

Coextinction and Persistence of Dependent Species in a Changing World

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Abstract

The extinction of a single species is rarely an isolated event. Instead, dependent parasites, commensals, and mutualist partners (affiliates) face the risk of coextinction as their hosts or partners decline and fail. Species interactions in ecological networks can transmit the effects of primary extinctions within and between trophic levels, causing secondary extinctions and extinction cascades. Documenting coextinctions is complicated by ignorance of host specificity, limitations of historical collections, incomplete systematics of affiliate taxa, and lack of experimental studies. Host shifts may reduce the rate of coextinctions, but they are poorly understood. In the absence of better empirical records of coextinctions, statistical models estimate the rates of past and future coextinctions, and based on primary extinctions and interactions among species, network models explore extinction cascades. Models predict and historical evidence reveals that the threat of coextinction is influenced by both host and affiliate traits and is exacerbated by other threats, including habitat loss, climate change, and invasive species.

Primary extinction:

extinction of a species in a network of interacting species that results in other extinctions, called secondary extinctions

Affiliate or

dependent species:

a species that depends directly on another for survival or reproduction, such as a parasite, commensal, or mutualist partner

Coextinction:

extinction of a species as a consequence of its dependence on another that has gone extinct or declined below some threshold abundance

Extirpation:

the extinction of a local or regional population; an indicator of species extinction risk

Extinction cascade:

extinction of multiple, interdependent species following the loss of a pivotal species or guild, such as top carnivores

INTRODUCTION

With the accelerating loss of species to extinction, much effort has been invested in identifying the life-history, morphological, and functional characteristics associated with extinction vulnerability for a wide range of taxa, ranging from tropical angiosperms (Sodhi et al. 2008) to coral reef fauna (Graham et al. 2011). Meanwhile, estimating the number of species already lost, in historical times, or predicted to go extinct in the future is complicated by our ignorance of the large proportion of living species that remain undescribed (Hubbell et al. 2008, Barnosky et al. 2011, Cardoso et al. 2011) and by weak support for most present estimates (Stork 2010).

Whatever their accuracy for primary extinctions, estimates of past and future extinction rates generally fail to take account of dependent species. Interred within the tombs of known and unknown species extinctions is the coterie of species dependent on the lost ones: parasites extinct with their hosts, specialist herbivores gone with their food plants, plants lost with their pollinators or seed dispersers. These coextinctions of affiliate species may exceed the number of primary extinctions (Koh et al. 2004a, Dunn et al. 2009). As a concept, coextinction in its simplest, binary form is straightforward. Two species can be linked by pure exploitation (one species benefits while the other is harmed), by mutualism (each partner bears a cost while reaping a net benefit), or by commensalism (one species benefits with negligible cost or benefit to the other). A species that obligately requires goods or services from another species faces coextinction when the other, its benefactor or codependant, meets its own demise (Stork & Lylal 1993).

The consequences of coextinctions extend beyond reduced biodiversity. Coextinctions have indirect consequences for the communities from which species have been lost. Interdependent species complexes are ubiquitous, and many ecological interaction networks are large and complex (May 2009). Some networks even connect species across biomes or link terrestrial and aquatic ecosystems. For example, fish abundance in ponds affects reproduction in a shoreline flowering plant (St John's wort, *Hypericum fasciculatum*) through consumption of dragonflies, which are important predators of bee pollinators of the plant (Knight et al. 2005). The threat of species extinction or population extirpation (local extinction, an indicator of species extinction risk) can propagate across such trophic and functional links. In a broader sense, then, secondary extinctions driven by trophic cascades (Estes et al. 2011) are also coextinctions. In the literature of ecological interaction networks, secondary extinctions of mutualists, consumers, and other affiliates are described as extinction cascades (e.g., Memmott et al. 2004, Eklöf & Ebenman 2006), and in a broad sense, we view these as further examples of coextinctions or indicators of coextinction risk.

Vulnerable ecological associations can simultaneously include multiple relationship modes, such as parasitism, commensalism, and mutualism. Ants in the genera *Atta* and *Acromyrmex* grow fungi to feed their larvae and in turn provide protection, nutrition, and dispersal for the fungi (Cafaro et al. 2011). But pathogens also depend on the fungi, whereas commensal mites and beetles (Navarrete-Heredia 2001), mutualist bacteria, and other species depend on the ants (Cafaro et al. 2011). In complex multitrophic associations like these, multiple coextinctions would likely follow the extinction of a key host species.

Sometimes we can anticipate the potential magnitude of coextinction risk from generalities. Roughly 78% of temperate and 94% of tropical plant species are pollinated by animals (Ollerton et al. 2011). Although many factors contribute to the vulnerability or resilience of such pollination networks in the face of potential coextinctions, the subset of those hundreds of thousands of species dependent on specialist pollinators are susceptible to coextinction should their pollinators fail, a troubling scenario given declines in the abundances of many native bees (Potts et al. 2010).

Despite longstanding interest in the numbers of primary extinctions, coextinctions remain a relatively unexplored but timely topic. In this review, which expands and updates earlier overviews

(Bronstein et al. 2004; Koh et al. 2004a; Dunn et al. 2009; Moir et al. 2010, 2012b), we provide theoretical constructs and empirical evidence for coextinctions and coendangerment following loss or decline of hosts or mutualist partners. We review the many impediments to documenting coextinction, discuss the implications of these limitations, and outline several approaches to modeling coextinction and extinction cascades. Because the risk of coextinction is exacerbated through interactions with other environmental stresses, we discuss coextinction in the contexts of habitat alterations, population declines, climate change, and invasive species. We evaluate circumstances, such as host-switching, that promote persistence of affiliate species despite the loss of hosts. We discuss the role of affiliates in ecological recovery and restoration and conclude by outlining challenges and suggesting ways forward.

Coendangerment: the endangerment of an affiliate species as a result of the endangerment or extinction of its host(s) or mutualist partner(s)

HISTORICAL AND CONTEMPORARY COEXTINCTIONS AND COENDANGERMENT

Challenges in Documenting Coextinctions

Dunn (2009) searched widely for credible examples of historical coextinctions and came up with a short list. Among the most cited examples of coextinction are parasites (particularly lice; Stork & Lyal 1993) of the passenger pigeon (*Ectopistes migratorius*) and a louse restricted to the black-footed ferret (*Mustela nigripes*) (Gompper & Williams 1998). These cases have come to illustrate the challenges of studying coextinction empirically: determining host specificity, the limitations of historical collections, the importance of resampling hosts, and the taxonomic impediment.

Determining host specificity. Assessing host specificity is a crucial step in evaluating the risk of coextinction or the likelihood of historical coextinction of an affiliate (Koh et al. 2004a, Moir et al. 2010). Two examples epitomize how difficult this can be. The lice of the passenger pigeon, once the most abundant bird in North America (Webb 1986) but extinct since 1914, provided the first published example of alleged coextinction. Stork & Lyal (1993) reported that two of these louse species, *Columbicola extinctus* and *Campanulotes defectus*, were likely to be extinct, as they were known from no other hosts. Louse species often include two or more closely related bird or mammal species among their acceptable hosts (Bush & Clayton 2006), but at the time Stork and Lyal published, the phylogenetic placement of the passenger pigeon was not yet clear. Not until 2010 was the closest living relative of the passenger pigeon identified as likely to be the band-tailed pigeon (*Patagioenas fasciata*) (Johnson et al. 2010), on which one of the two “extinct” passenger pigeon lice, *C. extinctus*, had already been found, very much alive (Clayton & Price 1999).

Taylor & Moir (2009) recently described two new species of rare, herbivorous insects in the genus *Acizzia* (Psyllidae: Hemiptera), each from a different rare, threatened Australian host plant. Taylor & Moir (2009) suggested these species be considered coendangered as a precautionary measure. Powell et al. (2011) later discovered a few individuals of one of them, *Acizzia keithi*, in the same region on a common, widespread, congeneric host plant, thereby reducing concern for this species. The second species, *Acizzia veski*, is still believed to be host specific, and its conservation listing has been approved at the state (Western Australia) level (M. Moir, personal communication).

Even though detailed study commonly reveals affiliates to be less specialized than assumed given published specimen records (Shaw 1994, Tompkins & Clayton 1999), it is unwise to assume further that all host ranges are underestimated. Coextinction is a process, not an event, and affiliates may often go extinct before their declining hosts (Moir et al. 2010, 2012b; Powell 2011). High host specificity is always a risk factor for coextinction when hosts are threatened.

Limitations of historical collections. In most cases, documenting coextinction depends on comparison of extant forms of a lineage (for example, a louse genus) to historical collections from an extinct host or partner. Such comparisons are only as dependable as the quality of the historical specimens and the accuracy of their associated collection data. For many reasons, collection data are often not reliable. In this regard, the passenger pigeon louse, *C. defectus*, also offered as an example of a coextinction, is illustrative, though perhaps extreme. The single specimen of this species reported to have been collected from a passenger pigeon appears to have become mislabeled during a World War II bombing episode in Germany. “*Campanulotes defectus*” appears to be a specimen of *Campanulotes flavens*, a parasite of the common bronzewing (*Phaps chalcoptera*), an Australian pigeon that has never occurred in the Americas (Price et al. 2000).

The importance of resampling hosts. If the passenger pigeon lice are synonymous with coextinction, the black-footed ferret louse has become emblematic of the special case of threatened parasites under captive rearing. In a growing number of cases, when the last individuals of rare species are brought into captivity for breeding with the aim of subsequent reintroduction of the species, they are immediately treated with biocides (pesticides, endectocides, or antihelminthics) to eliminate parasites (see sidebar, Extinction by Eradication?). When the last wild black-footed ferrets were brought into captivity in 1987 (Biggins et al. 2011), they may have carried a host-specific, but undescribed, louse species of the genus *Neotrichodectes*, last collected decades earlier. After pesticide treatment (delousing), no lice could be found on any of the captive ferrets, raising the possibility that this louse may now be extinct, despite the successful re-establishment of the ferret in the wild (Gompper & Williams 1998). No one has yet resurveyed the re-established black-footed ferret populations to examine whether the louse has reappeared, other ectoparasites have colonized, or the black-footed ferret now harbors any specialist parasite. Resampling hosts after release or translocation is an important but often neglected step in assessing the status of coendangered affiliates and host-species recovery.

The taxonomic impediment. Many, perhaps most, eukaryotic affiliates belong to hyperdiverse taxa (arthropods, helminths, protists, and fungi) (Dobson et al. 2008) that are not only poorly studied but also often difficult to distinguish and describe using only morphological characters.

EXTINCTION BY ERADICATION?

Captive breeding and other ex situ conservation programs for threatened or endangered hosts offer excellent opportunities for coextinction research (Moir et al. 2012a,b). In cases such as the black-footed ferret (Gompper & Williams 1998), in which the extinction of affiliates is threatened by insecticide or antihelminthic treatment of hosts, the total number of hosts to be sampled is usually small, and care for the host species in captivity is well funded. Tests of the role of parasites in stimulating and moderating host immune response upon release suggest a positive effect for some parasites in the captive setting (e.g., Van Oosterhout et al. 2007). A key experiment would compare the fitness of individuals from captive-rearing programs that are released after having been treated to exterminate parasites to the fitness of matched individuals that have been released without having been treated. The objectives of conservation of hosts and conservation of affiliates have the greatest potential for conflict in this setting, but these conflicts have been poorly explored, despite frequent pleas in both the biological (Windsor 1995; Nichols & Gomez 2011; Colwell et al. 2009; Moir et al. 2012a,b) and veterinary (Adler et al. 2011) literature to consider the ecological, evolutionary, ethical, and societal consequences of intentional or incidental eradication of parasites and other affiliate species.

As a result, it is now common for molecular studies to reveal lineages of multiple specialist species within what were previously viewed as single generalist affiliate species (Poulin & Keeney 2008). Detection of potentially coendangered or coextinct species may be aided by the increasing use of DNA barcoding and related approaches (Janzen et al. 2005). For example, the initial concerns of Gompper & Williams (1998) about the extinction of a potentially host-specific black-footed ferret louse were based solely on a record from a published host-parasite checklist. Had the historical louse samples been preserved or had sampling occurred at the time when ferrets were brought into captivity, current DNA-barcoding techniques could illuminate whether the species on the black-footed ferret was unique and now extinct. Nevertheless, systematists, even when using all available tools, face daunting obstacles in documenting the existence, much less the coextinction, of many affiliates. For example, Hamilton et al. (2010) estimate that 70% of terrestrial arthropods (nearly 3 million species), a large proportion of them dependent species, remain undescribed.

Additional Examples of Contemporary Coextinction and Coendangerment

Similar to the case of the black-footed ferret, when the last 22 wild California condors (*Gymnogyps californianus*) were brought into captivity in 1987 for rearing, they were deloused (Snyder & Snyder 2000). Three species of louse had previously been known from wild California condors, and two of them have not, so far, been found elsewhere. But, apparently, no one has systematically searched for these louse species on other bird species, not even on the California condor's closest relative (Wink 1995), the historically co-occurring black vulture (*Coragyps atratus*). Nor do there appear to have been attempts to resample the California condor in populations re-established from released, captive bred individuals.

Mihalca et al. (2011) considered the evidence for the extinction of ticks with the loss of their hosts and highlighted three potential examples, including the tick *Ixodes nitens*, known only from a single endemic rat species, *Rattus macraeri*, from Christmas Island. Ironically, the extinction of this endemic rat (sometime around 1900) appears to have been driven by the introduction of pathogenic trypanosomes vectored by fleas, themselves affiliates of the invasive black rat (*Rattus rattus*), as demonstrated by ancient-DNA evidence from museum specimens (Wyatt et al. 2008). Mey (2005) lists 12 bird lice species as probably coextinct, all but one from extinct island bird species. (The exception was the passenger pigeon louse, later rediscovered on band-tailed pigeons.)

Additional examples of coendangered species have steadily accumulated (e.g., Durden & Keirans 1996, Colwell et al. 2009, Daszak et al. 2011), although most tend to be based on literature review of host associations rather than field studies (e.g., Powell et al. 2012) and experiments (e.g., Moir et al. 2012a). An iconic example is the rhinoceros stomach bot, *Gyrostigma rhinocerotis* (Oestridae: Diptera), the largest fly in Africa, which is restricted to the critically endangered black (*Diceros bicornis*) and near-threatened white (*Ceratotherium simum*) rhinoceroses (Figure 1) (Colwell et al. 2009).

Experiments on Coendangerment and Coextinction

Although experiments on coendangerment and coextinction are not impossible, few have been reported. Experimental population translocation (or reintroduction) is increasingly discussed as a means of helping rare and poorly dispersing species to track climate change through "assisted migration" (McLachlan et al. 2007); experiments with affiliates could easily be integrated into such programs. Moir et al. (2012a) compared the arthropod affiliates associated with threatened plants in natural populations and affiliates of translocated populations of the same plants distant from the source populations. For some of the plant species studied, species composition of affiliates



Figure 1

The coendangered rhinoceros stomach bot fly (*Gyrostigma rhinocerotis*, Oestridae: Diptera), which is the largest fly in Africa (25–30 mm long, wingspan 50–57 mm), and one of its two host species, the critically endangered black rhinoceros (*Diceros bicornis*). The adult female fly attaches her eggs at the base of the horns or ears or on the neck or shoulders of the rhinoceros. The larvae enter the digestive tract of the rhinoceros and burrow into its stomach lining, where they feed until ready to emerge from the anus and pupate in rhinoceros dung piles. The other host is the near-threatened white rhinoceros (*Ceratotherium simum*) (Colwell et al. 2009; M. Hall, personal communication). Fly photograph by Harry Taylor, copyright Natural History Museum, London; rhinoceros photo from Ngorongoro N.P., Tanzania, copyright R.K. Colwell.

in translocated populations differed substantially from affiliates on hosts in natural populations, instead resembling the affiliate fauna of local, related plants. In some cases, host-specific affiliates appeared to be missing on the translocated plants.

A vast literature describes affiliates (both pests and beneficial species) of cultivated plants and domesticated animals introduced far from their place of origin, and an equally large literature covers invasive species and their affiliates. This work could be mined for quantitative patterns bearing on coendangerment and coextinction risk (Keane & Crawley 2002). For example, Torchin et al. (2003) showed that twice as many parasite species are associated with host species (molluscs, crustaceans, fishes, birds, mammals, amphibians, and reptiles) in the hosts' native range than on the same hosts living as exotics elsewhere, providing implicit evidence for extirpation of affiliate populations during range expansions. If source populations of the host were later lost from their native range (a common occurrence with cultivated and domesticated species), these missing affiliates would represent a special class of affiliate extinctions.

Anderson et al. (2011) considered the effects of a very different sort of natural experiment in New Zealand, involving a native bird-pollinated shrub (*Rhabdothamnus solandri*, Gesneriaceae) and its three endemic pollinators—bellbirds, tui, and stitchbirds. On small island sanctuaries where the birds are still abundant, pollination, fruit set, and plant density of the shrub were all greater than they were on the North Island of New Zealand, where two of the three pollinator species have been locally extinct since approximately 1870.

Host shift or host switch: expansion of an affiliate's host repertoire to include an additional, alternative host or the abandonment of one host for another

PERSISTENCE OF AFFILIATE SPECIES: HOST SHIFTS

In addition to the challenges of documenting coextinctions, some parasites and other affiliates may complicate matters by shifting or expanding affiliation from a rapidly declining host (or mutualist partner) to an alternative, more common host, even if such novel hosts are initially inferior in terms of the fitness benefits they offer (Dunn et al. 2009, Moir et al. 2010). Although we focus here on host shifts by parasites, analogous considerations apply to shifts in affiliation among mutualist partners (Bronstein et al. 2004). Ideally, in the context of coextinction, we must understand three

aspects of host shifts: how common they are, the host attributes that promote them, and the consequences they imply for novel hosts.

Real-Time Studies of Host Shifts

The most unambiguous way to document changes in the host specificity of affiliates is to see them in action, an increasingly frequent occurrence as infectious or parasitic organisms exploit humans and our domesticates, either as an additional host (host-range or niche expansion) or as sole host (host switch). The majority of diseases that affect humans worldwide originated from a nonhuman animal reservoir (Taylor et al. 2001). Recent examples of host shifts of eukaryote human affiliates include *Cyptosporidium* protists (Guerrant 1997) and helminths (Hotez et al. 1997) as well as a relatively long list of emerging zoonotic diseases (reviewed by Jones et al. 2008). Emerging zoonotic diseases in humans and our domesticates generally involve host shifts, or expansion of the affiliate's host repertoire, from relatively rare to relatively more common hosts. (We prefer the term host repertoire instead of host range, reserving "range" for its more general, geographical sense.)

Host repertoire: the set of alternative host species upon which an affiliate can survive and reproduce (also known as host range)

Are Affiliates More Likely To Switch When Their Hosts Become Rare?

If host rarity influences the probability of host switches, the endangerment of host species may drive a shift of parasites and other affiliates to more common hosts or mutualist partners, with consequences for those hosts or partners. A large literature considers the evolution of host preference among herbivores in light of host plant quality and density (e.g., Mayhew 1997). A few studies have examined experimentally how the local rarity and density of animal hosts influence the probability of host shift in their parasites. For example, in California, western fence lizards (*Sceloporus occidentalis*) serve as the blood-meal hosts for a large proportion of larval and nymphal western black-legged ticks (*Ixodes pacificus*). When Swei et al. (2011) removed lizards from enclosures and quantified ticks on alternative (mammal) hosts, the removal of lizards increased larval ticks on other hosts by only approximately 5%, leaving many larval ticks without any host.

Given the potential public health consequences (both for humans and our domesticated crops and animals) of host switches from rare to common hosts, a thorough literature review on host shifts as a function of decreasing host populations would prove useful, especially because both we and our domesticates tend to be among the most abundant potential hosts and the most likely to be in contact with dwindling species (particularly vertebrates) (Woolhouse et al. 2005, Wolfe et al. 2007). If host shifts occur, but do not tend to be directly influenced by the rarity or density of hosts, host shifts and coextinction are independent phenomena. By contrast, if host rarity influences the probability of a host shift, the two phenomena are coupled, with many potential implications.

Transitions Inferred from Phylogeny

Phylogenetic trees provide an additional means of assessing the propensity of affiliates to switch hosts, especially for taxa in which monitoring real-time host shifts is difficult (e.g., Reed et al. 2007). If host specificity is highly conserved, related affiliates would be expected to have the same or related hosts. Conversely, for affiliate taxa in which host specificity is a labile trait, closely related affiliate species often differ in their host preference, and host shifts may even be an important mode of speciation and radiation (e.g., Ziętara & Lumme 2002). The specificity of parasites is often, if not universally, well conserved among clades (Mouillot et al. 2006, Poulin et al. 2006) and in some cases in networks of mutualists (Rezende et al. 2007), but no comprehensive review appears

to have considered how labile host preferences are in general and whether differences in lability among taxa or functional groups (e.g., parasites versus mutualists) are statistically consistent.

MODELING COEXTINCTION

Given the difficulty of demonstrating individual events of contemporary coextinction or documenting coextinctions from the historical or fossil record, estimating the number of coextinctions, for past or future periods, calls for a modeling approach. A spectrum of approaches to modeling coextinction events can be described. At one extreme lie purely statistical methods that rely on estimating rates of affiliate coextinction as a function of primary extinctions of hosts or partners. At the other extreme, secondary extinctions and extinction cascades are modeled for hypothetical or empirical interaction webs. Here we attempt to link the two extremes conceptually, compare the challenges they face, and sketch out a middle ground.

Statistical Host-Extinction Models: Discrete Models

A species that obligately requires goods or services from any of several other species faces unequivocal extinction only when the last of its benefactors becomes extinct or falls below some critical population size or density threshold (Anderson & May 1986, Altizer et al. 2007, Dobson et al. 2008, Moir et al. 2010). Koh et al. (2004a,b) and Dunn et al. (2009) applied a simple, probabilistic extinction model to this scenario, treating host species (or populations) as either extant or extinct, ignoring density-threshold effects. This model relies on published data yielding “affiliation matrices” between hosts or mutualist partners and their affiliates, recording the binary association of S affiliate species with each of H hosts as a set of ones and zeros. A generalist affiliate will have several hosts, whereas a maximally specialized affiliate has only one. This simple approach assumes that no affiliate requires more than one host species to survive and ignores the complex life cycles of many parasites (taking them into account would increase predicted rates of coextinction). The number of coextinctions (extinctions of affiliates) as a function of b host extinctions can be estimated by randomly eliminating $1, 2, \dots, b, \dots, H$ hosts from the matrix without replacement. We refer to this model as a uniform random coextinction model (**Figure 2a**).

Mathematically, when hosts are chosen randomly for extinction, this approach is precisely equivalent to sample-based rarefaction (Colwell et al. 2012), widely used to estimate the number of species expected for a subset of sampling units (e.g., quadrats, traps, culture plates) for which only the presence or absence of each species has been recorded for each sample in a reference sample of H sampling units. An analytical (combinatoric) solution and unconditional variance estimators are available for this problem, allowing estimation of a confidence interval around the expected number of affiliates surviving after extinction of a specified number of hosts. The model is analogous to using a species-area relation “backwards” to estimate the expected number of extinctions given a certain loss of habitat area (the endemics-area curve) (Kinzig & Harte 2000, He & Hubbell 2011). As demonstrated by Colwell et al. (2004), sample-based (incidence-based) rarefaction is not biased by aggregation (in this application, by the aggregation of affiliates on certain hosts).

Building on this simple, uniform random extinction model, it is straightforward to condition the extinction of each host species on its intrinsic organismal traits (e.g., size, vagility, clade position) or on its susceptibility to extinction based on population size, geographical range size, habitat fragmentation, or other risk factors for primary extinction (e.g., Bunker et al. 2005, Srinivasan et al. 2007, Carpaneto et al. 2011). In addition, the cell probabilities in the affiliation matrix [zero or one in the model of Koh et al. (2004a)] could be based on quantitative, empirical patterns as estimates of probabilities of affiliation with hosts so that the effects of host loss on affiliate

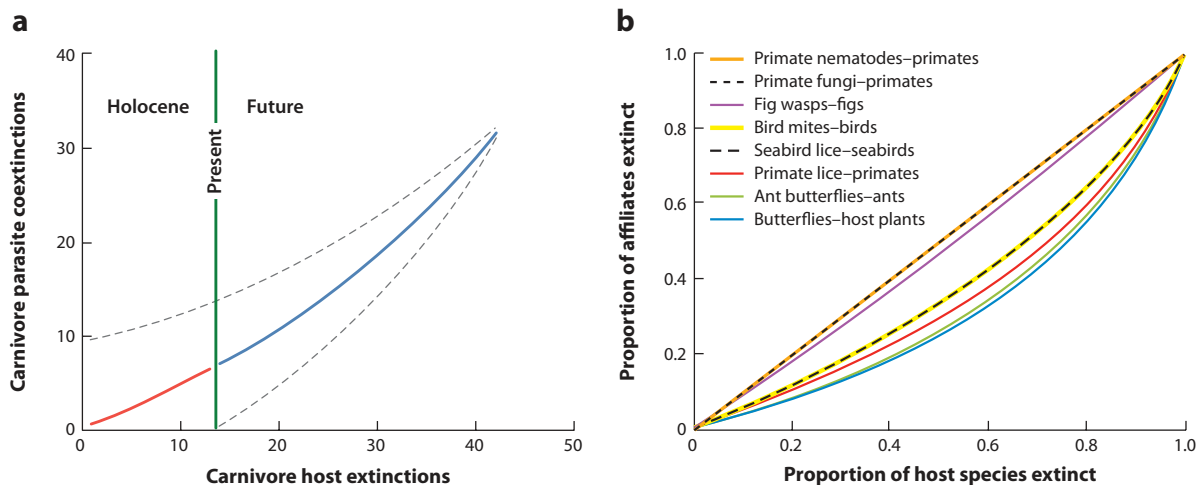


Figure 2

(a) Estimated number of coextinctions of louse, flea, and cestode (tapeworm) species as a function of the past and future extinctions of their hosts, 42 terrestrial North American Carnivora (NAC) species. Future coextinctions are based on the recorded affiliates of extant NAC, which are eliminated in random order in the model (Koh et al. 2004a). Dashed lines are estimated 95% confidence intervals (CI). Between 4 and 8 (mean 6.4, 4.3–8.5, 95% CI) NAC affiliate coextinctions are estimated to have occurred during the Holocene, on the basis of the known extinction of 13 NAC species since 11,000 years before present (Smith et al. 2003). Holocene coextinctions were estimated by extrapolating the future curve into the past using the statistical model of Colwell et al. (2012). The data considered here cover only metazoan ectoparasites and a small proportion of endoparasites (roughly one in 10 species), so the total number of coextinctions, past and future, would be greater. For the 10 NAC in the data set with ranges extending beyond North America, the losses should be considered coextirpations, unless the species is assumed extinct over its full range. Carnivora with ranges covering <10% of the Americas north of Panama were not considered. (b) The estimated proportion of affiliate species expected to face coextinction as a function of an increasing proportion of their hosts becoming extinct for eight affiliate-host systems: pollinating Agaonidae fig wasps—figs (*Ficus*), primate *Pneumocystis* fungi—primates, primate nematodes—primates, primate lice—primates, seabird lice—seabirds, bird mites—birds, butterflies—host plants, and Lycaenidae ant butterflies—ants. The curves were estimated on the basis of recorded affiliates for each host in each group, with hosts eliminated in random order in the model (figure from Koh et al. 2004a).

populations could be weighted (Vesk et al. 2010), akin to estimates of interaction strength in interaction-web models (e.g., Allesina & Pascual 2008).

Memmott et al. (2004) explored alternative host-elimination algorithms to estimate the expected number of plant coextinctions resulting from primary extinctions of their pollinators for two large pollination networks. Not surprisingly, when the deletion of pollinators from the affiliation matrix is ordered from the least-connected pollinators (specialists) to the most-connected pollinators (generalists), the number of plant coextinctions rises more slowly than in the uniform random coextinction model. In contrast, when deletions are ordered from generalist to specialist pollinators, the number of coextinctions rises more rapidly than they do in the uniform random model.

Using affiliation matrices for living species, Koh et al. (2004a) applied the uniform random coextinction model to estimate the number of undocumented, historical coextinctions of affiliates as a result of recorded, historical extinctions of their hosts. They modeled two cases: the coextinction of butterflies, as a result of known historical plant extinctions (assumed to be larval host plants), and the number of bird mite extinctions, as a function of the number of historical avian extinctions. This approach assumes that affiliates that have already become extinct had the same quantitative pattern of association with extinct hosts as living affiliates have with extant hosts, when, in fact, past host extinction [or even current threat (Altizer et al. 2007)] is likely to have increased the host

specificity of surviving affiliates through the extinction of some of their alternative hosts. A more rigorous approach would extrapolate the coextinction curve into the past [as Koh et al. (2004a) suggest in their supplemental online material].

With appropriate assumptions, recent advances in extrapolating sample-based species accumulation (rarefaction) curves beyond the empirical reference sample make this retrospective extrapolation feasible. Using sampling-theoretic, nonparametric predictors, Colwell et al. (2012) developed estimators (with unconditional confidence intervals) for the expected number of additional species to be found in b^* additional samples. By direct analogy, we can estimate the number of affiliate coextinctions that occurred as the result of the historical (or conjectured) extinction of b^* hosts. To demonstrate the method, **Figure 2a** shows an example for a subset of the parasites of North American Carnivora. The model estimates that between four and eight (unknown) species of fleas, lice, ticks, and cestodes were extirpated with the 13 known extinctions of North American Carnivora during the Holocene (Smith et al. 2003). Any affiliates that did not survive on non-Carnivora hosts or on non-North American Carnivora are now assumed globally extinct. Adding other parasitic taxa such as trematodes, nematodes, and protists would increase these estimates.

The critical statistics for all the above models are the numbers of hosts per affiliate (even if weighted for different hosts). Unfortunately, as for any measure of (statistical) range for finite samples, the observed host repertoire of an affiliate is a negatively biased estimator for its true host repertoire and, therefore, tends to overestimate coextinction risk, an issue of equal importance for interaction network models (Blüthgen 2010). Recognizing this problem, Veski et al. (2010; see also Moir et al. 2011) have explored a promising approach toward reducing the bias in estimates of host breadth that is based on a Bayesian, zero-inflated Poisson regression approach.

Statistical Host-Extinction Models: Curve-Fitting Models

When normalized by percentages, as in **Figure 2b**, the shape of coextinction curves based on uniform random host-extinction models (**Figure 2a**) depends entirely on the frequency distribution of hosts per affiliate. If every affiliate has exactly one host and every host one affiliate, as in the three groups of primate parasites in **Figure 2b**, the curve is a straight line with slope 1. Called the linear approach by Moir et al. (2010), the assumption of such a one-to-one relationship underlies early estimates of coextinction risk (e.g., Stork & Lyal 1993, Poulin & Morand 2004) and estimates that are intentionally confined to monophagous species (e.g., Thacker et al. 2006). For groups in which some or all affiliates have more than a single host per affiliate, the curve is shallower, because a typical affiliate tends to survive early host extinctions, succumbing only when its last, alternative host goes extinct (Koh et al. 2004a, Dobson et al. 2008).

Koh et al. (2004a, see their supplemental online material) showed that the distributions of hosts per affiliate are similar in shape for the groups in **Figure 2b** and took advantage of the similarity to fit a regression model for the ratio of affiliate extinctions to host extinctions (the instantaneous slopes of the curves in **Figure 2b**) as a function of host-extinction percentage and the mean number of hosts per affiliate. Koh et al. (2004a) used this empirical “nomographic model” to estimate the expected number of affiliate extinctions for groups such as herbivorous beetles and bird lice, for which complete affiliate matrices are not available but mean number of hosts can be estimated. They applied the model to project future extinctions, in the event that all currently endangered hosts were to be lost, as well as to estimate historical coextinctions as a function of recorded historical host extinctions. Using the same fitted equation, Dunn (2009) extended the historical extinction results for bird and mammal ectoparasites to estimate the number of coextinctions in these groups for the entire Holocene on the basis of estimated Holocene bird and mammal extinctions. Because the relation is data dependent, having been fitted for a particular set

of random host-extinction curves, these estimates of past and future extinctions depend closely on the assumption that affiliation matrices for all the groups to which they are applied are similar to the current distribution of number of hosts per affiliate in the “training” data sets. More work needs to be done comparing the host specificity distributions of different groups of affiliates, particularly to understand the extent to which taxa or classes of affiliates (e.g., parasites versus mutualists) differ systematically in the risk and rate of coextinction.

Linking Coextinction Matrix Models and Interaction Network Models

Coextinction models based on affiliation matrices, like those discussed in the previous sections, are conceptually a subset of ecological interaction network models (Bascompte & Jordano 2007), although this fact seems not to have previously been discussed in the literature. In both kinds of models, links between mutualist partners or between hosts and affiliates can be broken by extinctions (random or not), nodes can be unweighted or weighted, and the consequences interpreted as fragility or robustness.

A full account of food-web and interaction network studies would not be pertinent (or possible) here, and comprehensive reviews have recently appeared elsewhere (e.g., Bascompte & Jordano 2007, Bascompte 2009). From the point of view of coextinctions, the key consideration with food-web and interaction network studies is how the removal of species (primary extinctions) having identifiable characteristics leads to the secondary extinction of other species in the network. The characteristics of those consequential casualties are also of great interest (e.g., Petchey et al. 2008). Whereas the statistical coextinction models of Koh et al. (2004a) and Memmott et al. (2004) include only two trophic levels, many (but not all) food-web and interaction network models encompass multiple trophic levels and are thus capable of much more complex dynamic behavior. Here, we highlight the implications for coextinctions in a few pertinent network studies. We follow the literature of interaction networks in using “extinction” for local networks, recognizing that the species losses that the models predict are more accurately characterized as population extirpations.

Interaction Networks and Coextinctions

Examining three large empirical food webs, Solé & Montoya (2001) demonstrated that random deletion of species initially leads to few secondary extinctions, whereas [in accord with Memmott et al. (2004)] selective deletion of highly connected (i.e., keystone) species produces a rapid disintegration of the network and a high rate of secondary extinctions. Dunne et al. (2002) confirmed these conclusions for a larger set of empirical food webs, but they offered evidence that higher levels of connectance (more links per species independent of community size, the equivalent of decreasing host specificity in affiliation matrices) and increased species diversity (Dunne & Williams 2009) in model networks delay the nonlinear increase in secondary extinctions when highly connected species are targeted for primary extinction.

In a food-web study of 50 lakes in the Adirondack region of the United States, Srinivasan et al. (2007) found that deleting species according to prevalence (from least to most prevalent) among the lakes caused surprisingly few secondary extinctions until nearly all species were removed by primary extinction. Almost as few secondary extinctions resulted as when species were deleted according to increasing numbers of links. The reverse order of extinctions in both cases led to catastrophic cascades of extinction. For a very large collection of plant-pollinator and fruit-frugivore interaction networks, Rezende et al. (2007) showed that simulated secondary extinctions tend to eliminate species that are more closely related than would be expected at random, given the species in each network, presumably because of phylogenetic signaling in their niches.

Using dynamic population models (generalized Lotka-Volterra models) as well as topological analysis of empirical food webs, Petchey et al. (2008) showed that the primary extinction of species with unique trophic relationships is especially likely to drive secondary extinctions. Eklöf & Ebenman (2006) noted that topological analyses (unlike dynamic models) are blind to trophic cascades and other complex secondary interactions. Using dynamic models, they argued that trophic webs with higher connectance confer greater persistence (i.e., permanence) and that, within such high-connectance communities, species most vulnerable to secondary extinction tend to be in the middle of trophic webs.

Fundamental differences between mutualistic networks and trophic networks are under active exploration (Lewinsohn et al. 2006). On the basis of dynamic models and a meta-analysis of empirical pollination and herbivory networks, Thébault & Fontaine (2010) concluded that stability is promoted in mutualistic networks by highly connected and nested architectures, whereas stability in trophic networks is enhanced by weak connections and compartmentalization. By contrast, Allesina & Pascual (2008) argued on the basis of dynamic models that the stability of complex communities depends strongly on simple consumer-victim (including parasite-host) subsystems.

In summary, network studies indicate that the rate of secondary extinction is greater following the primary extinction of common species and highly connected species, whereas secondary extinction slows in networks with high average levels of connectance and high diversity. These results are closely in accord with conclusions from coextinction models, in which the extinction of hosts with many affiliates (such hosts tend to be widespread geographically; Lindenfors et al. 2007, Harris & Dunn 2010) drives faster affiliate coextinctions, whereas the presence of affiliates with many hosts slows the rate of coextinction. In both kinds of models, the survivors as well as the extinctions tend to be nonrandom subsets of the community.

FACTORS THAT INFLUENCE THE RISK OF COEXTINCTION

Host Specificity and Life Cycle

The factor most likely to influence the probability of coextinction directly is the host specificity of affiliates, including relative fitness on different hosts as well as the phylogenetic spectrum of hosts (Moir et al. 2010, Poulin et al. 2011) or mutualist partners (Bronstein et al. 2004). Host specificity is also both scale and context dependent (Krasnov et al. 2011). So far, coextinction models have ignored affiliates with complex life cycles (parasites, many free-living insects), which rely on different host species at different life stages. As hosts are lost, the risk of coextinction is assumed higher for such species than it is for affiliates with simple life cycles (Koh et al. 2004a, Poulin & Morand 2004, Lafferty 2012).

Coextinction is also a greater risk if specificity is evolutionarily inflexible. By evolving traits necessary for survival and reproduction on alternative or additional hosts, affiliates may escape extinction (Bronstein et al. 2004, Poulin et al. 2006). The characteristics of hosts that tend to have evolutionarily labile affiliates and of those affiliates could be better explored.

Affiliate and Host Traits

Affiliates predisposed to coextinction may share traits with species more generally vulnerable to extinction. If they are larger bodied, their total population size is likely to be smaller; larger-bodied affiliates also tend to depend on larger hosts (**Figure 1**) (Bush & Clayton 2006), which are also more vulnerable to extinction (e.g., Stork et al. 2009). Affiliates of hosts of higher trophic levels (**Figure 2**) share their host's vulnerability to extinction (Estes et al. 2011). Finally, just as for their hosts, affiliates with limited climatic tolerances will be at an increased risk of extinction if their

climatic niches are narrow or if the geographic area corresponding to their climatic niches is small (Moir et al. 2010).

Host traits may influence coextinction through host rarity or abundance and through their influence on affiliate diversity. Hosts vary dramatically in their rarity: Some species consist of fewer than ten individuals in the wild, whereas others have hundreds of millions and perhaps even billions of individuals. Large, abundant, geographically widespread hosts tend to have the greatest diversity of parasites (Lindenfors et al. 2007, Harris & Dunn 2010), even though a high diversity of parasites on a single host species may increase interspecific competition among its affiliates (e.g., Moore & Simberloff 1990). Such competition notwithstanding, parasites and other affiliate species dependent on abundant, widespread, invasive, pest, and domestic species may be relatively unlikely to face coextinction under current regimes.

Although hosts with wide geographic ranges and large populations may offer affiliates a low probability of extinction, the consequences of their extinction in terms of the number of coextinctions may be disproportionately greater. This principle is encoded in the idea that the extinction of well-connected species is more likely to cause cascading extinctions (as discussed in Modeling Coextinction; see section above). *Eciton burcbellii*, a wide-ranging Neotropical army ant species, hosts no fewer than 300 and perhaps even thousands of affiliate species (including mites, beetles, millipedes, and ant birds), many of which are likely to be host specific to *E. burcbellii* (Rettenmeyer et al. 2011). *E. burcbellii* is just one of more than 150 New World army ant species (Formicidae: Ecitoninae) and nearly as many species in the Old World army ant clade (Dorylinae), each of which likely hosts many unique species. The extinction of species such as *E. burcbellii* has the potential to drive a remarkably large number of coextinctions. In all but a handful of cases, these coextinctions will be of unstudied species that, if known at all before their demise, will be found only in museum collections.

INTERACTIONS WITH OTHER THREATS AND CONDITIONS

Habitat Alterations

As with other threats to biodiversity, the risk and rate of coextinctions can be exacerbated by additional perturbations (Bronstein et al. 2004, Dunn et al. 2009, Moir et al. 2010). Such synergisms not only add complexity to any effort to reduce the risk of coextinction, but also complicate documenting its occurrence. Loss and alteration of habitat remain the predominant threat to species persistence and thus to ecological associations. On the island of Singapore, observed or inferred estimates of the historical “local extinction” rate for some taxa approach 90%, corresponding to rapid loss of tropical forest exceeding 95% (Brook et al. 2003). Koh et al. (2004a) estimated the historical local extinction of at least 56 butterfly species, which they suggested was a consequence of both direct impacts on their populations and the loss of 208 potential butterfly larval host plants.

Climate Change

Because shifts in geographic distributions of species in response to changing climates may often prove discordant among species (Gilman et al. 2010, Sheldon et al. 2011), shifts in the geographic range of hosts may drive spatial or temporal mismatches among previously co-occurring species, dramatically altering interactions between hosts and affiliate species (Traill et al. 2010). Although many affiliate species can be expected to survive by range shifts in step with their hosts or partners, host switches and conversion by affiliates to independent lifestyles may also allow survival. The abandonment of mutualisms has been documented, for example, when available pollinators are infrequent and plants switch from animal to wind dispersal (Kaiser-Bunbury et al. 2010).

In the larval stage, freshwater mussels (Unionoida) obligately parasitize fish. Spooner et al. (2011) modeled the effects of decreased river flow (expected under ongoing climate change) on the coextirpation of mussel species in rivers of the eastern United States, predicting that up to 43% of mussel populations may fail owing to loss of host-fish populations. Phenological mismatch of partner interactions, such as plants and their pollinators, may also alter key ecosystem processes under climate change scenarios (Yang & Rudolf 2010).

Exploitation

Given the continued reliance of human societies on natural resources, coextinction dynamics may be accelerated through harvest. Bushmeat harvest decimated vertebrate seed dispersers in Thailand, resulting in diminished seed dispersal, population growth, and heightened extinction risk of a canopy tree (*Choerospondias axillaris*, Anacardiaceae) (Brodie et al. 2009). Wood et al. (2010) showed that marine protected areas, which generally prohibit fishing and trolling activities, harbor greater parasite richness and host abundances than fished areas support (e.g., Loot et al. 2005). Not surprisingly, multiple threats may interact, as evident in the increased vulnerability of the affiliates of coral reef fishes to coextinction through fishing pressure and climate change (Graham et al. 2011).

Invasive Species

Invasions of exotic species continue to threaten biological diversity globally, and affiliate species are not spared. Native to Asia, emerald ash borer (*Agrilus planipennis*, Buprestidae: Coleoptera) is an epidemic pest on ash (*Fraxinus*) species of eastern North America that causes significant mortality and restructuring of forests. The native arthropod fauna, including an estimated 15% (43 species) of ash-dependent invertebrate species, has also suffered (Gandhi & Herms 2010). According to the IUCN Red List (Gandhi & Herms 2010), the extirpation of American chestnut by chestnut blight, an Asian fungus, drove the extinction of at least two specialist arthropods, American chestnut moth (*Ectodemia castaneae*, Nepticulidae: Lepidoptera) and phleophagan chestnut moth (*Ectodemia phleophaga*), and possibly others (Opler 1978; D.L. Wagner, personal communication). The coextinction of the endemic Christmas Island rat and its parasites (discussed above) after the introduction of the black rat with its flea-vectored trypanosome parasites (Wyatt et al. 2008) may represent an underappreciated scenario applicable to other settings.

Invasive species may disrupt mutualistic interactions among native species (Bronstein et al. 2004). In South Africa, invasive Argentine ants profoundly altered floral visitation by native arthropods (Lach 2008). A contrary, yet growing, literature documents the ability of invasive species to replace the function of lost native species, maintaining interactions to the benefit of affiliates (Bronstein et al. 2004). For example, following their recent arrivals to New Zealand, the black rat (*Rattus rattus*) and silvereye bird (*Zosterops lateralis*) have partially compensated for missing native vertebrate pollinators by pollinating some plant species, thereby sustaining species interactions and function (Pattimore & Wilcove 2011).

SPECIES CONSERVATION, RECOVERY, AND RESTORATION

Coextinction matters not only because of the intrinsic value of all species, but also because of the broader consequences of the loss of dependent species. Every class of affiliates, whether parasites (Hudson et al. 2006), commensals (Howells et al. 2011), or mutualists (Forup et al. 2008, Menz et al. 2011), provides ecosystem services (Cardoso et al. 2011). Thus the conservation or restoration of

these services may often require attention to affiliate species and the dynamics of coextinction. For example, during rainforest regeneration in the Biological Dynamics of Forest Fragments Project (Laurance et al. 2011) in the Brazilian Amazon, processes linked to affiliate species lagged in their recovery: Research shows that decomposition of vertebrate feces by dung beetles required 20 years to recover fully (Quintero & Roslin 2005), whereas dispersal of large seeded trees dependent on large vertebrate dispersers has yet to recover fully after 30 years (Cramer et al. 2007).

The return of the ecological function of affiliates may be the ultimate measure of success in recovery or restoration projects (Huspeni & Lafferty 2004, Dixon 2009, Menz et al. 2011). Likewise, the continued functioning of affiliates may be a sensitive indicator of successful conservation programs; conserving affiliates in the first place will always be easier than restoring them once they are gone. As an obvious starting point, the fate of affiliate species of threatened hosts—whether the California condor (Snyder & Snyder 2000) or an endangered pitcher plant (Folkerts 1999)—deserves immediate attention (Moir et al. 2012a,b).

SUMMARY POINTS

1. The extinction of a single species that is large or conspicuous enough to be detected is rarely, if ever, an isolated loss. Parasites, commensals, and mutualists (affiliates), many of them hard to study and poorly known, face coextinction with the demise of their hosts or partners.
2. Coextinctions are difficult to document because of sampling difficulties, taxonomic uncertainty, the limitations of historical collections, and the potential for host shifts. Experimental studies of host-affiliate interactions are possible, but rare.
3. Statistical models based on patterns of association between hosts and affiliates can be used to estimate the rates of past coextinctions and the patterns and rates of future coextinctions.
4. Network models of species interactions explore secondary extinctions and extinction cascades driven by primary extinctions of specified categories of hosts and mutualist partners.
5. Coextinction risk and its management depend on the host specificity and evolutionary lability of affiliates and on the ecological traits of hosts or mutualist partners and of their affiliates. The risk of coextinction interacts with other threats, including habitat loss, climate change, and invasive species.
6. Restoration and recovery of ecosystems can depend on and be measured by the return of ecosystem services delivered by dependent species.

FUTURE ISSUES

1. Better understanding of the risk and rate of coextinction depends, unequivocally, on increased study and documentation of the natural history of affiliates and better support for the training and research of systematists working on understudied affiliate groups.
2. Intensified experimental study of hosts and affiliates in the laboratory and field would substantially increase understanding of coextinction dynamics.

3. Integration of statistical and network approaches to the modeling of coextinctions and extinction cascades, incorporating demographic and evolutionary dynamics, host switching, affiliate phylogeny, and risk factors for affiliate extinction, is likely to advance our ability to predict and prevent future coextinctions under conditions of ongoing global change.

DISCLOSURE STATEMENT

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