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Tolerance of pollination networks to species extinctions

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Mutually beneficial interactions between flowering plants and animal pollinators represent a critical 'ecosystem service' under threat of anthropogenic extinction. We explored probable patterns of extinction in two large networks of plants and flower visitors by simulating the removal of pollinators and consequent loss of the plants that depend upon them for reproduction. For each network, we removed pollinators at random, systematically from least-linked (most specialized) to most-linked (most generalized), and systematically from most- to least-linked. Plant species diversity declined most rapidly with preferential removal of the most-linked pollinators, but declines were no worse than linear. This relative tolerance to extinction derives from redundancy in pollinators per plant and from nested topology of the networks. Tolerance in pollination networks contrasts with catastrophic declines reported from standard food webs. The discrepancy may be a result of the method used: previous studies removed species from multiple trophic levels based only on their linkage, whereas our preferential removal of pollinators reflects their greater risk of extinction relative to that of plants. In both pollination networks, the most-linked pollinators were bumble-bees and some solitary bees. These animals should receive special attention in efforts to conserve temperate pollination systems.

Keywords: conservation; food webs; generalization; nestedness; pollination; redundancy

1. INTRODUCTION

The healthy functioning of natural and managed ecosystems provides gratis 'services' essential to humankind (Costanza *et al.* 1997; Daily 1997). Both ecosystem functioning and delivery of ecosystem services are positively related to biodiversity (Loreau *et al.* 2001), and thus both are at risk from species loss. Unfortunately, the biosphere is entering a period of greatly increased extinction of local populations and entire species, caused by anthropogenic changes in habitats and climate, and the introduction of alien organisms (Hughes *et al.* 1997; Sala *et al.* 2000). One task facing ecologists is to predict how this 'sixth mass extinction' will affect ecosystems and their functioning.

We model extinction cascades for a critical ecosystem service, the pollination of flowering plants by animals. Pollination by animals is a ubiquitous ecological interaction in virtually all terrestrial ecosystems, involving more than 90% of flowering plant species by some estimates (Nabhan & Buchmann 1997; Renner 1998) and, by virtue of the high diversity of flowering plants and pollinating insects, a large fraction (approximately one third) of described species on earth (e.g. Wilson 1992; Kearns *et al.* 1998). Given the tendency of plants to use multiple pollinators and *vice versa* (e.g. Waser *et al.* 1996), pollination can be viewed at the level of an entire ecological community as a web, or network, of mutually beneficial (mutualistic) interactions between two trophic levels. In this context, the plants are primary producers and the animals are a special subset of primary consumers that feed on nectar and pollen. Pollination systems can thus be examined in light of the

theory of food webs (e.g. Memmott & Waser 2002; Dicks *et al.* 2002), and more generally of complex networks (e.g. Bascompte *et al.* 2003; Jordano *et al.* 2003).

Our intention is to analyse how pollination networks respond to loss of component species. Evidence is accruing that pollinator loss can lead to extinction of plant species (Bond 1995). By contrast, loss of floral resources is a key threat facing pollinating insects (e.g. Kearns *et al.* 1998). However, the patterns of extinction within entire pollination networks remain unknown. We ask the following questions. (i) How does cumulative depletion in the ranks of one mutualistic partner within a network lead to secondary depletion in the ranks of the other partner? As a starting point we explore the loss of pollinating animals and consequent extinction of non-pollinated plants; this reflects the evidence that most pollinators are at more immediate risk of extinction than plants (Tepedino 1979; Kevan 1991; Nabhan & Buchmann 1997; Kearns *et al.* 1998; Renner 1998). (ii) How do patterns of secondary extinction depend on the pollinators' degree of linkage with plants (or stated differently, their degree of specialization or generalization)? (iii) What properties of plant-pollinator networks contribute to observed patterns of extinction? (iv) Which groups of plants and pollinators are most important for conserving the network of interactions?

2. MATERIAL AND METHODS

(a) *The data*

We made use of the exhaustive records of flowers and their visitors provided in the classic studies of Clements & Long (1923) on Pikes Peak in the Rocky Mountains of Colorado, USA (hereafter referred to as C&L), and of Robertson (1929) in the prairie-forest

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transition of western Illinois, USA (hereafter referred to as R). Computerizing these data allowed construction of large pollination networks: 97 plant species forming 918 unique pairwise interactions with 275 pollinator species in C&L, and 456 plant species forming 15 265 unique pairwise interactions with 1428 pollinator species in R. This latter network is more than tenfold larger than most other available pollination networks, including C&L. Both webs were finely resolved, with no lumping of species by taxon or functional similarity. In C&L the data were collected in various subalpine habitats at *ca.* 2500 m elevation over 11 years (Clements & Long 1923), whereas in R they were collected within *ca.* 10 km of Carlinville, Illinois over 22 years (Robertson 1929).

(b) Extinction patterns

We simulated extinction by removing pollinator species and observing which plants were left non-pollinated as a result. This was carried out separately for each of the two pollination networks. Plant species were considered to go extinct within the local community upon loss of all their pollinators, due to failure of sexual reproduction.

We used three different algorithms to remove pollinators from C&L and R. For *random removal* (Albert *et al.* 2000) we removed increasing proportions of all pollinator species chosen at random and without replacement. This process was repeated 300 times for each web. Random removal represents a ‘null model’ with which to contrast two types of *systematic removal*, in which pollinator species were removed according to their number of links, i.e. the number of plant species that they visit. We systematically removed pollinators from the least-linked (most specialized) pollinator to the most-linked (most generalized); and conversely, from the most- to least-linked. The first approach is the same as that first used by Dunne *et al.* (2002), and here simulates a probable extinction sequence, because specialist pollinators, which also tend to be the rarest species (e.g. Vázquez & Aizen 2003), appear at greatest risk of real-world extinction (Rathcke & Jules 1993; Olesen & Jain 1994; Bond 1995). The second approach explores ‘attack tolerance’ of networks to loss of highly connected nodes (see Albert *et al.* 2000; Solé & Montoya 2001; Dunne *et al.* 2002). This represents a ‘worst case scenario’ but one that unfortunately is within the realm of possibility, for example with simultaneous declines in highly-connected pollinators such as honeybees (e.g. Watanabe 1994) and bumble-bees (e.g. Williams 1982).

Our simulation approach is a first attempt to predict extinction cascades in animal-pollinated networks. While this seems justified in the face of looming extinctions, we note several caveats. Simulated removal of animal species assumes that all flower visitors are equally effective pollinators of the plants they visit, so that a plant must lose all visitors before its rate of population growth becomes negative. Violation of this assumption means that our method may underestimate the consequences of losing animal species, but the assumption is forced upon us by lack of data for *any* pollination web on the relative effectiveness of all flower visitors, much less on how mutualistic interactions affect population dynamics of individual plant species. We also tacitly assume that all plants require pollination to reproduce. In fact, some fraction of species can propagate clonally or apomictically, or can self-pollinate, but in most cases these alternatives will not ultimately prevent extinction following loss of sexual reproduction (Holsinger 2000). Finally, we assume that pollinators remaining after an extinction do not expand their floral diets, which could ‘rescue’ some plant species that otherwise would go unpollinated (Kondoh 2003). Although the sampling in both C&L and R is extensive enough to include most plant–pollinator links that actually occur, new links might

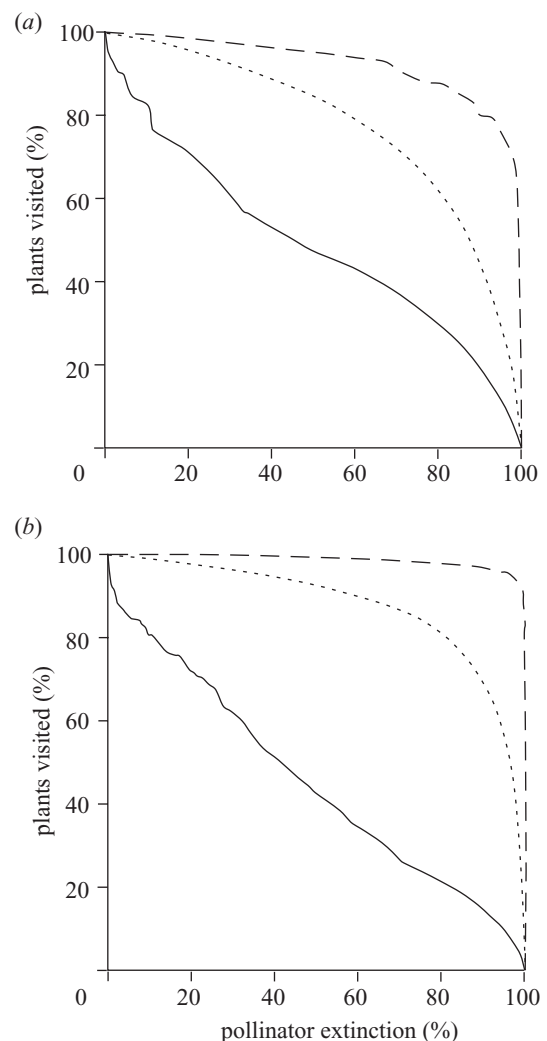


Figure 1. Extinction patterns for the pollination networks of (a) Clements & Long (1923; C&L) and (b) Robertson (1929; R). The solid line is most to least linked, the dashed line least to most and the dotted line is random extinctions. The error bars for random extinctions are extremely small and so are not shown.

arise during actual extinctions, if pollinators are released from competitors that formerly excluded them from some flowers. However this effect, which would moderate the impact of pollinator loss for plant extinctions, may be counterbalanced by relaxing the assumption that all visitors to flowers are pollinators of equivalent efficiency. Hence our approach seems a good first approximation even though it ignores some complexities of actual pollination systems.

3. RESULTS

Removal of pollinators by the three different algorithms (at random; from least- to most-linked; from most- to least-linked) caused different patterns of secondary plant extinction, and the C&L and R networks were qualitatively similar in their behaviour (figure 1). Random removal of pollinators elicited a steadily accelerating decline in plant species, with the bulk of plant extinctions occurring only after 70–80% of all pollinator species had perished. Systematic removal beginning with the least-linked (most specialized) pollinators yielded even more

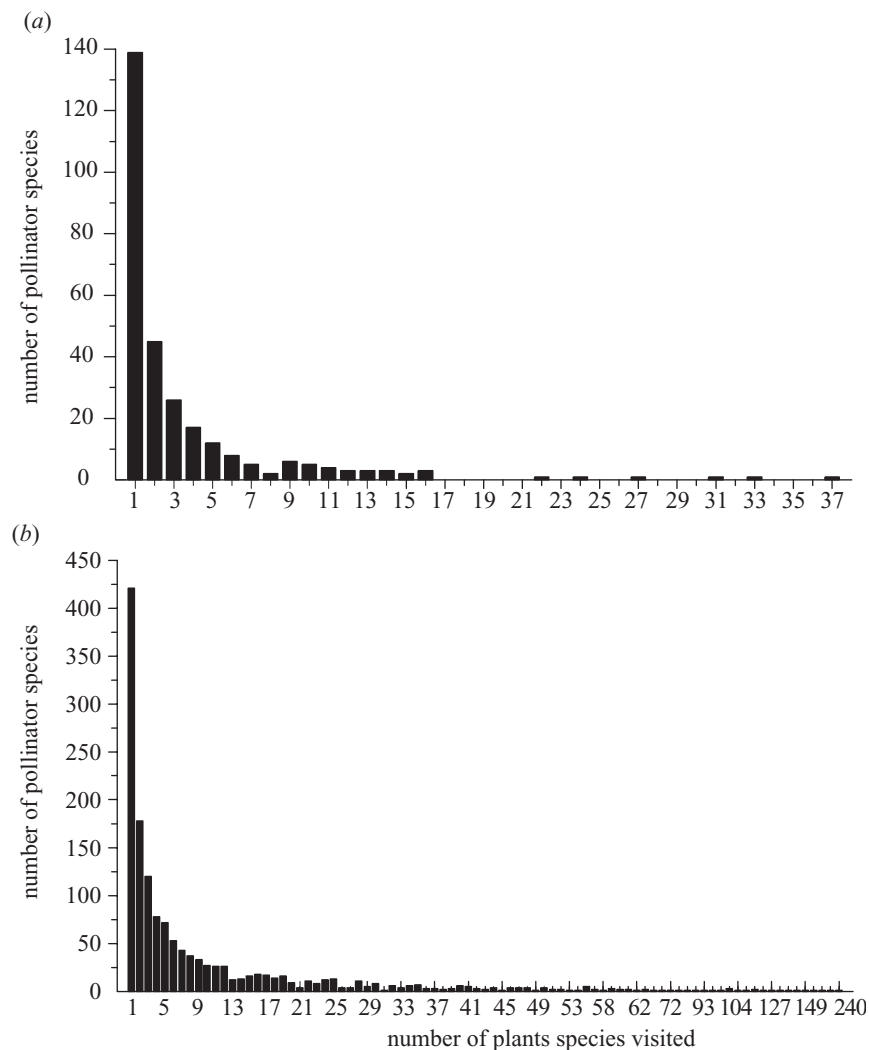


Figure 2. The distributions of plant species visited per pollinator species for (a) Clements & Long (1923; C&L), and (b) Robertson (1929; R).

dramatic nonlinearity, with very slow loss of plant species until almost all pollinators had perished, at which point plant species numbers dropped precipitously to zero. This was especially true in R: plants in this network were virtually unaffected until removal of the last ten most generalized pollinators, representing less than 1% of 1430 total animal species (figure 1b). Finally, systematic loss beginning with the most-linked pollinators deviated from random removal in the opposite direction, i.e. with a more rapid cumulative loss of plant species. However, the extinction functions for plants were essentially linear in this case, rather than dropping precipitously in one or more large steps.

4. DISCUSSION

Both pollination networks were relatively tolerant to extinction of component species. Loss of pollinators at random with respect to their linkage, and loss of pollinators beginning with the least-linked (most specialized in use of plants), caused only gradual declines in plant diversity. Even preferential loss of the most-linked (most generalized) pollinators elicited no worse than a linear decline. This last result differs from the extinction dynamics reported for standard antagonistic (predator–prey, host–parasite) food webs, in which

removal of the most-linked species quickly caused a collapse to low diversity (Solé & Montoya 2001; Dunne *et al.* 2002). In what follows we discuss topological features of the two pollination networks that contribute to their relative tolerance to extinction, and then explore why they behave differently to standard food webs. We conclude with recommendations for the conservation of pollination interactions and thoughts on assembly rules for pollination networks.

(a) *Tolerance to extinction and its causes*

Many networks are characterized by frequency distributions of the number of links per node ('degree distributions') that are *long tailed*, and such networks tolerate loss of random and least-linked nodes (e.g. Albert *et al.* 2000; Solé & Montoya 2001; Dunne *et al.* 2002). The best studied examples are scale-free networks with degree distributions that follow the power law $P(k) \propto k^{-\gamma}$, where $P(k)$ is the frequency of nodes (or species) with k links and γ is a constant, the 'degree exponent' (Albert *et al.* 2000). Jordano *et al.* (2003) examined several small qualitative mutualistic networks (both plant–pollinator and plant–seed disperser) and found that degree distributions for the animals were scale free over the entire observed range of k values, or else deviated beyond some value of k in the direction of fewer super-generalist animals than predicted (i.e. the power law

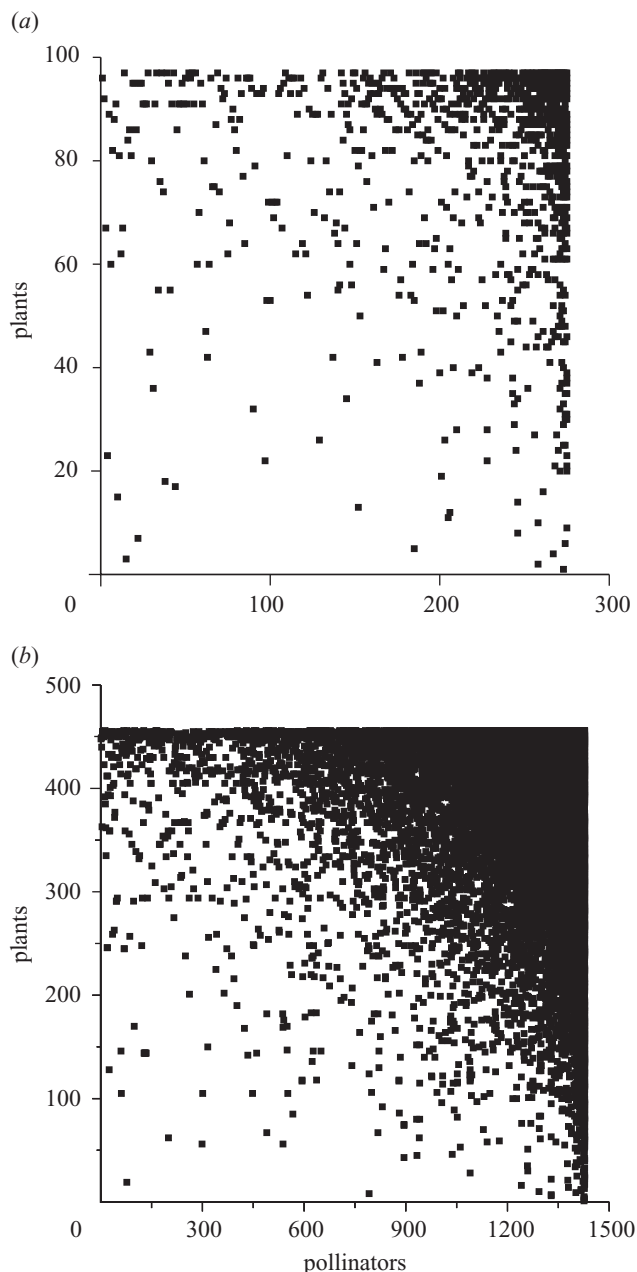


Figure 3. Nestedness in the C&L and R networks (*a* and *b*, respectively). Each figure arrays the plants upward along the *y*-axis from least- to most-linked (most specialized to most generalized), and the pollinators left to right along the *x*-axis from least- to most-linked. Each square denotes a link between a given plant species and pollinator species. The most-generalized (right-most) pollinator uses a substantial fraction of the plants; use of plants by the next most-generalized pollinator tends to be a nested subset, and so on.

fit was 'truncated'). In agreement with this, the distributions of plants visited per pollinator species are scale free in our much larger and more completely characterized pollination networks (figure 2):

For C&L: $y = 0.289t^{-1.2739}$, $r^2 = 0.877$

For R: $y = 0.3388t^{-1.4263}$, $r^2 = 0.896$

Tolerance of the C&L and R networks to loss of random and least-linked pollinator species therefore seems unsurprising.

By contrast, the fact that neither C&L nor R collapsed even when highly linked nodes (highly generalized pollinators) were first to go extinct suggests that additional properties must contribute to tolerance. One property is *redundancy* in the use of pollinators by plants. Pollinators outnumber plants by approximately 3 : 1 in both networks, and only 18% and 11% of the plant species in C&L and R, respectively, are limited to a single visitor species. This means that most plants are protected from extinction until the last of the multiple pollinators has gone extinct (although it should not be inferred, recalling the long-tailed degree distribution, that three pollinators per plant is the usual condition). An additional contributor to tolerance upon removal of the most-linked pollinators is *nestedness* (Atmar & Patterson 1993; Bascompte *et al.* 2003). Both C&L and R are significantly nested ($p < 0.001$ in both cases); that is, the second most generalized pollinator tends to interact with a subset of plant species visited by the most generalized, the third most generalized tends to interact with a subset visited by the second most generalized, and so on (figure 3). Nestedness in turn confers two important properties (as can be discerned from figure 3): a tendency of specialist plants to associate with generalist pollinators, and *vice versa*; and a lack of pronounced *compartments* (*sensu* Dicks *et al.* 2002), in which groups of plants and pollinators form associations largely or wholly disconnected from other such groups. Nestedness yields an essentially linear loss of plant species as pollinator species are 'peeled away' in order of decreasing generalization, because upon each such removal only a small subset of plants stands to lose the last pollinator.

(b) Comparison with previous network studies

In contrast to our results, removal of some intermediate fraction of the most-linked species caused the collapse of standard food webs studied by Solé & Montoya (2001) and Dunne *et al.* (2002). This difference is largely explained by how species were removed in simulations. We removed species at one trophic position only (pollinators), whereas Solé & Montoya (2001) and Dunne *et al.* (2002), whose goal was to explore 'attack tolerance', removed the most-linked species without regard to trophic position or other determinants of extinction risk. This difference has a profound effect. If we pool plants with pollinators and remove species from C&L and R according only to their linkage, the dynamics resemble those reported previously for standard food webs (compare figure 4*a,b* with 4*c,d*). Thus C&L collapses upon removal of the top 21% of most-linked species, and R collapses upon removal of the top 22%. These results make intuitive sense: redundancy and nestedness cannot protect a network from simultaneous removal of the most-linked plants (which take multiple specialist pollinators with them) as well as the most-linked pollinators (which take multiple specialist plants with them).

In general, secondary extinction patterns depend critically on how one assigns risk of primary extinction across species. Risk is not equal for all species, but instead will be greater for species of high trophic position, rare species, and specialists (e.g. Gilbert *et al.* 1998). As noted earlier (see § 1), pollinators are judged to be more at risk of anthropogenic extinction than plants, due to their higher trophic position and other aspects of their biology (including in

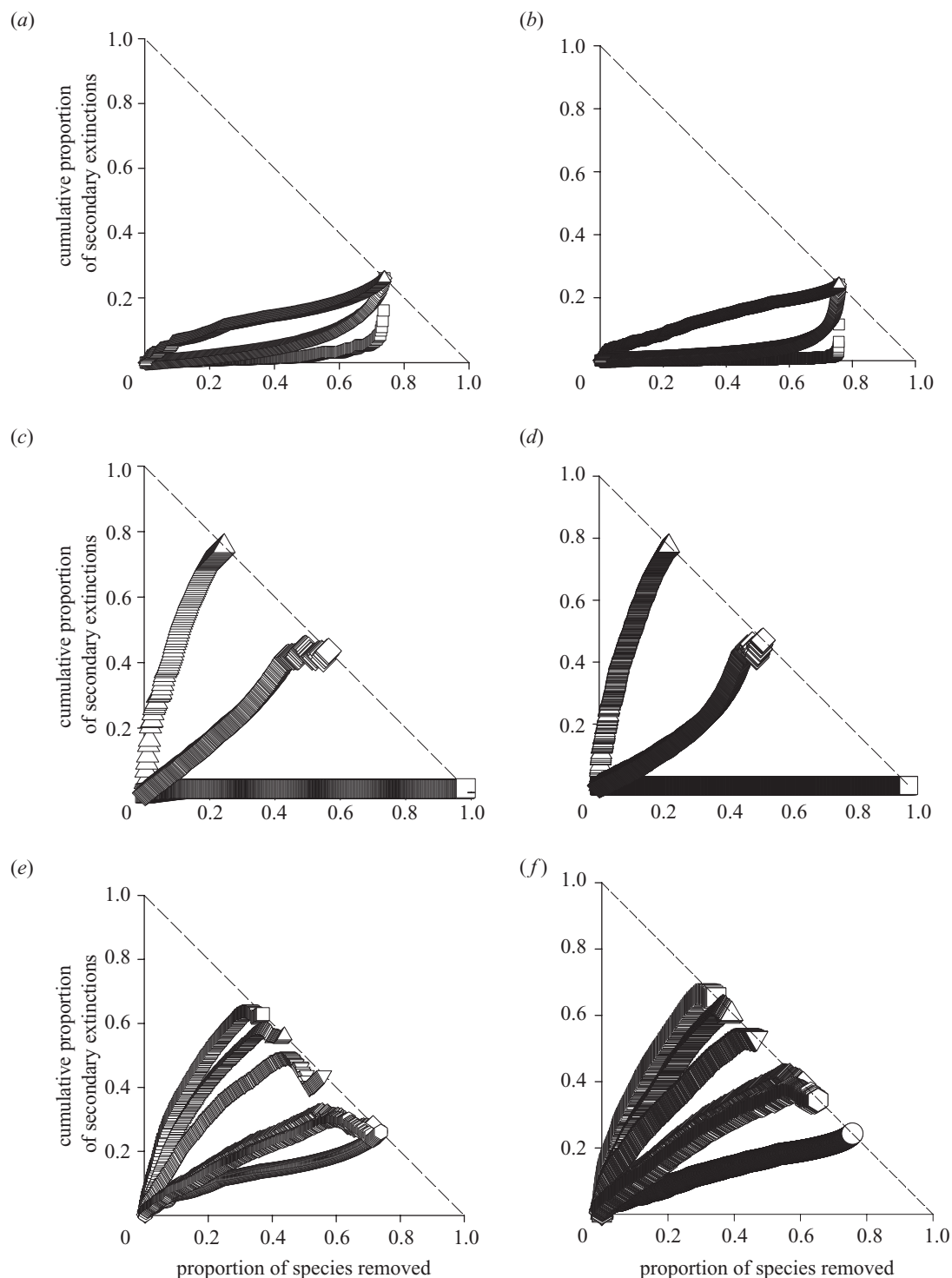


Figure 4. Proportion of species lost to secondary extinctions as a function of proportion of species removed (primary extinction) from C&L (left) and R (right). The diagonal dashed lines connect points at which all species in the network are lost, triangles = most-connected species removed first, squares = least-connected removed first, diamonds = random removal. In (a) and (b) pollinators alone are removed, and secondary extinctions are solely of plants (these are the same data as in figure 1, in different form). In (c) and (d) plants and pollinators are equally at risk of being removed. Intermediate cases (e,f) in which plants experience non-zero risk of primary extinction, but lower risk than for pollinators; only removal of most-connected species first is shown in these figures. Each curve in (e,f) represents the average of 300 replicate simulations, the error bars are smaller than the symbols and are not shown. Moving from the uppermost to lowermost curve in (e,f) represents the pollinators having twice the extinction risk, five times the risk, 10 times the risk, 40 times the risk, and 60 times the risk of the plants. Some curves dip downwards as they approach the diagonal as not all of the replicate simulations persist equally long before the whole pollination web becomes extinct. Those that persist longest have slower accumulation of secondary extinctions, so the mean of the cumulative secondary extinctions tends to be lower towards the end.

most cases small size, short lifespan, and lack of perennial habit).

These considerations suggest that the simulated secondary extinction would be less dramatic for standard food

webs if risk were assigned according to the attributes of component species. By contrast, pollination networks should be less tolerant if plants are assigned some risk. This last prediction is borne out by simulations in which plants have non-zero risk relative to pollinators: tolerance of the network declines as relative risk to plants is increased (figure 4e,f). Although some such intermediate risk is probably more realistic than simulated removal of pollinators alone, since herbivory, disease, climate change and other factors also threaten plants, we have focused on pollinators because no quantitative estimates are available of relative risk for plants versus pollinators, and the best qualitative estimates assign greater risk to the latter. Our approach is probably more realistic biologically than removal of plants and pollinators with equal probability, and thus yields a more realistic picture of likely extinction dynamics.

(c) *Implications for the conservation of pollination ecosystem services*

Relative tolerance of pollination systems is no argument for complacency about the ongoing extinction crisis, because tolerance is not synonymous with immunity to extinction. Rather than waiting for actual extinctions of pollinators, plants, and their interactions, we advocate management decisions formulated in advance from the best available information. Our simulations illustrate one possible approach. The simulations confirm an intuitive conclusion, that loss of generalist pollinators constitutes the gravest danger to pollination networks. In both R and C&L networks, these core pollinators derive mainly from insect orders Hymenoptera and Lepidoptera. Within Hymenoptera, they are the honeybee (*Apis mellifera*), bumble-bees (genus *Bombus*), and solitary bees (families Andrenidae, Colletidae, Halictidae, and Megachilidae and subfamily Anthophorinae within family Apidae). Thus, six of the 18 bee families in R and C&L are included in the core pollinator group. Within Lepidoptera, they are predominantly skippers (family Hesperiidae). These groups should be given high priority for research and management in an effort to conserve the pollination interactions in northern temperate ecosystems.

5. CONCLUDING REMARKS

Our intent here has been to explore how pollination networks behave when they are 'disassembled' via extinction. Some of the conclusions reached raise questions about the reverse process. Are pollination networks usually assembled through evolutionary and ecological time with long-tailed degree distributions, and if so, why? The continuum from specialization to generalization is highly correlated with the abundance of different pollinating animals, with common species appearing as generalists, perhaps as a sampling artefact or perhaps as a true reflection of diet breadth (Vázquez & Aizen 2003). Thus the question, in part, devolves to one of relative abundances. But does this suffice to explain the nested topology of the pollination network? The result is a striking pattern: rather than the compartments predicted by the classical view that plants are grouped according to specific associations with pollinators (e.g. Fægri & van der Pijl 1966), from which one expects specialists to associate with specialists and generalists with generalists, we find that specialists tend to associate with generalists. This result has been reported previously for

networks in general (Newman 2002) and for other pollination networks (Petanidou & Ellis 1996; Bascompte *et al.* 2003), but we are just beginning to understand its implications for ecosystem structure and function.

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