directions for future research on the dynamics of extinction.

2. MODELS

The concept of coextinction was hinted at by Darwin (1862). In Madagascar, he was fascinated by the specialist-moth pollinators of an endemic orchid. ‘If such great moths’, he wrote, ‘were to become extinct in Madagascar, assuredly the *Angraecum* (the orchid) would become extinct’. Both the moths and the orchids appear to live on, but in considering their possible demise, Darwin raised the possibility that coextinctions could occur. Other authors would later echo Darwin’s sentiment (e.g. Diamond 1989), but the potential magnitude of coextinctions was not highlighted until a short paper by Stork and Lyal (1993), who suggested that ‘as a host species goes extinct, so does one or more species of parasites’, such that parasite extinctions might be at least as common as host extinctions.

Koh *et al.* (2004) were the first to attempt to estimate the frequency of coextinctions. They used two approaches. In the first approach, they considered empirical matrices of host species and their affiliate species (e.g. parasites and mutualists), and examined the consequences for affiliate

* Author and address for correspondence: Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Republic of Singapore (dbsns@nus.edu.sg).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.0413> or via <http://rspb.royalsocietypublishing.org>.

diversity of removing, at random, a given number of hosts. This approach makes the assumptions that hosts go extinct randomly, that the sampling of host and affiliate relationships is perfect, and that, as hosts become rare, affiliates do not evolve. This approach revealed a simple pattern: affiliate extinction rates generally depend on two factors, host extinction rates and the host specificity of the affiliate (number of host species an affiliate can survive on). Furthermore, Koh *et al.* (2004) found that nearly all of the host specificity distributions they considered were approximately lognormal, which allowed them to develop a second, heuristic approach of estimating coextinction rates, formalized as a nomographic model whereby \bar{A} , the affiliate extinction probability, is described by the equation

$$\bar{A} = \bar{E}[1 + (0.35\bar{E} - 0.43) \ln s],$$

where \bar{E} is the host extinction probability and s is the mean host specificity of the affiliate species. This second approach, while requiring additional assumptions regarding the host specificity distribution of affiliates, allows coextinction rates to be estimated even for poorly studied affiliate groups. Given a known (or estimated) mean host specificity of an affiliate taxon, it is possible to predict the expected number of coextinctions for a given number of host extinctions (figure 1).

The models of Koh *et al.* (2004) and extensions in Dunn (in press) suggest that not only had coextinctions probably occurred in large numbers during the Holocene (hundreds of species) and during the last hundred years (thousands of species), but coextinction rates will increase in the near future (potentially tens of thousands of species) given current rates of habitat and biodiversity losses. Yet these studies have considered only a proportion of the parasites found on a given host. In figure 2, we consider the proportion of parasite coextinctions as a function of host extinctions for all known parasite taxa (including protozoa, viruses and bacteria) of terrestrial carnivores (order Carnivora) in North America (data S2 in the electronic supplementary material). Based on the first approach of Koh *et al.* (2004), we estimate the number of coextinctions for increasing numbers of randomized extinctions of carnivore host species. We repeated each number of host extinctions (1, 2, 3, etc.) five hundred times to generate the mean number of parasites extinguished for a given number of host extinctions.

For North American carnivores, the predicted number of coextinctions of parasite species is more than an order of magnitude greater than the number of coextinctions of hosts. Extinction of just five North American carnivore species, for example, is predicted to lead to 56 parasite extinctions from carnivores (figure 2; see data S2 in the electronic supplementary material). Globally, the IUCN Red List currently classifies 1141 (25%) mammal species as threatened (Schipper *et al.* 2008). If the numbers and host specificities of parasites on other mammals are similar to those for parasites of North American carnivores, the number of co-endangered parasite species, including mites and protists, may be in the tens of thousands. Finally, a similar analysis performed on angiosperms and their herbivores suggests the current coendangerment of 200 000 plant-dependent animals (data S3 in the electronic supplementary material). In short, coextinction models predict that tens of thousands of parasites and mutualists may have already

succumbed to coextinction and that most endangered host species have coendangered obligates.

3. EVIDENCE (AND THE PARADOX)

Although tens or even hundreds of thousands of coextinctions and coendangered species are predicted on the basis of coextinction models, few recent coextinctions have been empirically documented (reviewed by Dunn in press). It is noteworthy that several of the best-known examples have either been shown to be false (the passenger pigeon lice are alive and apparently common) or are poorly studied. Other evidence from coextinction comes from the fossil record, where widespread extinctions of plants are associated with extinctions of insects. Labandeira *et al.* (2002), for example, found that specialist herbivore extinctions followed host plant extinctions. Some authors have taken this result as strong evidence of the historical significance of coextinctions (Bascompte & Jordano 2007). However, Labandeira *et al.* (2002) were quick to point out that the links in their own results between host extinctions and herbivore extinctions are correlative and do not preclude alternative explanations.

Only one study has taken the step of considering which parasite species are endangered, based on lists of hosts and their parasites and the conservation status of hosts. Thacker *et al.* (2006) found that 24 aphid or scale species (out of 2728 considered) are restricted to threatened tree species and hence are coendangered (or perhaps co-threatened). It is noteworthy that none of the species Thacker *et al.* (2006) found to be coendangered is listed by the IUCN Red List, an indication of more fundamental problems with the listing of small species and insects in particular (Dunn 2005). Just one parasite species is listed in the IUCN Red List as endangered because of the rarity of its host, the pygmy hog-sucking louse (*Haematopinus oliveri*), known only from the world's smallest (and rarest) pig (Whiteman & Parker 2005).

To date, the general evidence for coextinction presents a conundrum. Models indicate coextinctions should be extremely common, in fact the most common form of extinction, but empirically they appear rare. What is going on?

4. WHERE ARE THE MISSING COEXTINCTIONS?

There are two potential resolutions to the discrepancy between predicted and empirical numbers of coextinctions. Coextinctions may be occurring in large numbers, undetected. Given that most parasites and mutualists are small and poorly studied, such undocumented extinctions are entirely possible. Alternatively, host–parasite or mutualist–mutualist networks may be more stable than is assumed in coextinction models. Measurement error in estimating host specificity, poor assumptions about the adaptability of parasites or mutualists and loss of parasites and mutualists from rare (but still extant) hosts may all influence coextinction rates. We consider each in turn.

(a) *Measuring host specificity*

In models of coextinction, whether or not the extinction (or even rarity) of a host leads to coextinction, depends on few things. Arguably, the most important determinant is the host specificity of the parasite in question. At the heart of the concept of host specificity is the idea of

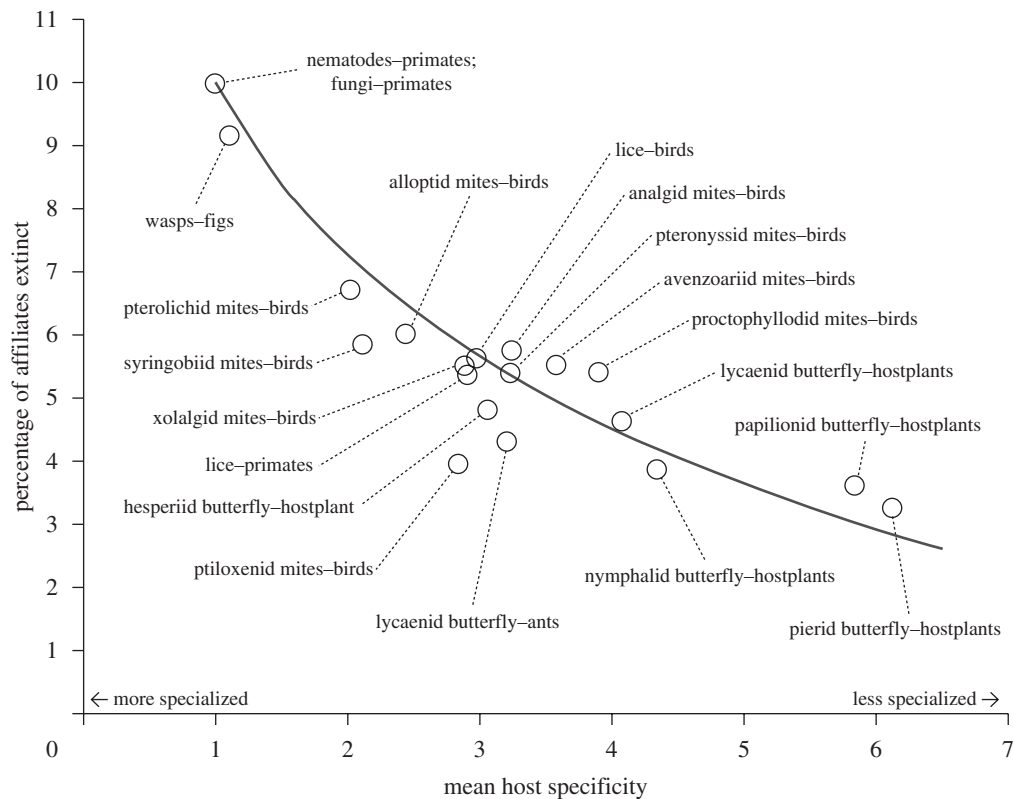


Figure 1. Relationship between mean host specificity (number of host species associated with a given affiliate species) and the proportion of affiliate species estimated to go extinct given that 10 per cent of host species go extinct. Open circles represent affiliate extinction rates derived from simulated random extinction of host species based on empirical affiliate–host matrices; the solid line represents predicted affiliate extinction rates based on a nomographic model (Koh *et al.* 2004).

tradeoffs for parasites or mutualists between the traits that enable survival on alternative hosts (Rausher 1984; Jaenike 1990; Joshi & Thompson 1995). A trait that allows a parasite to do well on (or simply find) one host can compromise its ability to do so on another (Joshi & Thompson 1995). For example, it has been argued that feather lice specialized on cave swiftlet (*Apodiformes: Collocaliini*) species with thin feather barbs cannot hold on to the feathers of swiftlet species with thicker feather barbs and vice versa. When tradeoffs are strong, survival on non-preferred hosts approaches zero (Tompkins & Clayton 1999).

Ideally, one would like to estimate host specificity distributions by studying the fitness of parasites on each of their potential hosts. In practice, host specificity is usually estimated on the basis of a limited number of samples (usually observations of parasites feeding or even just found on hosts) across a limited number of potential hosts. As a consequence, true host specificity may differ greatly from what is assumed in coextinction models. More study often, but not always, reveals that parasites are more generalist than assumed (Clayton & Price 1999; Price *et al.* 2000; Dunn 2002). In some cases, species are found to feed only on a subset of those hosts from which they have been recorded (Shaw 1994) or occasionally disperse to non-preferred hosts, but once on those hosts have reduced fitness or are unable to breed (e.g. Tompkins & Clayton 1999). Alternatively, well-sampled generalist ‘species’ may actually consist of a number of hard-to-distinguish specialists, as recent molecular genetic studies have revealed to often be the case (e.g. Poulin & Keeney 2008), and even these molecular genetic techniques may reveal only part of the story.

Because parasite species vary genetically, it is not the mean host specificity within a species that is relevant to understanding coextinction, but is instead some measure of the range of variation in host specificities. If some individuals in a population are less host specific, they may, in effect, protect populations against coextinction. In the path of coextinction, much depends on how much variation populations have for finding and feeding on hosts. As a final twist, in some relationships, particularly mutualisms, partners may be not be obligate in their need for each other. For example, at least some plants that require a specific pollinator species can also reproduce clonally, have great longevity or can engage in facultative self-pollination (Bond 1994).

(b) Evolution

Imagine, G. C. Williams once said, there was a flea found only on passenger pigeons (Maynard Smith 1977). ‘As the pigeons became rarer, the fleas would have been under stronger and stronger selection pressure to exploit an ever-dwindling resource. But no matter how rapidly they improved their adaptation to their way of life, nothing could prevent their extinction’. When parasites or mutualists are inescapably tied to their hosts and cannot disperse, Williams is clearly right. But fleas, like many parasites and mutualists, can disperse from host to host. If parasite and mutualist populations have genetic variation that permits some individuals to find and survive on alternative hosts (hosts not assessed in estimating host specificity), then those parasites may initially persist with reduced fitness even when the primary hosts go extinct. It is on those

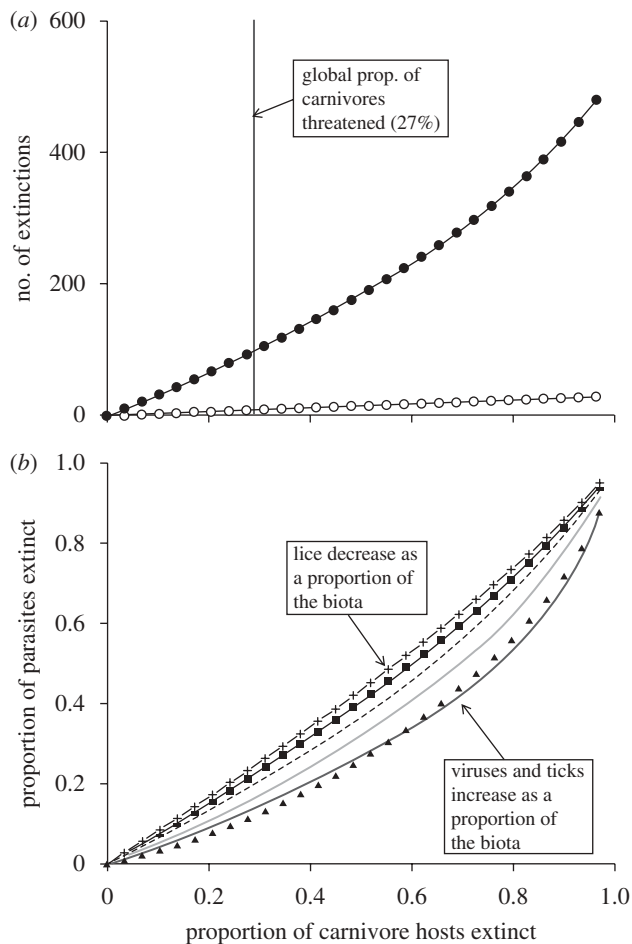


Figure 2. The number of parasite and host extinctions and the proportion of parasites extinct as a function of the proportion of hosts extinguished. (a) The vertical line indicates the current proportion of carnivore hosts listed as threatened (IUCN 2008), filled circles the parasite extinctions (max.=518) and open circles the host extinctions (max.=29). (b) Each line represents a parasite taxon (triangles, viruses; squares and black solid line, trematodes; black solid line, ticks; grey solid line, nematodes; crosses and solid line, lice; dashed line, bacteria). Lines show the number (a) or proportion (b) of parasites extinct after random extinctions of different numbers of hosts. In (b), select parasite taxa are shown, since most taxa (including the result when all taxa are considered together) fall on a line coincident with the line shown for nematodes. Data in both panels are for all North American carnivores.

new hosts that selection 'will be stronger and stronger' for adaptation. Whether species persist in the long term on new hosts will depend on how quickly they are able to evolve to increase their fitness. Understanding the likelihood that a rare parasite or mutualist will adapt to an initially inferior new host is difficult. On the one hand, growing numbers of studies find evidence of rapid evolution of the ability to survive and reproduce on new hosts (host shifts) or, more generally, new foods or environments (Woolhouse *et al.* 2005; Jones *et al.* 2008; Smith & Bernatchez 2008; Zaffarano *et al.* 2008). Yet, in order to understand the significance of evolutionary responses to estimates of coextinction rates, one needs to know how often such events occur.

One measure of the historical frequency of host shifts is the conservatism of host specificity within clades. All else

being equal, if parasites or mutualists tend to adapt quickly to novel or alternative hosts when their primary hosts become rare, then host specificity should vary greatly within clades. Conversely, if host specificity evolves slowly (as is the case for many traits; e.g. Peterson *et al.* (1999)), species within clades should tend to be similar with regard to their host specificity. To date, empirical studies of fleas (Mouillot *et al.* 2006; Poulin *et al.* 2006), helminths (Mouillot *et al.* 2006) and networks of mutualists (Rezende *et al.* 2007) suggest that host specificity, and more generally the number of species with which each species interacts, is moderately well conserved within clades, such that the rapid evolution of a more generalist lifestyle or rapid host shifts in light of host rarity may be relatively uncommon. Ultimately, however, the conservatism of a clade depends both on its genetic variation for traits related to host specificity and on the costs and benefits of being a generalist versus a specialist. Clades may differ in the extent to which they show conservatism in host specificity simply as a result of differences in the extent to which there has been selection for generalism. Differences among clades in the conservatism of host specificity could therefore reflect differences in the genetics of the traits associated with specialization or differences in the extent to which those clades have been confronted with selection pressures (such as host loss) that favour generalism. In this regard, it is tempting to regard examples in which host specificity is not conserved (Poulin *et al.* 2006), or where generalism is a derived trait (Stireman 2005), as evidence of clades in which there has been recent selection for generalism, perhaps because of changes in host dynamics.

(c) *Population dynamics and coendangerment*

Nearly all models of coextinction rates (as opposed to dynamics) are incidence models. Parasites or mutualists are assumed to go extinct when all of their hosts go extinct. However, the truth may be that in some cases parasites and mutualists go extinct even before their hosts (de Castro & Bolker 2005). Where rare host species have been well surveyed for parasites, the most host-specific parasites tend to be among the rarest of the species recorded (Millan *et al.* 2007). Perhaps as a consequence, threatened primates tend to have fewer parasite species than do more common primates (Altizer *et al.* 2007). Similarly, extinction of even a single host population could lead to coextinctions, if some parasites are narrowly restricted in terms of their geographical ranges. To the extent that parasites are lost from rare hosts, incidence-based estimates of coextinction rates could actually be underestimates.

(d) *Chains of extinction and trophic cascades*

Attempts to estimate the empirical frequency of coextinctions have tended to focus on the extinctions that result directly from the loss of a mutualist partner or host. However, extinctions may cascade beyond species directly dependent on the extinguished species (e.g. Dunn *in press*). Diamond *et al.* (1989), an example of such cascades the extinction of top predators on Barro Colorado Island (Panama), which caused an increase in the population sizes of meso-predators and, as a consequence,

extinctions of ground nesting birds. However, cascades of extinctions may also follow from coextinctions. Also on Barro Colorado Island, the local extinction of army ants led to the coextinction of a species of ant-following bird (Harper 1989). That bird is, in turn, exploited by host-specific lice (Price & Clayton 1996; Price *et al.* 2006) that may have gone locally extinct.

A body of research often called network theory has considered which aspects of communities influence their proneness to trophic cascades (in which changes at one trophic level propagate to others) and chains of extinctions. This large literature (reviewed in Bascompte & Jordano 2007) outlines many scenarios in which the order of extinctions in food webs or mutualist networks (Petchey *et al.* 2008) and other attributes of the structure of mutualistic networks affect rates of extinctions and extinction dynamics. Just as in the study of coextinction, the factors that most influence extinction dynamics in models tend to be measures of host specificity (species degree) and the number of interacting species. And just as for coextinctions, whether such cascades are empirically an important general aspect of extinction dynamics or merely an interesting theoretical possibility occasionally borne out in reality remains poorly understood.

It remains conceivable that coextinction is the most common form of extinction. It is also possible, however, that many parasites and mutualists are more resistant to the loss of their hosts or partners than is immediately apparent.

5. INTERACTIONS AND SYNERGIES: RIDING WITH THE OTHER HORSEMEN

One aspect of coextinction that distinguishes it from other drivers of extinction is that it rarely acts alone. Except perhaps for cases in which host populations naturally decline, coextinction acts in concert with other drivers of extinction—Diamond's other horsemen. Thus, coextinction dynamics are strongly influenced by habitat loss, overkill, invasion and potentially, by climate change—the fifth horseman. Overkill and invasion can lead to coextinction, but their effects are primarily direct (i.e. host loss leads to parasite or mutualist loss). Habitat loss and climate change can either have direct effects on coextinction or interact with coextinction.

(a) *Habitat loss*

Habitat loss and degradation have directly or indirectly resulted in many extinctions (Brook *et al.* 2003). In the dominant model of species loss with reductions in the area of habitat, population sizes of species are related to available resources, which are in turn a function of habitat area (Sekercioglu *et al.* 2002). At lower trophic levels, area and resource availability are closely linked. For plants, the two variables are essentially equivalent. The magnitude of coextinctions may be captured within this framework, with coextinctions simply representing a special case of extinction because of resource loss. For example, obligate ant-following birds (e.g. the rufous-throated antbird, *Gymnopithys rufigula*), restricted to the Neotropics, disappear from forest fragments following the local extinctions of the army ants on which they depend and reappear if the ants are experimentally re-introduced (Harper 1989). The ants appear to disappear from fragments, at least in

part, as a function of loss of habitat area and food resources, and so the coextinction of ant-birds is ultimately a consequence of the loss of habitat area. What is missing from the habitat-loss model, however, is an understanding of which species go extinct, which seems influenced in this case and in others (e.g. Koh *et al.* 2004) by coextinction. It may often be true that habitat loss is the ultimate cause of the extinction of parasites or mutualists, but coextinction, in effect, determines which species are lost.

(b) *Climate change*

Just as with habitat loss, host–parasite or mutualist–partner dynamics interact in complex ways with the direct effects of climate change. Global climate change has left a clear imprint on the distribution of species over recent decades (Walther *et al.* 2002; Parmesan & Yohe 2003). Shifts in plant phenology, in the timing of migration and reproduction in birds, and in emergence times in insects are early warnings of biological responses to warming. Geographical range shifts follow as demography responds more slowly to changing fitness differentials between the warmer edges and cooler edges of species ranges (Franco *et al.* 2006). At temperate and subtropical latitudes, where temperature declines steeply with elevation and more slowly, but steadily, with increasing latitude, insect, vertebrates and plants have shifted polewards (Parmesan 2006) and higher up mountain slopes (e.g. Wilson *et al.* 2005, 2007; Moritz *et al.* 2008). Within the tropics, because there is virtually no latitudinal temperature gradient between 21° N and 21° S, range shifts for terrestrial species can be expected to be almost exclusively upslope, where such shifts are topographically feasible and not interdicted by habitat fragmentation (Colwell *et al.* 2008; Raxworthy *et al.* 2008; Chen *et al.* 2009).

On the one hand, if hosts and parasites or mutualists and their partners shift together with climate change, there may be little interaction between climate change and coextinction. But what can we realistically expect for species closely linked by ecological interactions under climate-change scenarios? Will their ranges shift, lock-step, polewards at higher latitudes and upslope at all latitudes? Studies of the elevational distribution of plants over Pleistocene glacial cycles, based on pollen cores and plant microfossils, speak eloquently against this view of what one writer (Marris 2007) dubbed 'the Escalator Effect'. At temperate latitudes, neither plant communities during glacial maxima nor transitional communities during cooling and warming periods come near matching contemporary plant communities of the current warm interglacial (Davis & Shaw 2001). At mid-elevations in tropical wet forests, pollen cores show a shuffling of plant communities with warming and cooling glacial cycles that indicates an idiosyncratic shift of individual species, albeit with the expected net upward shift in warm periods and downward shifts in cool periods (Bush 2002; Bush & Hooghiemstra 2005). Idiosyncratic variation in range shifts among formerly sympatric species has now been documented for elevational shift among temperate vertebrates (Moritz *et al.* 2008) and insects (Wilson *et al.* 2007). Such idiosyncratic shifts increase the probability that hosts will move faster,

more slowly, or in different directions than the species that depend on them.

Regardless of the specifics of the outcome, empirical patterns of range shift argue against the facile assumption that closely interacting pairs or sets of species will remain together simply by tracking climate zones across the map. Indeed, many authors have warned that contemporary communities of species will be disassembled by individualistic range shifts (Bush 2002; Walther *et al.* 2002; Parmesan 2006; Wilson *et al.* 2007). In the case of mutualists and their partners or parasites and their hosts, such individual range shifts may result in coextinctions. Importantly, such coextinctions will not be predicted on the basis of models of host responses to climate change alone or even necessarily when both hosts and parasites or different mutualist partners are modelled separately. Together, these facts and projections suggest that climate change may interact with coextinction to disproportionately affect closely interacting species, either by direct coextinction of one partner, following the climate-driven extinction of the other, or by dramatically lowered fitness of both partners, when their response to climate change is discordant.

6. CONSEQUENCES (WHY SHOULD WE CARE?)

Discussions of coextinction consistently raise the question, 'why should we care?', particularly because most coextinction events are likely to target parasites (e.g. figure 1; Dunn *in press*). Given that the extinction crisis is dire and conservation resources are scarce, one might argue that we should ignore parasites. Albeit through inaction rather than conscious decision, this is the approach that has been taken to date. But the choice is not nearly this simple. Although, in the popular view, parasites tend to lack charisma, their loss bears consequences perhaps just as great as those of the loss of their hosts. We consider each of the potential consequences of coextinction in turn.

(a) *Loss of biological diversity and diversification*

Perhaps 50 per cent of known species and a larger percentage of unnamed species have relatively host-specific relationships in at least one of their life stages (Poulin & Morand 2000). As such, to the extent that we care about 'biodiversity', much of biodiversity and consequently diversification is influenced by coextinction dynamics. Further, for a given number of species, parasites are phylogenetically much more diverse than are their hosts, whether we consider mammals and their parasites (e.g. herein) or potentially even bacteriophages and their bacterial hosts (Breitbart *et al.* 2003). Coextinctions may influence not only parasite and mutualist diversification, but also that of hosts. It has been plausibly argued (Nunn *et al.* 2004) that parasites facilitate host diversification through processes associated with sexual selection, such that loss of parasites might even reduce host diversification rates.

(b) *Loss of history*

Extinctions of hosts are clustered both in terms of the traits that rare hosts share (large body size, slow reproduction, etc.) and the relatedness of hosts (e.g. Rezende *et al.* 2007). Such phylogenetic clumping of extinctions has the consequence of extinguishing more evolutionary history

(measured in terms of phylogenetic branch lengths or the differences in the nucleotide sequence between species) than would random extinction (Purvis *et al.* 2000). Like host extinction, affiliate extinctions are likely to be phylogenetically non-random. First, to the extent that host and affiliate phylogenies are similar, the extinction of related parasites will tend to lead to the extinction of related hosts (e.g. Rezende *et al.* 2007). In strict co-cladogenesis, for example, host and parasite (or mutualist and partner) phylogenies match identically or nearly so (Light & Hafner 2008). Additionally (and just as for hosts), the traits related to host specificity may be conserved phylogenetically, such that even if host extinction were phylogenetically random, affiliate extinction might not be. As a consequence, the loss of evolutionary history by coextinction is very likely to be greater than the loss expected were species to go extinct at random with respect to their phylogenetic position.

(c) *Loss of traits*

If coextinctions are phylogenetically clustered, it is likely that coextinction will produce non-random loss of traits. One can imagine a suite of parasite and mutualist traits (other than host specificity) that might be at greater risk of loss during coextinctions. Species at risk of coextinction might be expected to be larger because, at least in some taxa, rare hosts tend to be larger and large hosts have large parasites (Lindenfors *et al.* 2007). They might also be expected to have longer generation times (Cardillo *et al.* 2008) or higher trophic position (such as hyperparasitoids), all things being equal. Trait extinction might be non-random even if host extinction were phylogenetically random, as long as host extinction is in some way related to host traits (such as size) that influence parasite or mutualist traits.

The most obvious consequences of coextinctions are evident in examples of mutualism, as suggested, for example, by the loss of food production with declines in threatened pollinators. Yet, losses of parasites can also have negative consequences, even for humans or the species we tend to care more about. In rare hosts, we speculate that losses of specialist parasites may predispose hosts to infection by their generalist competitors or emergent parasites. In line with our speculation, most of the cases in which diseases have caused significant mortality in rare species are attributable to generalist rather than specialist parasites (Dobson & Foufopoulos 2001; Gog *et al.* 2002; de Castro & Bolker 2005). While we know of no clear examples in which the prevalence of the generalist disease or parasite can be directly linked to the absence of the specialist, the mere possibility of such cases should give pause to thought to those actively removing parasites from captive rare species. One wonders whether the few remaining California condors (*Gymnogyps californianus*), from which the host-specific parasites appear to have been intentionally removed (e.g. Koh *et al.* 2004), are really bereft of parasites or whether those host-specific parasites have been replaced by generalists, with equal or greater health impacts. Yet, current practices in most zoos require and uncritically accept the practice of parasite removal from rare hosts.

Changes in the composition of parasite biotas may affect captive-bred animals, but they could also have

effects on host assemblages more generally. In considering the parasites of North American carnivores, for example, we found that, although many carnivore parasites have similar host specificities and hence similar probabilities of coextinction for a given level of host extinction, some parasite taxa are much more and others much less host specific. Lice, for example, are very host specific, a pattern true within our carnivore dataset (figure 2) and apparently more generally (figure 1). However, ticks and viruses are much less host specific, both for carnivore parasites (figure 2) and for the other mammal parasites that have been considered (Pedersen *et al.* 2005). As a consequence, host extinctions will tend to shift the parasite biota towards a composition more dominated by ticks and viruses (and less by lice) than would otherwise be the case. This shift in composition could severely impact both host species conservation and human health, given that most emerging parasites are viruses (Woolhouse & Gowtage-Sequeria 2005) and ticks are efficient vectors of disease (Gage *et al.* 2008). Similar consequences may be expected to occur within taxa (for example within bacteria), wherein generalist parasites, a non-random set of species within the biota, persist and specialists disappear. Many parasites of carnivores and of mammals more generally are zoonotic (have the ability to infect humans). Because zoonotic parasites have a host specificity of at least two (humans + some carnivores in our dataset), they are unlikely to be the first taxa to go extinct. As such, it seems likely that host extinction will drive the parasite fauna towards a greater dominance of zoonotic parasites.

Related to the potential consequences of removing specialist parasites from rare hosts is the associated problem of where generalist parasites go when their rarest hosts go extinct. Imagine for a moment that each vertebrate has a specialist parasite species (on average not an unlikely scenario). Schipper *et al.* (2008) estimated that more than 1000 (roughly 1 in 5) mammals are at risk of extinction. If, as simple models suggest, the host-specific parasites of those mammals are dependent only on those species, then there are roughly 1000 mammal parasite species at risk of extinction through co-endangerment. If, on the other hand, those specialists are able, in some way, to find new hosts, there are now 1000 mammal parasites, once confined to their hosts, switching onto alternative hosts. Those alternative hosts are, in many cases, likely to be humans or human domesticates, which together represent the vast majority of all individual mammals on Earth. It is possible that the increase in the rate of emerging pathogens and parasites both for humans and for domesticates is in part a consequence of the declining abundance of those species' 'natural' hosts. Many emerging parasites and pathogens are known to have undergone host shifts (Woolhouse *et al.* 2005). A number of these emerging diseases have shifted from relatively rare species to humans (e.g. the Nipah virus from bats to pigs and humans). In shifting to novel hosts, parasites and pathogens often have increased virulence (because of a lack of coevolutionary relationship with the new hosts), such that these shifts may be of great epidemiological concern (Woolhouse *et al.* 2005). Either scenario—whether the loss of parasites because of coextinction or the acquisition of new parasites by abundant hosts—is obviously a problem.

7. WAYS FORWARD

We find ourselves with a superficially paradoxical situation. Models continue to predict that many thousands of coextinctions must be occurring (a mass coextinction event), but only a handful of coextinctions have been documented. These results relate not only to the current extinction event but also, presumably, to historical mass extinctions. It may be that coextinctions are very common, both in the context of contemporary extinctions and more generally (Labandeira *et al.* 2002), but we have missed most of them. At the opposite extreme, it may be that coextinctions are actually rare and that parasites and mutualists adapt more quickly and are more plastic than we give them credit for. The truth almost certainly lies between these two extremes, but just where is unclear. Great uncertainty exists in the predictions of the probable number of extinctions of vertebrates such as birds or mammals (e.g. Cardillo *et al.* 2008), but by far the greatest uncertainty in the total number of species likely to be lost is in the smaller species, among which parasites and specialist mutualists number in the millions.

Whether many or few coextinctions are occurring bears on our understanding of both historical and current extinction dynamics, with important implications for the health of humans and persistence of rare hosts. We suggest three steps towards understanding the significance of coextinctions. We need to search harder for empirical examples of coextinctions and document them better when found. We need to better understand the host specificity of entire populations of parasites and mutualists. How much variation is there among individuals? On what does that variation depend? Finally, we need to develop better ways to integrate the effects of Diamond's four (plus one) drivers of extinction on wild species. Climate change, habitat loss, species invasion, overkill and coextinctions all interact. But what are the dynamics of these interactions? We know that whatever factors influence hosts also indirectly influence their parasites. Is the reverse also true? If specialist parasites are lost on rare hosts, are there costs to the hosts? Given our current and preliminary understanding of coextinction, one can imagine scenarios in which coextinctions amplify dramatically the effects of host extinctions, but one can also imagine scenarios in which parasites and mutualists, through both redundancy and rapid evolutionary rates, stabilize and minimize the effects of host loss. Much remains to be learned.

L.P.K. was supported by an ETH fellowship (FEL-05 08-2) and a Swiss National Science Foundation research grant (105314_125186/1). R.K.C. was supported by US NSF (DEB-0639979). R.R.D. was supported by a DOE-NICCR grant and DOE-PER grant DE-FG02-08ER64510. N.C.H. was supported by a Department of Forestry and Environmental Resources fellowship at North Carolina State University. N.S.S. was supported by the Sarah and Daniel Hrdy Fellowship.

REFERENCES

- Altizer, S., Nunn, C. L. & Lindenfors, P. 2007 Do threatened hosts have fewer parasites? A comparative study in primates. *J. Anim. Ecol.* **76**, 304–314. (doi:10.1111/j.1365-2656.2007.01214.x)
- Bascompte, J. & Jordano, P. 2007 Plant-animal mutualistic networks: the architecture of biodiversity. *Annu. Rev.*

- Ecol. Evol. Syst.* **38**, 567–593. (doi:10.1146/annurev.ecolsys.38.091206.095818)
- Bond, W. J. 1994 Do mutualisms matter: assessing the impact of pollinator and disperser disruption on plant extinction. *Phil. Trans. R. Soc. Lond. B* **344**, 83–90. (doi:10.1098/rstb.1994.0055)
- Breitbart, M., Hewson, L., Felts, B., Mahaffy, J. M., Nulton, J., Salamon, P. & Rohwer, F. 2003 Metagenomic analyses of an uncultured viral community from human feces. *J. Bacteriol.* **185**, 6220–6223. (doi:10.1128/JB.185.20.6220-6223.2003)
- Brook, B. W., Sodhi, N. S. & Ng, P. K. L. 2003 Catastrophic extinctions follow deforestation in Singapore. *Nature* **424**, 420–423. (doi:10.1038/nature01795)
- Brook, B. W., Sodhi, N. S. & Bradshaw, C. J. A. 2008 Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**, 453–460. (doi:10.1016/j.tree.2008.03.011)
- Bush, M. B. 2002 Distributional change and conservation on the Andean flank: a palaeoecological perspective. *Global Ecol. Biogeogr.* **11**, 463–473. (doi:10.1046/j.1466-822X.2002.00305.x)
- Bush, M. B. & Hooghiemstra, H. 2005 Tropical biota responses to climate change. In *Climate change and biodiversity* (eds T. E. Lovejoy & L. Hannah), pp. 125–137. New Haven, CT: Yale University Press.
- Cardillo, M., Mace, G. M., Gittleman, J. L., Jones, K. E., Bielby, J. & Purvis, A. 2008 The predictability of extinction: biological and external correlates of decline in mammals. *Proc. R. Soc. B* **275**, 1441–1448. (doi:10.1098/rspb.2008.0179)
- Chen, I. C., Shiu, H. J., Benedick, S., Holloway, J. D., Cheye, V. K., Barlow, H. S., Hill, J. K. & Thomas, C. D. 2009 Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proc. Natl Acad. Sci. USA* **106**, 1479–1483. (doi:10.1073/pnas.0809320106)
- Clayton, D. H. & Price, R. D. 1999 Taxonomy of New World Columbicola (Phthiraptera: Philopteridae) from the Columbiformes (Aves), with descriptions of five new species. *Ann. Entomol. Soc. Am.* **92**, 675–685.
- Colwell, R. K., Brehm, G., Cardelus, C. L., Gilman, A. C. & Longino, J. T. 2008 Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* **322**, 258–261. (doi:10.1126/science.1162547)
- Darwin, C. 1862 *The various contrivances by which orchids are fertilized by orchids*. London, UK: John Murray.
- Davis, M. B. & Shaw, R. G. 2001 Range shifts and adaptive responses to Quaternary climate change. *Science* **292**, 673–679. (doi:10.1126/science.292.5517.673)
- de Castro, F. & Bolker, B. 2005 Mechanisms of disease-induced extinction. *Ecol. Lett.* **8**, 117–126. (doi:10.1111/j.1461-0248.2004.00693.x)
- Diamond, J. M. 1989 Overview of recent extinctions. In *Conservation for the twenty-first century* (eds D. Western & M. Pearl), pp. 37–41. Oxford, UK: Oxford University Press.
- Diamond, J. M., Ashmole, N. P. & Purves, P. E. 1989 Present, past and future of human-caused extinctions [and discussion]. *Proc. R. Soc. Lond. B* **325**, 469–477.
- Dobson, A. & Foufopoulos, J. 2001 Emerging infectious pathogens of wildlife. *Phil. Trans. R. Soc. Lond. B* **356**, 1001–1012.
- Dunn, R. R. 2002 On parasites lost-and found: passenger pigeon lice rediscovered. *Wild Earth* **12**, 28–31.
- Dunn, R. R. 2005 Modern insect extinctions, the neglected majority. *Conserv. Biol.* **19**, 1030–1036.
- Dunn, R. R. In press Coextinction: anecdotes, models, and speculation. In *Holocene extinctions* (ed. S. Turvey). Oxford, UK: Oxford University Press.
- Franco, A. M. A., Hill, J. K., Kitchke, C., Collingham, Y. C., Roy, D. B., Fox, R., Huntley, B. & Thomas, C. D. 2006 Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biol.* **12**, 1545–1553. (doi:10.1111/j.1365-2486.2006.01180.x)
- Gage, K. L., Burkot, T. R., Eisen, R. J. & Hayes, E. B. 2008 Climate and vectorborne diseases. *Am. J. Prevent. Med.* **35**, 436–450. (doi:10.1016/j.amepre.2008.08.030)
- Gog, J., Woodroffe, R. & Swinton, J. 2002 Disease in endangered metapopulations: the importance of alternative hosts. *Proc. R. Soc. Lond. B* **269**, 671–676. (doi:10.1098/rspb.2001.1667)
- Harper, L. H. 1989 The persistence of ant-following birds in small Amazonian forest fragments. *Acta Amazon.* **19**, 249–264.
- IUCN 2008 *An analysis of mammals on the 2008 IUCN Red List*. Conservation International, Arizona State University, Texas A&M University, University of Rome, University of Virginia, Zoological Society of London.
- Jaenike, J. 1990 Host specialization in phytophagous insects. *Annu. Rev. Ecol. Syst.* **243**–273. (doi:10.1146/annurev.es.21.110190.001331)
- Jones, K. E., Patel, N. G., Levy, M. A., Storeygard, A., Balk, D., Gittleman, J. L. & Daszak, P. 2008 Global trends in emerging infectious diseases. *Nature* **451**, 990–994. (doi:10.1038/nature06536)
- Joshi, A. & Thompson, J. N. 1995 Trade-offs and the evolution of host specialization. *Evol. Ecol.* **9**, 82–92. (doi:10.1007/BF01237699)
- Koh, L. P., Dunn, R. R., Sodhi, N. S., Colwell, R. K., Proctor, H. C. & Smith, V. S. 2004 Species coextinctions and the biodiversity crisis. *Science* **305**, 1632–1634. (doi:10.1126/science.1101101)
- Labandeira, C. C., Johnson, K. R. & Wilf, P. 2002 Impact of the terminal Cretaceous event on plant-insect associations. *Proc. Natl Acad. Sci. USA* **99**, 2061–2066. (doi:10.1073/pnas.042492999)
- Laurance, W. F. 2007 Have we overstated the tropical biodiversity crisis? *Trends Ecol. Evol.* **22**, 65–70. (doi:10.1016/j.tree.2006.09.014)
- Light, J. E. & Hafner, M. S. 2008 Codivergence in heteromyid rodents (Rodentia: Heteromyidae) and their sucking lice of the genus *Fahrenholzia* (Phthiraptera: Anoplura). *Syst. Biol.* **57**, 449–465. (doi:10.1080/10635150802169610)
- Lindfors, P., Nunn, C. L., Jones, K. E., Cunningham, A. A., Sechrest, W. & Gittleman, J. L. 2007 Parasite species richness in carnivores: effects of host body mass, latitude, geographical range and population density. *Global Ecol. Biogeogr.* **16**, 496–509. (doi:10.1111/j.1466-8238.2006.00301.x)
- Marris, E. 2007 The Escalator Effect. *Nature Reports Climate Change*. (doi:10.1038/climate.2007.70)
- Maynard Smith, J. 1977 The limitations of evolution theory. In *The encyclopaedia of ignorance* (eds R. Duncan & M. Weston-Smith), pp. 235–242. London, UK: Pergamon.
- Millan, J., Ruiz-Fons, F., Marquez, F. J., Viota, M., Lopez-Bao, J. V. & Mateo, M. P. M. 2007 Ectoparasites of the endangered Iberian lynx *Lynx pardinus* and sympatric wild and domestic carnivores in Spain. *Med. Vét. Entomol.* **21**, 248–254.
- Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C. & Beissinger, S. R. 2008 Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* **322**, 261–264. (doi:10.1126/science.1163428)
- Mouillot, D., Krasnov, B. R., Shenbrot, G. I., Gaston, K. J. & Poulin, R. 2006 Conservatism of host specificity in parasites. *Ecography* **29**, 596–602. (doi:10.1111/j.0906-7590.2006.04507.x)
- Nunn, C. L., Altizer, S., Sechrest, W., Jones, K. E., Barton, R. A. & Gittleman, J. L. 2004 Parasites and the

- evolutionary diversification of primate clades. *Am. Nat.* **164**, S90–S103.
- Parmesan, C. 2006 Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669. (doi:10.1146/annurev.ecolsys.37.091305.110100)
- Parmesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42. (doi:10.1038/nature01286)
- Pedersen, A. B., Altizer, S., Poss, M., Cunningham, A. A. & Nunn, C. L. 2005 Patterns of host specificity and transmission among parasites of wild primates. *Int. J. Parasitol.* **35**, 647–657. (doi:10.1016/j.ijpara.2005.01.005)
- Petchey, O. L., Eklof, A., Borrvall, C. & Ebenman, B. 2008 Trophically unique species are vulnerable to cascading extinction. *Am. Nat.* **171**, 568–579.
- Peterson, A. T., Soberon, J. & Sanchez-Cordero, V. 1999 Conservatism of ecological niches in evolutionary time. *Science* **285**, 1265–1267. (doi:10.1126/science.285.5431.1265)
- Pimm, S. L. & Raven, P. 2000 Biodiversity: extinction by numbers. *Nature* **403**, 843–845. (doi:10.1038/35002708)
- Poulin, R. & Keeney, D. B. 2008 Host specificity under molecular and experimental scrutiny. *Trends Parasitol.* **24**, 24–28. (doi:10.1016/j.pt.2007.10.002)
- Poulin, R. & Morand, S. 2000 The diversity of parasites. *Q. Rev. Biol.* **75**, 277–293.
- Poulin, R., Krasnov, B. R., Shenbrot, G. I., Mouillot, D. & Khokhlova, I. S. 2006 Evolution of host specificity in fleas: is it directional and irreversible? *Int. J. Parasitol.* **36**, 185–191. (doi:10.1016/j.ijpara.2005.09.017)
- Price, R. D. & Clayton, D. H. 1996 Revision of the chewing louse genus *Formicaphagus* (Phthiraptera: Philopteridae) from Neotropical antbirds and gnateaters (Aves: Passeriformes). *J. Kansas Entomol. Soc.* **69**, 346–356.
- Price, R. D., Clayton, D. H. & Adams, R. J. 2000 Pigeon lice down under: taxonomy of Australian *Campanulotes* (Phthiraptera: Philopteridae), with a description of *C. durdeni* n. sp. *J. Parasitol.* **86**, 948–950. (doi:10.1645/0022-3395(2000)086[0948:PLDUTO]2.0.CO;2)
- Price, R. D., Arnold, D. C. & Bush, S. E. 2006 Five new species of *Myrsidea* (Phthiraptera: Menoponidae) from Asian babblers (Passeriformes: Timaliidae). *J. Kansas Entomol. Soc.* **79**, 369–377. (doi:10.2317/0602.14.1)
- Purvis, A., Agapow, P. M., Gittleman, J. L. & Mace, G. M. 2000 Non-random extinction and the loss of evolutionary history. *Science* **288**, 328–330. (doi:10.1126/science.288.5464.328)
- Rausher, M. D. 1984 Tradeoffs in performance on different hosts: evidence from within- and between-site variation in the beetle *Deloya guttata*. *Evolution* **38**, 582–595. (doi:10.2307/2408708)
- Raxworthy, C. J., Pearson, R. G., Rabibisoa, N., Rakotondrazafy, A. M., Ramanamanjato, J. B., Raselimanana, A. P., Wu, S., Nussbaum, R. A. & Stone, D. A. 2008 Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Global Change Biol.* **14**, 1703–1720. (doi:10.1111/j.1365-2486.2008.01596.x)
- Rezende, E. L., Lavabre, J. E., Guimaraes, P. R. J., Jordano, P. & Bascompte, J. 2007 Random coextinctions in phylogenetically structured mutualistic networks. *Nature* **448**, 925–928. (doi:10.1038/nature05956)
- Schipper, J. et al. 2008 The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* **322**, 225–230. (doi:10.1126/science.1165115)
- Sekercioglu, C. H., Ehrlich, P. R., Daily, G. C., Aygen, D., Goehring, D. & Sandi, R. F. 2002 Disappearance of insectivorous birds from tropical forest fragments. *Proc. Natl Acad. Sci. USA* **99**, 263–267. (doi:10.1073/pnas.012616199)
- Shaw, M. R. 1994 Parasitoid host ranges. In *Parasitoid community ecology* (eds B. A. Hawkins & W. Sheehan), pp. 111–114. Oxford, UK: Oxford University Press.
- Smith, T. B. & Bernatchez, L. 2008 Evolutionary change in human-altered environments. *Mol. Ecol.* **17**, 1–8. (doi:10.1111/j.1365-294X.2007.03607.x)
- Stireman, J. O. 2005 The evolution of generalization? Parasitoid flies and the perils of inferring host range evolution from phylogenies. *J. Evol. Biol.* **18**, 325–336. (doi:10.1111/j.1420-9101.2004.00850.x)
- Stork, N. & Lyal, C. H. C. 1993 Extinction or 'co-extinction' rates?. *Nature* **366**, 307.
- Thacker, J. I., Hopkins, G. W. & Dixon, A. F. G. 2006 Aphids and scale insects on threatened trees: coextinction is a minor threat. *Oryx* **40**, 233–236. (doi:10.1017/S0030605306000123)
- Tompkins, D. M. & Clayton, D. H. 1999 Host resources govern the specificity of swiftlet lice: size matters. *J. Anim. Ecol.* **68**, 489–500. (doi:10.1046/j.1365-2656.1999.00297.x)
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395. (doi:10.1038/416389a)
- Whiteman, N. K. & Parker, P. G. 2005 Using parasites to infer host population history: a new rationale for parasite conservation. *Anim. Conserv.* **8**, 175–181. (doi:10.1017/S1367943005001915)
- Wilson, R. J., Gutierrez, D., Gutierrez, J., Martinez, D., Agudo, R. & Monserrat, V. J. 2005 Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol. Lett.* **8**, 1138–1146.
- Wilson, R. J., Gutierrez, D., Gutierrez, J. & Monserrat, V. J. 2007 An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biol.* **13**, 1873–1887. (doi:10.1111/j.1365-2486.2007.01418.x)
- Woolhouse, M. E. J. & Gowtage-Sequeria, S. 2005 Host range and emerging and re-emerging pathogens. *Emerg. Infect. Dis.* **11**, 1842–1847.
- Woolhouse, M. E. J., Haydon, D. T. & Antia, R. 2005 Emerging pathogens: the epidemiology and evolution of species jumps. *Trends Ecol. Evol.* **20**, 238–244. (doi:10.1016/j.tree.2005.02.009)
- Zaffarano, P. L., McDonald, B. A. & Linde, C. C. 2008 Rapid speciation following recent host shifts in the plant pathogenic fungus *Rhynchosporium*. *Evolution* **62**, 1418–1436. (doi:10.1111/j.1558-5646.2008.00390.x)