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LETTER

The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour

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Abstract

Species extinctions pose serious threats to the functioning of ecological communities worldwide. We used two qualitative and quantitative pollination networks to simulate extinction patterns following three removal scenarios: random removal and systematic removal of the strongest and weakest interactors. We accounted for pollinator behaviour by including potential links into temporal snapshots (12 consecutive 2-week networks) to reflect mutualists' ability to 'switch' interaction partners (re-wiring). Qualitative data suggested a linear or slower than linear secondary extinction while quantitative data showed sigmoidal decline of plant interaction strength upon removal of the strongest interactor. Temporal snapshots indicated greater stability of re-wired networks over static systems. Tolerance of generalized networks to species extinctions was high in the random removal scenario, with an increase in network stability if species formed new interactions. Anthropogenic disturbance, however, that promote the extinction of the strongest interactors might induce a sudden collapse of pollination networks.

Keywords

Behaviour, complex networks, extinction, habitat restoration, Mauritius, mutualism, network re-wiring, pollination.

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INTRODUCTION

The stability of ecological networks has been a focus of empirical and theoretical studies over several decades. Most of our current understanding of interactions in ecological communities derives from advances in predator–prey relationships in food web analyses (Polis 1998; Solé & Montoya 2001; Dunne *et al.* 2002; Kondoh 2003; Ives & Cardinale 2004; Montoya *et al.* 2006; Rooney *et al.* 2006). Although equally important, knowledge on the stability of mutualistic interaction networks is less developed, not least due to a lack of extensive and highly resolved quantitative datasets of pollination and seed dispersal communities.

Memmott *et al.* (2004) modelled the effect of mutualist extinctions on the stability of two temperate qualitative pollination networks and showed that preferential removal of the most-linked pollinators, considered as the worst-case scenario, resulted in a linear decline of plant species diversity. With the recent increase in data quality, quantitative analyses of ecological networks has revealed that simply focusing on diversity and richness metrics may disguise important changes in community structure and ecosystem functions (Bascompte *et al.* 2006; Bascompte & Jordano 2007; Tylianakis *et al.* 2007). In analyses of mutualistic networks, for example, the use of quantitative data has revealed strong asymmetrical dependencies (Bascompte *et al.* 2006; Vázquez *et al.* 2007). Furthermore, quantitative network parameters have revealed substantial changes in food web structure depending on the degree of habitat modification, which were not detected by their qualitative counterparts (Tylianakis *et al.* 2007). To provide accurate predictions of the stability of mutualistic networks to human-induced extinctions, the ideal approach is to use data from highly resolved, quantitative networks assembled over entire field seasons.

The lability of species interactions presents another challenge when analysing mutualistic systems. Like other ecological networks, the structure of pollination networks changes continually as pollinators switch plant species in response to the availability of resources and plant species attracting a changing pollinator assemblage throughout the season depending on pollinator phenology. The importance of such behavioural shifts to community persistence was clearly shown for food webs where switches in food choice were shown to stabilize food webs (Kondoh 2003). So far, few studies have considered behaviour in mutualistic networks, and those studies that have considered it, have analysed qualitative data (Petanidou 1991; Medan *et al.* 2002, 2006; Lundgren & Olesen 2005; Basilio *et al.* 2006; Fortuna & Bascompte 2006; Olesen *et al.* 2008; Petanidou *et al.* 2008). Plant–pollinator communities are dynamic systems in which species enter and exit frequently, causing interactions to establish, break down or vary substantially in frequency. This 're-wiring' has not yet been investigated in plant–pollinator communities despite its known prevalence. Moreover, re-wiring does not only include shifts of entire interactions but also shifts in the frequencies of mutual dependencies meaning that the standard network parameters do not change, but quantitative parameters such as interaction evenness could undergo large changes (see Tylianakis *et al.* 2007).

The stability of mutualistic networks can be affected by a range of human-induced processes. Species and population extinctions, the introduction of invasive species, and habitat restoration are only a few examples of anthropogenic changes in community composition and function. While advances in the analysis of complex ecological networks have furthered understanding of invasion processes (Morales & Aizen 2006; Lopezaraiza-Mikel *et al.* 2007; Aizen *et al.* 2008) we know little about how habitat restoration rebuilds ecological interactions in the system (but see Forup *et al.* 2008). Human-induced extinctions of populations and species impose a serious threat to biodiversity (Hughes *et al.* 1997; Sala *et al.* 2000), and by working with ecological networks, ecologists can begin to predict how the current wave of extinctions will affect ecosystems and their functioning (Tylianakis 2008).

In this study, we investigate the stability of mutualistic interactions by using two of the most comprehensive and temporally highly resolved pollination networks collected to date, and by accounting for behavioural processes in these communities. We draw on two published, fully quantitative pollination networks from Mauritius (Kaiser-Bunbury *et al.* 2009) to predict the resistance of dynamic mutualistic networks to species extinction. We ask two basic questions: (1) are quantitative networks more sensitive in detecting biological processes and therefore show different and potentially more realistic extinction patterns under different modelling scenarios compared with qualitative networks? (2) accounting for behaviour, do networks with re-wiring prove more stable compared with networks without re-wiring, as species loss will be ameliorated by newly established connections? We selected the two Mauritian networks – one restored site from which all introduced plants were removed, and one unrestored invaded site – to assess the impact of dominant exotic plant species on the robustness of plant–pollinator communities to extinction.

METHODS

Study system

The pollination networks were collected between September 2003 and March 2004 at two sites at Pétrin on Mauritius (20°42′ S, 57°44′ E). One of the communities, the restored site (6.2 ha), has been regularly managed since 1994 by manual removal of all exotic plants. The unrestored, heavily invaded site was of equal size and located *c.* 0.54 km from the restored site. In terms of native plant species richness and abundance both sites represent a similar sample of the original heath community in Mauritius (Vaughan & Wiehe 1937). The major difference between the plant communities of the two sites was the dominance of exotic plants at the unrestored site. While the pollination webs differed in size, reflecting higher floral and pollinator species richness and abundance at the restored site, network structure appeared to be similar. For a detailed description of site characteristics and plant–pollinator communities see Kaiser-Bunbury *et al.* (2009).

Data collection and quantification

The networks contained 74 and 64 species of woody flowering species and 135 and 100 pollinator species with a total of 744 and 534 species interactions at the restored and the unrestored site respectively. Flowering herbaceous species were almost absent from both sites, and those that were present, primarily orchids, occurred in such low numbers and with unpredictable flowering times that they could not be included in the network. Floral abundance was recorded following a stratified sampling scheme along 23 parallel transects at each site. We conducted random flower counts in 10 cubic metres along each transect every 2 weeks for 12 consecutive fortnights (230 cubes/site/fortnight). Pollination interactions were recorded by timed observations, of 30 min duration, on randomly selected flowering individuals across the study site. Each flowering species was observed on average for 1.84 ± 0.5 h (mean ± SD; restored) and 1.72 ± 0.6 h (unrestored) during each 2-week period, amounting to 471 and 387.5 h across the full season in the restored and the unrestored site respectively. We recorded the identity of all flower visitors that touched the sexual parts of flowers, the number of flowers observed, and the number of visits by each pollinator. Each visitor approaching a flowering plant was considered a separate visit and the majority of pollinators were pollen collectors/feeders such as beetles and flies (see Kaiser 2006; Kaiser-Bunbury *et al.* 2009). We used the total number of visits of each animal species as pollinator abundance.

Floral abundance is expressed as the mean number of flowers (F) per cubic metre ($F\,\mathrm{m}^{-3}$). We used visitation frequency as a measure of mutual interaction strength between a plant and an animal species (Vázquez *et al.* 2005; Sahli & Conner 2007), and defined normalized interaction strength $L_N(i,j)$ as the total number of visits (V) per flower per hour (h) ($V/F \times h$) of animal species i. Absolute interaction strength $L_A(i,j)$ between animal species i and plant species j is then defined as $L_N(i,j)$ times the floral abundance $F\,\mathrm{m}^{-3}$ of plant j. That is, each visit was quantified based on the floral abundance of the interaction partner, thus the unit of L_A is $V\,\mathrm{hm}^{-3}$. The interaction strength of a *species* then corresponds to the sum of the strengths of all interactions in which a species is involved, i.e. $N_A(i)=\sum_j L_A(i,j)$ and $N_A(j)=\sum_i L_A(i,j)$ for animals and plants, respectively, and the total interaction strength present in the network sums up to $N_A=\sum_i N_A(i)=\sum_j N_A(j)$. Both networks are strongly asymmetrical, with a few highly generalized abundant species and many specialized rare species (Kaiser-Bunbury *et al.* 2009), whereby the level of generalization refers to the number of mutualistic partners in the community.

In addition to the full-season networks, we used 12 temporal networks each representing a 2-week subsection of the full-season networks. The recording of floral abundance and pollinator activity was carried out repeatedly at 2-week intervals throughout the flowering season. Thus, each temporal network represents a defined temporal sub-unit of the full-season networks (see also Kaiser 2006; Kaiser-Bunbury *et al.* 2009). These 2-week webs are referred to forthwith as 'temporal snapshots'. In comparison with full-season networks, the temporal snapshots reflect more realistic network structures as they include only species with existent phenological or morphological overlap, i.e. no forbidden links (sensu Vázquez 2005). While forbidden links have often been overlooked in the analysis of mutualistic networks (Olesen & Jordano 2002), they may act as an obstacle when modelling species extinction as they inflate the number of potential links and, consequently, overestimate network stability. In addition, as plant–pollinator communities are subject to continuous spatial and temporal change in species composition, temporal snapshots can be used to investigate whether network structure is inherent to the system or if it changes throughout the season.

Qualitative and quantitative species removal simulations

We removed plants and pollinators from both networks following three extinction scenarios: systematic removal from the strongest interactor (either plant or pollinator species), systematic removal from the weakest interactor and random removal without replacement, where a species was considered to be extinct if it was left without plant host or animal pollinator. Similar to Memmott *et al.* (2004) and Dunne *et al.* (2002), random removal represents a null model with which to compare two types of systematic removal. Removal from the weakest interactor simulates a potential extinction sequence as weakly linked plants and pollinators appear at greatest risk of real-world extinction (Rathcke & Jules 1993; Olesen & Jain 1994), and the removal from the strongest interactor explores the 'attack tolerance' of networks to loss of highly connected nodes (see Albert *et al.* 2000; Solé & Montoya 2001; Dunne *et al.* 2002).

We use both full-season networks and temporal snapshots to assess the effect of species removal on interaction partners under a restoration scenario, the plot where the dominant introduced plant species have been removed and the adjacent control plot. While there is no replication of the treatment effect, this analysis provides a first approximation of the short-term impact of removing dominant food supplies (see Lopezaraiza-Mikel *et al.* 2007; Bartomeus *et al.* 2008) from a pollination network. The removal of alien plants is a feature of most restoration programmes, but the impact of this management approach on ecological networks is rarely considered (Carvalheiro *et al.* 2008; Dixon 2009).

Qualitative models

Qualitative interaction data (i.e. presence/absence of interactions) was used to model the effect of pollinator removal on plant species diversity and vice versa. In this model each species was considered to contribute equally to the fraction of extinction among pollinators or plants, e.g. if originally the network contains 10 plant species and one species becomes extinct, 10% of the plants are considered to be extinct. These analyses were carried out on both entire networks and on the 12 temporal snapshots of each full-season network.

Quantitative models

Having fully-quantitative interaction networks allows a more sophisticated model scenario than the qualitative models described above. These are closer to natural processes because each species shows different interaction frequencies and abundances in the system. Here, abundant and highly linked pollinators or plants are considered more important to the system than rare or specialized ones. Thus, the extinction of a species i as a result of not being visited was given the impact corresponding to its interaction strength $N_A(i)$, meaning that the total interaction strength present in the network N_A declines immediately by the amount $N_A(i)$ once the species i dies out. Thus, the removal of different species leads to different levels of surviving interaction strength N_A. As above, the analyses were carried out on the two entire networks and the 12 temporal snapshots of each network (for network data see Appendix S6).

Adding behaviour to the networks

The two full-season networks provide an estimate of all the potential interactions in the network and this information can be used to add behavioural shifts to the 12 snapshots as follows. All interactions observed at least once in each full-season network were considered *potential* links and these were used as 're-wiring' options for potentially disrupted links of the respective temporal networks, i.e. dietary switches leading to new links in the 12 temporal snapshots.

We applied models described above to the temporal snapshots accounting for re-wiring processes. Models were calculated for temporal snapshot based on the species and interaction strength observed in the respective fortnight, and the *potential* links derived from the full-season networks accounting for re-wiring. For example, when a pollinator species i in the temporal snapshot t_1 lost all interactions as a consequence of the extinction of its mutualistic partners, i will remain in the model with its full interaction strength if t_1 contains plant species with which i interacted at any other time throughout the season. Thus, in contrast to previous studies which used additional re-wiring modelling assumptions, such as preferential attachment (e.g. Olesen *et al.* 2008), we applied information on potential re-wiring links derived from the empirical information available in the full-season networks. No species were added to temporal snapshots to avoid false assumptions on phenological overlap. Similarly, species interaction strength did not change following re-wiring in the models. Interactions strength N_A was used to define the importance of mutualistic species in the network, and the species' properties remained the same throughout the modelling.

RESULTS

Qualitative and quantitative species removal simulations

Qualitative models

For both communities, the decay of pollinator- and plant species richness with mutualist loss for the three extinction scenarios (systematic removal from the strongest interactor, systematic removal from the weakest interactor and random removal) are depicted in Fig. 1. The extinction patterns of plant and pollinators in the qualitative models were, at most, linear (removal of strongest interactors), and the decay was much slower than linear as plant and pollinators were removed randomly from the networks (Fig. 1a,b).

We used temporal snapshots from each site to investigate whether the observed patterns were consistent throughout the season and independent of network size and phenological

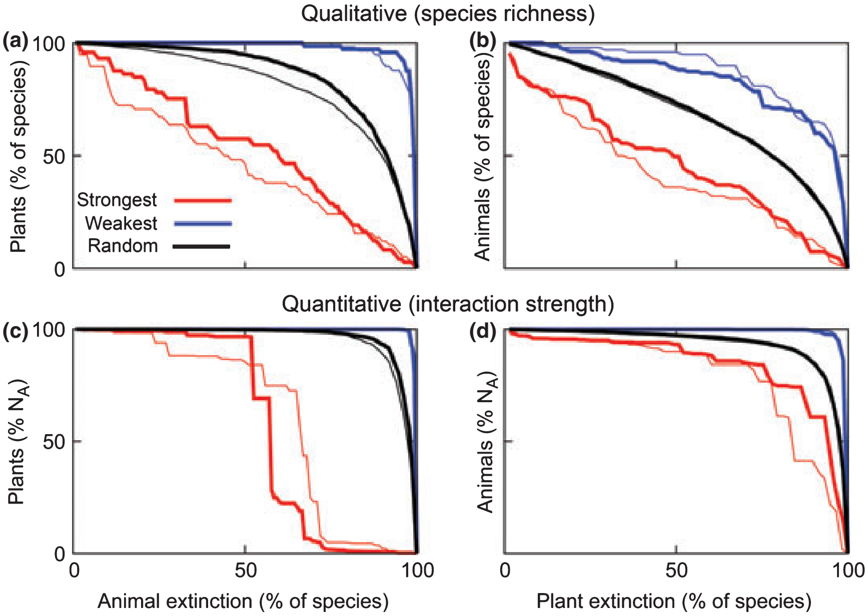

Figure 1 Extinction plots upon systematic removal from the strongest or weakest interactor, and random removal. (a, b) Qualitative data, i.e. presence/absence of interactions; (c, d) quantitative data, i.e. interaction strength, both for the full-season networks. Thick lines (restored site) and thin lines (unrestored site) show extinction patterns of the different restoration schemes. The left panels (a, c) displays the decline of plant species and interaction strength following the removal of animal species, and the right panels (b, d) display the decline of animal species and interaction strength following the removal of plant species.

mismatches in the networks. Across all temporal snapshots we observed extinction patterns similar to those observed in the full-season networks. The qualitative models showed in 92% (secondary plant extinction; Appendix S1) and 58% (secondary animal extinction; Appendix S3) of the snapshots a linear or less than linear relationship between mutualist extinctions when the strongest interactors were systematically removed from the networks.

Quantitative models

In contrast to the qualitative models, the quantitative models depicting the decay in interaction strength showed that animal removal according to their importance to the network leads to a sigmoidal decline with a rapid collapse of the overall interaction strength (N_A) of plant species in the system (Fig. 1c). This sudden decline – the removal of 20% of animal species (between 40% and 60% total animal removal) resulted in the loss of 95% of plant interactions – was caused by the secondary extinction of a few disproportionately dominant plant species (three and five species in the restored and unrestored site respectively). These species dropped in large steps from the networks as the interactions with their pollinators were systematically removed. Both systematic removal from the weakest animal interactor and random removal appeared to affect interaction strength of plant species less than in the qualitative removal scheme; a decline occurred only after 80–90% of all pollinator species had been removed. Interestingly, animal interaction strength appeared to be more resistant to plant species extinction. Given that even when the strongest plant interactors were removed first, a noticeable but gentle decline in animal interaction strength set in only after 50–60% of plant species had vanished (Fig. 1d).

Similar to the qualitative networks, the quantitative extinction patterns of the temporal snapshots resembled the patterns observed in the full-season quantitative networks. The decline of plant interaction strength as a consequence of animal extinction followed a sigmoidal shape in 75% of temporal snapshots, and the extinction curves of the systematic removal of the weakest interactors indicated a high robustness of the networks to the removal of weak links throughout the season (Appendices S1 and S2). Comparing qualitative and quantitative models that depict the proportion of mutualist species and their interactions that need to be removed from the temporal network to cause a 50% secondary extinction, robustness to extinction was significantly greater in quantitative models throughout the random removal scenarios at both sites and for animals and plants (Fig. 2b,d–f). During the systematic removal of the strongest interactors, however, quantitative models showed an inconsistent pattern (Fig. 2a,c,e,g). For plant species, quantitative models suggested significantly greater robustness than qualitative models (restored: 0.74 ± 0.15 vs. 0.51 ± 0.13 mean ± SD; unrestored: 0.75 ± 0.17 vs. 0.57 ± 0.13), while this pattern was reversed when pollinators were systematically removed (restored: 0.48 ± 0.22 vs. 0.64 ± 0.14; unrestored = non-significant; Fig. 2a,e). Thus, pollinators appeared to react less sensitively to secondary extinction than plant species.

The quantitative models indicated that the effects of targeted extinctions may be exacerbated by within-season fluctuations in network susceptibility to secondary extinctions. Simulated random loss of mutualists showed a low level of within-season fluctuation [coefficient of variation (CV) = 0.06 ± 0.015 SD] in comparison to the systematic removal of species and interactions (CV = 0.28 ± 0.09 SD). There was no indication for greater network stability in the middle of the flowering season in comparison to the beginning or the end of the season, when community assembly and disassembly could reduce network stability.

The restored and the unrestored site showed similar extinction patterns in the full-season networks (Fig. 1), and inconsistent or marginal differences in the temporal networks (Fig. 2; Appendices S1–S4). For example, modelled animal extinction resulted in a similar secondary extinction of plant species interactions in six of the 12 temporal snapshots (quantitative data; Appendix S2, plots 2, 5, 8–10, 12), while in four snapshots plant species interactions started to decay at lower levels of pollinator extinction in the restored site compared with the unrestored site (Appendix S2, plots 1, 3, 6–7).

Adding behaviour to the networks

Re-wiring consistently increased the stability of networks when strong interactors were systematically removed, both in qualitative and quantitative models (Fig. 3; $P < 0.05$, Wilcoxon paired signed-rank test). Stability, expressed as the percentage of species and interactions removed to cause a 50% secondary extinction, increased on average by 22.7% in qualitative and quantitative models. The relative change in stability through re-wiring between both models was equal because species interaction strength remained the same throughout the modelling, and species or interactions were removed from the model at once when the last link was lost. The degree of increase in stability, however, fluctuated depending on the type of data and removal scheme. An increase in stability due to re-wiring in qualitative networks did not generally correspond to patterns observed in the quantitative networks; there was no significant relationship between the changes over time in the qualitative and the quantitative models with re-wiring (Spearman rank correlation, $P > 0.05$; see Fig. 3e,f, snapshots 1–3,6–7; Fig. 3a,b, snapshots 7–8; Appendix S5: compare black and red lines in the plot showing 90% secondary plant extinction risk). Also,

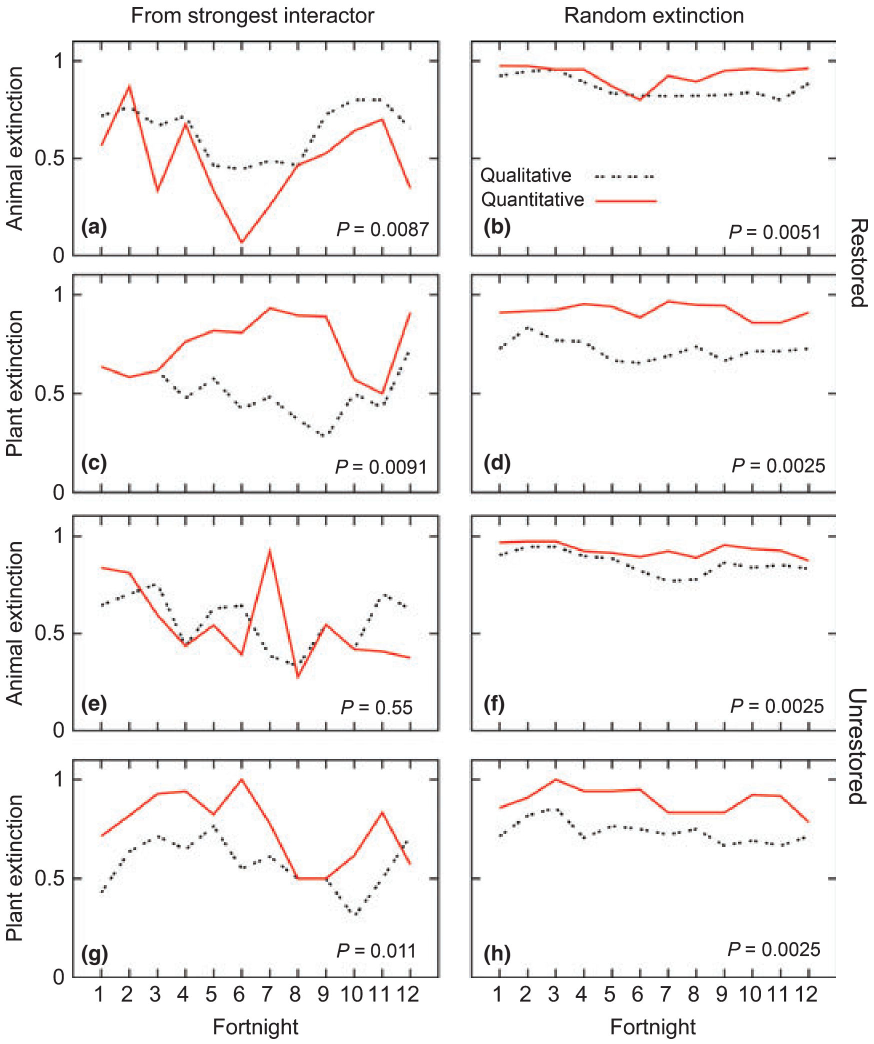

Figure 2 Summary plots of qualitative and quantitative extinction models in temporal networks of the restored (a–d) and the unrestored (e–h) site. Each plot displays the amount pollinator (a, b, e, f) and plant (c, d, g, h) species or interaction strength to be removed (*y*-axis; proportion to be removed) to cause 50% secondary extinction of plants and pollinators, respectively, across the 12 temporal snapshots. Shown are only extinction models with systematic removal from strongest interactor and random removal; systematic removal from weakest interactor was omitted from the figure as it showed consistently low secondary extinction throughout the season. Dashed black lines: qualitative models based on species richness; thick red lines: quantitative models based on interaction strength. *P* values refer to the comparison of mean proportion of plant and animal extinctions of qualitative and quantitative models by Wilcoxon paired ranked test in R 2.9 (R Development Core Team 2009).

when the weakest interactors were systematically removed, re-wiring added little to the stability of the networks in contrast to when the strongest interactors were removed first. The higher number of species and interactions in the restored site did not result in a significant increase in system stability through re-wiring (Fig. 3b,d,f,h; animals – restored: 0.86 ± 0.12, unrestored: 0.85 ± .017; plants – restored: 0.89 ± 0.10, unrestored: 0.82 ± 0.12; $P > 0.05$).

DISCUSSION

Our data demonstrates the value in using quantitative data when considering the effect of species loss in ecological networks. In the worst-case scenario (i.e. systematic removal from the strongest interactor) the quantitative models revealed that the networks may experience a sudden collapse, a pattern not seen in the qualitative models. Furthermore, accounting for the ability of pollinators to perform behavioural shifts, e.g. pollinators switch hosts and plants attract other pollinators, following the loss of their mutualistic partners substantially increased the stability of the networks, and the effect was largest when the strongest interactors were being removed from the networks. There are no marked differences in the models between the restored and the unrestored site, suggesting that exotic plant removal does not affect the tolerance of pollination networks to extinction. In the following section we discuss the limitations of our models, the difference in qualitative and quantitative species removal simulations, the importance of behaviour for the tolerance of networks to extinction and the implications of restoration for mutualistic networks.

Model limitations

While we are well aware of the constraints of simulated removal of plant and pollinators, this study attempts to minimize the impact of any assumption on the outcome of the models by using highly resolved, fully quantified, and

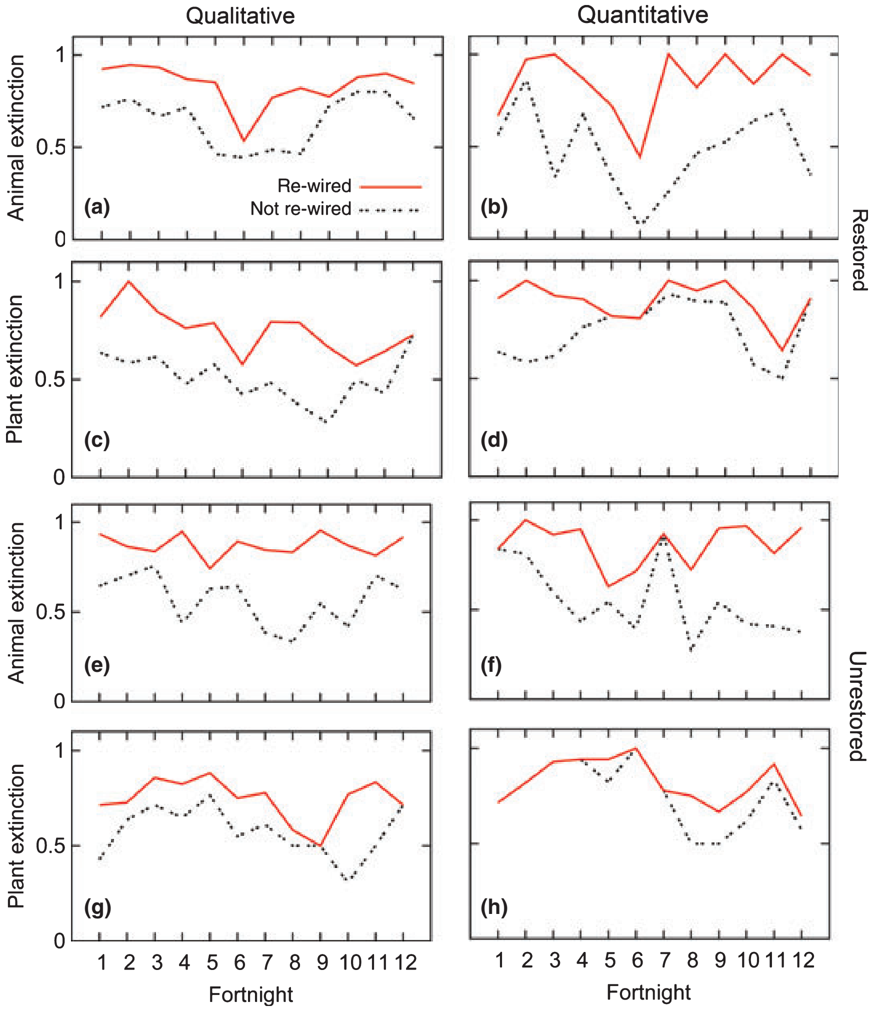

Figure 3 Plots of qualitative and quantitative extinction models with systematic removal from strongest interactor in temporal networks of the restored (a–d) and the unrestored (e–h) site. Each plot displays the amount pollinator (a, b, e, f) and plant (c, d, g, h) species (qualitative) or interaction strength (quantitative) to be removed (*y*-axis; proportion to be removed) to cause 50% secondary extinction of plants and pollinators, respectively, across the 12 temporal snapshots. Dashed black lines: re-wiring was not permitted; thick red lines: re-wiring was permitted. Systematic removal from weakest interactor and 10% and 90% secondary extinction scenarios are displayed in Appendix S5. For further interpretation see text.

temporally and spatially extensive pollination networks. As in Memmott *et al.* (2004), though, we do not have data on the relative effectiveness of pollinators, and thus risk underestimating the consequences of losing a pollinator species. Vázquez *et al.* (2005) and Sahli & Conner (2007) demonstrated that the most abundant flower visitor was likely to be the most important pollinator, providing that the observed flower visitors in the networks are a subset of all potential pollinators and thereby limiting the between-species variation in pollination quality. Data on pollinator abundance is clearly incorporated into our models, and by recording only visitors that touched the reproductive parts of the flowers, the Mauritian networks satisfy the conditions of relatively even pollination quality between species. Lastly, we assume that all plant species require pollinators to reproduce instead of relying on self-pollination or vegetative means of propagation, which may underestimate plant survival following pollinator removal. In the long term, however, all plant species need to reproduce sexually to secure survival as vegetative reproduction and self-pollination are only short-term survival strategies which prohibit evolutionary adaptation to environmental changes.

Qualitative and quantitative species removal simulations

Our qualitative analysis of Mauritian pollination networks shows a response in tolerance to extinction in mutualistic networks similar to the previous qualitative models (Memmott *et al.* 2004) and to other studies which explore the consequences of species removal on mutualistic networks (Fortuna & Bascompte 2006; Jordano *et al.* 2006). Memmott *et al.* (2004) explained network stability with certain topological features, such as a long-tailed degree distribution, nestedness and a high degree of redundancy, and comparable values were also described from the Mauritian networks (Kaiser 2006). However, our networks showed rather different secondary extinction patterns in the quantitative models. While most quantitative models suggested a higher degree of stability compared with the qualitative models, one scenario in particular, systematic removal of the most frequently visiting pollinator species, triggered a sharp drop in plant visitations when 50–60% of pollinator species were removed from the system. The lack of quantitative information is likely to have been the reason why Memmott *et al.* (2004) did not observe the collapse of the system, which had previously been described in food web studies (Solé & Montoya 2001; Dunne *et al.* 2002). One possible explanation for this pattern is that many mutualistic interactions are highly asymmetrical (Bascompte & Jordano 2007; Kaiser-Bunbury *et al.* 2009). Our models suggest that under random removal scenarios, interaction asymmetry contributes substantially to the stability of systems. For example, the qualitative model of the full-season network (Fig. 1b) shows that for 45% of animal species to be affected by secondary extinction 75% of plant species need to go extinct. In comparison, for 45% animal extinction in the quantitative model, 98% of plants must be lost (Fig. 1d). In contrast to qualitative data, which assume that observed interactions are equally important, quantitative data account for asymmetries in mutualist dependence measured as interaction strength. Although it was suggested that strong asymmetrical interactions in food webs can destabilize networks (May 1973; McCann *et al.* 1998; Albert *et al.* 2000; but see Rooney *et al.* 2006), it is now widely considered that asymmetry in fact contributes to the stability of mutualistic systems (Vázquez & Aizen 2004; Bascompte *et al.* 2006; Vázquez *et al.* 2007). This can also be seen in the higher sensitivity of plants to secondary extinction compared with pollinators (see Fig. 1). Abundant and highly linked pollinators interacted both with a few dominant and many rare plant species, while dominant plant species were visited to a higher degree by equally dominant pollinator species (see also Kaiser 2006). Consequently, the systematic removal of the strongest interactors affected the plant community more severely than pollinator community. Thus, neglecting quantitative data on interaction frequency is likely to result in an underestimate of network stability when extinction acts at random, over evolutionary timescales, and an overestimate when key pollinators die out selectively, either induced by humans or through rare natural catastrophes.

In natural communities, the systematic removal of the strongest animal mutualist is less probable than random or selective extinctions of rare and specialized mutualists. Nevertheless, anthropogenic actions and ecological processes can indeed result in the selective decline and local extinction of the most abundant species in the system. Bumble bees, for example, which are important pollinators of many crops and wildflowers, have declined rapidly in many parts of Europe and North America (Williams 1982; Goulson *et al.* 2008 and reference therein), causing associated plant species to decline in the Netherlands and the UK (Biesmeijer *et al.* 2006). Although those scenarios are likely to be rare events, the modelling of such worst-case scenarios furthers our understanding of complex network structure and clearly demonstrates that quantitative data is crucial for modelling species loss in ecological networks.

Rather predictable was the insignificant impact of the systematic removal of weakest interactors on secondary extinction in qualitative and quantitative models of the full-season networks. The qualitative models of the temporal snapshots, however, depicted a pattern similar to that described by Dunne *et al.* (2002); a quarter of the snapshots showed relatively high secondary extinctions (Appendices S1 and S3; plot 7 and plots 1, 6, 8–9, 11 respectively) indicating a disproportionately large negative effect caused by topologically insignificant species. Such patterns were absent in the quantitative models (Appendices S2 and S4), which suggests that the impact of rare and specialized species on secondary extinction was overrated in the qualitative models, and that natural systems are relatively resistant to the systematic removal of weak interactors.

Adding behaviour to the networks

In our models, we made use of the extensive information on pair-wise interactions provided by the full-season networks and used this information to incorporate behaviour (re-wiring) into the temporal networks. Although pollinator behaviour is not accounting for the only potential shift in mutualistic networks, e.g. a change in plant phenology due to global warming can result in temporal shifts within networks, such shifts are far less likely to occur and happen on a larger temporal scale than re-wiring processes due to changes in pollinator behaviour. Along with behavioural and phenological shifts in pollinators and plants respectively, changes in abundance can increase absolute morphological and phenological variability of both plants and pollinators, which can further result in alterations in mutualistic interactions on a relatively short temporal scale. While these temporal fluctuations may play a role in the stability of pollination networks, we focus here primarily on the behavioural changes of pollinators which can, due to their mobility, react quickly to alterations in resource availability.

Our results suggest that re-wiring buffers the impact of species loss by indirectly increasing connectance and, thereby, adds to the stability of the system (Dunne *et al.* 2002). Re-wiring relies heavily on the presence of a sufficient diversity of species and interactions to create a pool for potential re-wiring options. For example, Mauritian pollinators appeared to be more vulnerable to secondary extinction at times when few plant species were flowering in the community (e.g. Appendix S3, plots 1, 9). Such fluctuations in flowering species can occur naturally at the beginning and the end of the season or they can be human-induced through, e.g. regular mowing of meadows, habitat destruction, or logging.

Re-wiring processes may be easier in generalized systems with fewer forbidden links due to long overlapping phenophases in plants and the presence of pollinators with broad diets. Re-wiring allows species to change their tolerance to perturbations in the systems and consequently modifies the order of secondary extinction. Rare species and specialists are at greater risk of extinction (e.g. Gilbert *et al.* 1998), but through re-wiring they may become more important to the system after other species go extinct. Those species may ameliorate the stability of the networks and may have contributed to the greater robustness of the models in which behavioural shifts were permitted (see Fig. 3).

Comparison of the two networks

There was no consistent difference between the response of the restored and control plot to simulated species loss. Forup *et al.* (2008) reported a trend towards increased robustness in restored plots, but they were limited in their analysis by a small sample size, a limitation even more apparent here. In reality, the only way to determine the impact of restoration on network structure is to have a sample size sufficient for a robust statistical analysis (e.g. see Henson *et al.* 2009). There is a trade-off between network quality and network quantity, and it is simply time- and cost-prohibitive to construct a large number of detailed biotic networks. However, there are ways around this problem. For example, Tylianakis *et al.* (2007) solved it by using a simple, replicable method of bioassaying the local parasitoid community at 48 sites. While their method entailed intensive rearing of natural enemies, it did not require long hours of observation in the field.

CONCLUSION

We used quantitative interaction data to investigate the effects of the loss of species and interactions at the community level on pollination networks in Mauritius. These data revealed that species loss had a strong impact on the networks, with the loss of 50–60% of the 24 most connected animals (but not plants) causing a sudden and rapid collapse of the total interaction strength, a pattern which was not seen using the qualitative models. While this is an extreme scenario, anthropogenic modifications and disturbances to natural systems may create the conditions that increase the probability of these worst-case scenarios, for example the simultaneous declines of bumble bees and honey bees (e.g. Williams 1982; Oldroyd 2007). Our work has shown that having detailed qualitative networks is not necessarily sufficient when predicting the effects of species loss on network structure. Including quantitative information on the frequency of interactions in our simulations significantly changed the impact of species loss on the networks. Moreover, adding behaviour to the networks also affected the simulation output, substantually ameliorating the impact of species loss. Increasing the realism of the ecological networks we use when predicting the expected impacts of environmental changes is likely to amplify our prediction powers and thereby our understanding of natural ecosystems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Plant species extinction patterns following animal extinction scenarios of systematic removal from the strongest interactor and systematic removal from the weakest interactor of 12 consecutive temporal snapshots.

Appendix S2 Same as Appendix S1. The quantitative models are based on interaction strength data.

Appendix S3 Same as Appendix S1 for animal species extinction patterns following plant extinction scenarios.

Appendix S4 Same as Appendix S2 for animal species extinction patterns following plant extinction scenarios and quantitative models are based on interaction strength data.

Appendix S5 Summary plots of extinction models in temporal networks of the restored and the unrestored site without and with re-wiring.

Appendix S6 Data of 12 temporal networks for qualitative and quantitative extinction models.

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