Species Coextinctions and the Biodiversity Crisis

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To assess the coextinction of species (the loss of a species upon the loss of another), we present a probabilistic model, scaled with empirical data. The model examines the relationship between coextinction levels (proportion of species extinct) of affiliates and their hosts across a wide range of coevolved interspecific systems: pollinating *Ficus* wasps and *Ficus*, parasites and their hosts, butterflies and their larval host plants, and ant butterflies and their host ants. Applying a nomographic method based on mean host specificity (number of host species per affiliate species), we estimate that 6300 affiliate species are "coendangered" with host species currently listed as endangered. Current extinction estimates need to be recalibrated by taking species coextinctions into account.

Rapid population declines and extinctions of species following the widespread destruction of natural habitats have been reported across the natural world (*1*). Up to 50% of species are predicted to be lost in the next 50 years (*2*, *3*). This seemingly inevitable biodiversity crisis has galvanized the study of population and species extinctions (*4*). However, while investigations have focused on the pathology of independent taxon-based extinctions, the possible cascading effects of species loss, while acknowledged (*5–7*), have not been estimated quantitatively for extinct or endangered taxa. Such a view underestimates the intricate processes of species extinctions, especially in complex ecosystems such as tropical rainforests, where many species obligately depend on one another.

The term "coextinction" was first used to describe the process of the loss of parasitic insects with the loss of their hosts (*5*). The concept has been expanded to describe the demise of a broader array of interacting species,

including predators with their prey (*6*) and specialist herbivores with their host plants (*7*). Here, we define coextinction as the loss of a species (the affiliate) upon the loss of another (the host). The most often cited example is that of the extinct passenger pigeon (*Ectopistes migratorius*) and its parasitic louse (*Columbicola extinctus*) (*5*), although the latter has been shown to be alive and well on other hosts (*8*, *9*). More recently, the loss of tropical butterfly species from Singapore was attributed to the loss of their specific larval host plants (*7*).

Here, we apply a simple probabilistic model to empirical "affiliation matrices" (host by affiliate presence/absence matrices) to examine the relationship between affiliate and host extinctions across a range of coevolved interspecific systems: pollinating *Ficus* wasps and *Ficus*, primate parasites (*Pneumocystis* fungi, nematodes, and lice) and their hosts, parasitic mites and lice and their avian hosts, butterflies and their larval host plants, and ant butterflies and their host ants. The model estimates the number of affiliate extinctions as a function of the number of host extinctions, assuming a random order of host extinction (*10*). Figure 1 shows the predicted coextinction curves for eight relatively well studied affiliate-host systems. The coextinction curve is linear for affiliate-host systems in which each affiliate species was associated with only one host, such as *Pneumocystis* fungi and their primate hosts, and curvilinear for systems in which at least some affiliate species have multiple hosts, such as butterflies and their larval host plants.

This probabilistic model relies on fully specified affiliation matrices and thus is not useful for estimating expected numbers of affiliate extinctions in affiliate-host systems for which host specificity distributions are unavailable. To estimate coextinction levels for these affiliate-host systems, we have developed a nomographic model of affiliate extinctions that expresses affiliate extinction
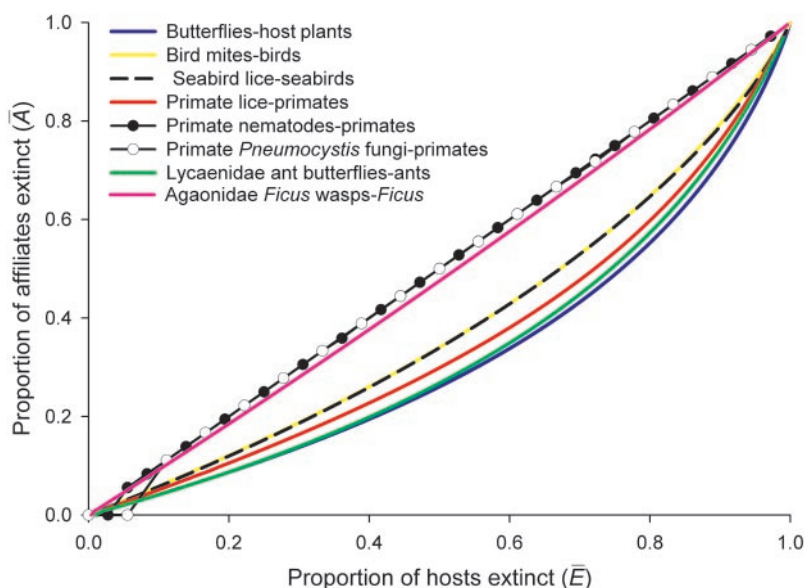
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Fig. 1. Proportion of affiliate species expected to go extinct through coextinction for a given proportion of host extinction in eight affiliate-host systems: pollinating Agaonidae *Ficus* wasps–*Ficus*, primate *Pneumocystis* fungi–primates, primate nematodes–primates, primate lice–primates, seabird lice–seabirds, bird mites–birds, butterflies–host plants, and Lycaenidae ant butterflies–ants. Coextinction curves were estimated with a rigorous probabilistic model. Briefly, we used an explicit combinatorial model (*20*) as implemented in EstimateS 7 (*21*) to estimate, for each data set, the number of affiliate species expected to survive, given a decreasing number of surviving host species. The estimated number of affiliate extinctions for a given number of host extinctions was then computed by subtracting the number of surviving species from the respective total number of species. See (*10*) for details.

probability as a function of host extinction probability and mean host specificity (Fig. 2) (10). This alternative approach is useful for estimating coextinction levels because mean host specificity is easier to approximate than complete host specificity distributions for many affiliate-host systems. The nomographic model reveals that affiliate extinction levels can be expected to decrease approximately log-linearly as the mean number of hosts increases, for any given level of host extinction (Fig. 2). The estimated affiliate extinction probability, $\overline{A}$, is described by the equation

$$\overline{A} = (0.35\overline{E} - 0.43)\overline{E}\ln(\overline{s}) + \overline{E} \quad (1)$$

where $\overline{E}$ is the host extinction probability and $\overline{s}$ is the mean host specificity of the affiliate species. Affiliate extinction levels estimated by this equation are highly concordant (concordance correlation $R_c >$ 0.99) with those predicted by the probabilistic model for all 20 affiliate-host systems we analyzed (10).

For selected affiliate-host groups, we estimate the magnitude of historical affiliate extinctions due to the documented loss of their hosts, as well as future affiliate extinctions if all their currently endangered hosts [International Union for Conservation of Nature and Natural Resources (IUCN) categories of "critically endangered," "en-dangered," and "vulnerable" (11)] were to go extinct. We estimate that at least 200 affiliate species have become extinct historically from the extinction of their hosts in these groups (Fig. 3A), and another 6300 affiliate species are currently "coendangered"—likely to go extinct if their currently endangered hosts in these groups become extinct (Fig. 3B).

For all but the most host-specific affiliate groups (e.g., primate *Pneumocystis* fungi and primates), affiliate extinction levels may be modest at low levels of host extinction but can be expected to rise quickly as host extinctions increase to levels predicted in the near future (2, 3). This curvilinear relationship between host and affiliate extinction levels may also explain, in part, why so few coextinction events have been documented to date (10). We modeled extinction risk as a probability. The actual numbers of affiliate extinctions depend on the species richness of affiliate groups at risk and can be expected to be substantial for species-rich affiliate taxa (e.g., beetles, Fig. 3B). Affiliate extinctions may already have resulted from historical extinctions of their hosts (Fig. 3A). However, only a small proportion of the number of affiliate extinctions that we predict on probabilistic grounds have been documented (10). The study of the skins or other remains of extinct potential host organisms (e.g., birds and mammals) would likely yield many more coextinct parasites or mutualists.

Organisms with complex life histories would be expected to have higher risks of coextinction over evolutionary time than those with simpler life histories. For example, hummingbird flower mites face extinction if either the hummingbirds they use for transport or the flowers on which the mites depend for nectar and pollen go extinct (12). Conversely, in interactions where hosts are associated with many obligately dependent affiliate species, the loss of the host will result in the coextinctions of all its affiliated organisms. For example, the army ant, *Eciton burchelli*, hosts no fewer than 100 affiliate species, including springtails, beetles, mites, and ant birds (13). Many of these affiliate organisms would hence be lost were *E. burchelli* to go extinct (14). Because a disproportionate number of affiliate species obligately depend upon them for their continued existence, species like *E. burchelli* may be considered a "keystone mutualist," a keystone species in an evolutionary sense (15). The ecological importance and conservation implications of keystone mutualists deserve further investigation because their loss will likely result in multiple extinction cascades.

It might be argued that there is no need to focus on the endangerment of affiliate species, because their protection follows automatically from the protection of their endangered hosts. Although this may be the case for some categories of affiliates (e.g., obligate endoparasites with simple life cycles), affiliates that depend on complex ecological interactions between multiple hosts, or affiliates that have demographic thresholds more sensitive than those of their hosts (7, 12) may be at greater risk of extinction than their hosts. Further, some affiliates may be lost when their hosts are intentionally fumigated (16). On the other hand, in some cases declines in host populations threatened by human activities may be exacerbated by the negative effects of affiliates. For example, forest habitat fragmentation in North America has favored the parasitic brown-headed cowbird (*Molothrus ater*) at the expense of some of its declining hosts (17). In such cases, if other threats to hosts cannot be remedied, control of affiliates, even at the risk of their possible extinction, must be contemplated. There is no point in attempting to save an affiliate if its host(s) become extinct in the process. Although this study is about species coextinctions, we expect the loss of host populations to result in the loss of affiliate populations. For example, Koh *et al.* (7) recently reported that local extinc-
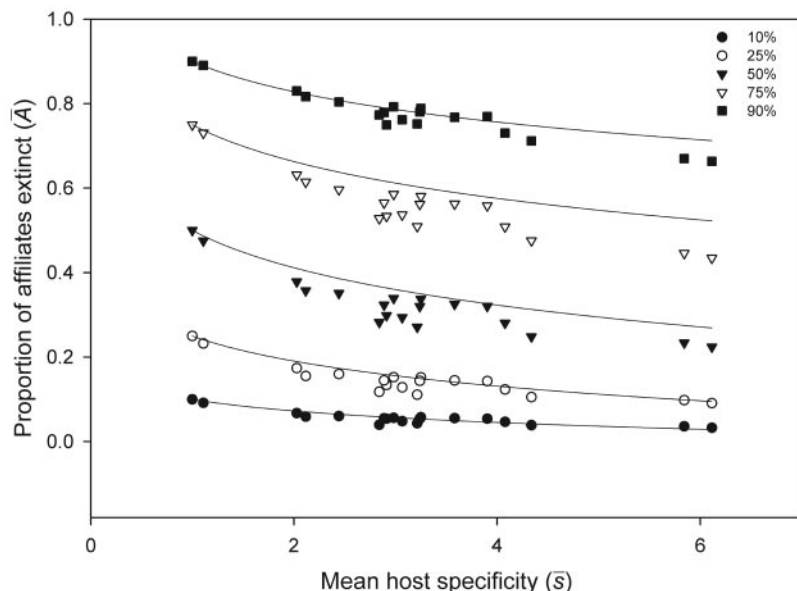

Fig. 2. Nomographic model expressing affiliate extinction probability as a function of host extinction probability and mean host specificity for 20 affiliate-host systems of varying mean host specificities: pollinating Agaonidae *Ficus* wasps–*Ficus*, primate *Pneumocystis* fungi–primates, primate nematodes–primates, primate lice–primates, seabird lice–seabirds, bird mites (including Avenzoariidae, Alloptidae, Analgidae, Proctophyllodidae, Pterolichidae, Pteronyssidae, Ptiloxenidae, Syringobiidae, and Xolalgidae)–birds, butterflies (including Papilionidae, Nymphalidae, Pieridae, Lycaenidae, and Hesperiidae)–host plants, and Lycaenidae ant butterflies–ants. See (10) for method. The affiliate extinction levels predicted by the nomographic model were highly concordant (concordant correlations $R_c >$ 0.99) with those predicted from the probabilistic model (10). Symbols and lines represent predicted affiliate extinction levels from the probabilistic and nomographic models, respectively.

A

Plants (99, <0.1%) — Beetles (69, <0.1%)
Fish (90, 0.3%) — Monogenean (71, 0.3%)
Birds (132, 1.3%) — Bird lice (36, 0.9%)
Birds (132, 1.3%) — Bird mites (20, 0.7%; 19, 0.7%)
Mammals (78, 1.7%) — Mammal lice (6, 1.0%)
Plants (99, <0.1%) — Butterflies (2, <0.1%; 2, <0.1%)

Number of extinct host species — Estimated number of affiliate species extinctions

B

Plants (6279, 2.0%) — Beetles (4672, 0.4%)
Fish (746, 2.6%) — Monogenean (593, 2.4%)
Birds (1194, 12.1%) — Bird lice (342, 8.7%)
Birds (1194, 12.1%) — Bird mites (193, 7.1%; 194, 7.1%)
Plants (6279, 2.0%) — Butterflies (136, 0.8%; 142, 0.8%)
Mammals (1130, 24.4%) — Mammal lice (92, 16.6%)
Primates (114, 48.9%) — Primate nematodes (20, 48.9%; 20, 48.9%)
Primates (114, 48.9%) — Primate lice (12, 35.4%; 10, 30.0%)
Primates (114, 48.9%) — Primate *Pneumocystis* fungi (9, 48.9%; 9, 48.9%)
Ficus (23, 3.1%) — *Ficus* wasps (9, 2.9%; 8, 2.8%)
Ants (142, 1.4%) — Ant butterflies (Lycaenidae) (5, 0.7%; 5, 0.7%)
Canadian fish (22, 11.5%) — Metazoan parasites (5, 2.5%)

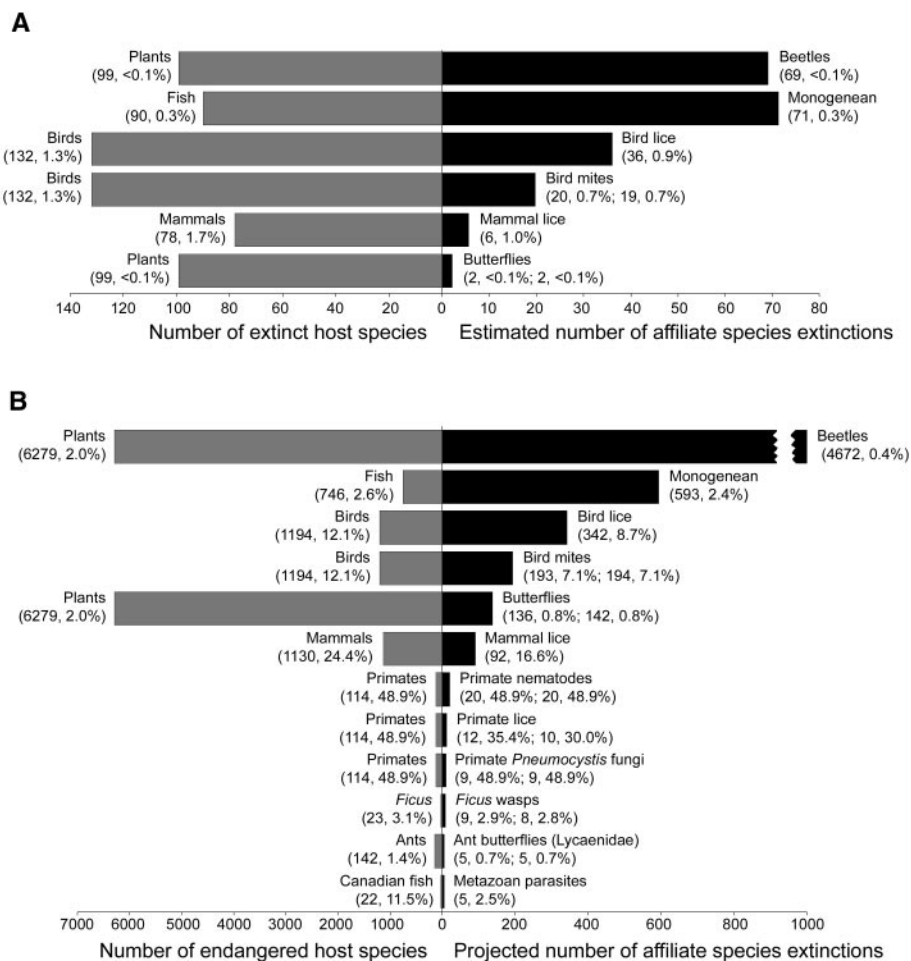Number of endangered host species — Projected number of affiliate species extinctions

Fig. 3. Predictions of affiliate extinctions from the nomographic and combinatorial models. (**A**) Estimated numbers of historically extinct affiliate species based on the number of host species recorded as extinct. (**B**) Projected numbers of affiliate species extinctions, were all currently endangered hosts to go extinct. The first value in parentheses represents the absolute number and the second value the percentage of species extinct or endangered as predicted by the nomographic model; the second set of values in parentheses represents predictions from the combinatorial model for selected affiliate-host groups for which affiliation matrices are available. See (*10*) for details.

tions of butterfly species were significantly correlated with local extinctions of specific larval host plants (*7*). The issue of species or population coextinction has immediate implications for local conservation and management decisions.

Species coextinction is a manifestation of the interconnectedness of organisms in complex ecosystems. The loss of species through coextinction represents the loss of irreplaceable evolutionary and coevolutionary history (*18, 19*). In view of the global extinction crisis (*3*), it is imperative that coextinction be the focus of future research to understand the intricate processes of species extinctions. While coextinction may not be the most important cause of species extinctions, it is certainly an insidious one.

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