

Extremes: understanding flower-visitor interactions in a changing climate

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ABSTRACT

We argue here that climate change studies which focus only on single species will be inadequate to address the complexity of causal mechanisms, as climate effects will percolate through entire ecological communities. Changes in species distributions may be considered as: 1) fully independent, in which case each species will respond directly to environmental factors; 2) dependent upon a set of biological interactions among species; or 3) of a combination of both environmental and biological factors.

Our second point is that climate extremes will drive substantial change beyond any changes in averages – and that it is these rare outlier events that are most likely to be relevant for Australia and for the arid zone in particular.

A corollary of this point is that at present, the extremes, e.g. rainfall in the arid zone, are currently unpredictable and this unpredictability is likely to further increase as the extremes increase. This could lead to events of greater severity, more frequent extreme events of current magnitude, or a combination of both. It is not known to what extent the Southern Oscillation Index and the El Niño/La Niña cycles will be altered.

We illustrate our case by considering the interactions among flowering plants and their floral visitors in the Simpson Desert.

Key words: species interactions, ecological communities, climate change, extreme climate, interaction networks, flower-visitor interactions, arid zone.

Introduction

Climate change presents new challenges for delivering robust conservation strategies for wildlife. Current changes are well documented (IPCC 2007 and reviewed for Australia in Hughes 2011) but uncertainties in the projected degree of future change, the appropriate modelling framework to use (Araujo and Rahbek 2006; Elith *et al.* 2006) and the expected response of ecological communities limit our ability to predict which species will persist and where. Furthermore, our current approach to modelling the relationship of distributions of species and climate assumes that species are in equilibrium with current climates and that climate, above all other factors, is responsible for their realised distributions. We know this to be untrue as species exist in communities and participate in a complex array of interactions to obtain food, compete for habitat, disperse seeds, or achieve effective pollination (Gotelli *et al.* 2010). These networks of interactions play an important role in the maintenance of biodiversity, the mediation of community responses to perturbations such as climate change, and the stability of ecosystem services (Bascompte and Jordano 2007).

Species interactions have, however, received relatively little attention in research investigating the effects of climate change (but see Gotelli *et al.* 2010; Kissling *et al.* 2010). Progress has been made on the direct effects of changed climatic averages on the potential for changes in species distributions, abundances and local

extinctions (Bertin 2008; Hughes 2003). In turn, as the combinations of species and distributions adjust to the new climatic regime, novel interactions and communities will eventuate. We propose that interactions are useful to detect the first evidence of altered environments before a species declines in numbers, shifts in distribution or even disappears. Interactions are commonly climate dependent as they are sensitive to the phenology, behaviour, physiology and relative abundances of multiple species (Gilman *et al.* 2010; Tylianakis *et al.* 2008). Climate-driven changes in species interactions can manifest themselves as completely novel interactions or as a change in the type or strength of an interaction, if previously interacting partners no longer spatially or temporally overlap. Therefore, our understanding of the potential effects of climate change will improve if we incorporate our knowledge of the ecological interactions among species into future projections and management frameworks. Quantifying changes in interactions at a system level and detecting climate-driven signals over other environmental drivers will be difficult, but this difficulty can be overcome with sufficient effort and resources given the importance of such findings.

Changes in mean temperatures and rainfall, and increases in the frequency and intensity of extreme weather events have already been recorded around the globe (IPCC 2007). Despite predictions that extreme weather events

will change in intensity and frequency, the effects of such events on species and ecological communities have received relatively little attention, perhaps because they are episodic and brief. Yet extreme events are likely to have pervasive and dramatic effects on community structure and dynamics (Chesson *et al.* 2004; Jentsch *et al.* 2009; Kreyling *et al.* 2008; Thibault and Brown 2008).

In this paper, we aim to contribute to the understanding of the mechanisms by which ecological communities and the species within them will respond to climate change. We start by highlighting that, in general, species interactions are already considered an important factor in shaping the distribution and abundance of species. We demonstrate how climatic changes have already affected ecological communities by altering species interactions. By using flower – visitor interactions in the Simpson Desert as a case study, we outline the importance of extreme climatic events as a driver of change; we illustrate how species interactions can be studied on a community level; and we highlight the advantages and insights this approach provides.

Climate change, ecological communities and species interactions

Interactions are one of the most important factors structuring ecological communities, and are often central in determining species' distribution, abundance and fitness (Bruno *et al.* 2003; Hairston *et al.* 1960). Cascade effects, bottom-up effects, ecological release, and facilitation are a few common ways interactions structure ecological communities. Climate change has influenced virtually every type of species interaction (Tylianakis *et al.* 2008), which means the outcomes of interactions frequently depend on climate. For instance, an increase in water temperature reduced rates of predation by a predatory fish on claddisfly larvae (Kishi *et al.* 2005). Changes in interactions between two species can have flow-on effects throughout a community. In the previous example, increased abundance of the herbivorous claddisfly larvae led to a decrease in the abundance of benthic algae due to herbivory. Interestingly, a single species study showed that under conditions of warming, benthic algae increased in abundance (Kishi *et al.* 2005). The use of a simple food chain demonstrates that any response a species has to a change in climate does not exist in isolation. Rather, other members of the community (which may or may not be directly affected by climate change) can be indirectly affected via species interactions. These effects can be more important than direct effects (Gilman *et al.* 2010).

Altered interactions affect simple food chains in relatively predictable ways, provided a good understanding exists of the interactions within the food chain. Effects on a community, however, are not necessarily consistent with species-specific and simple food chain projections (Tylianakis *et al.* 2008). In contrast, the ecological community comprises a greater number of species, multiple pathways and complex feedbacks. This can make the effects of change unexpected and drastic. For instance, a combination of warming climate and fire suppression in

Alaska led to the conversion of spruce forest to grassland due to a change in interactions (Walker *et al.* 1999). Warming enabled the spruce bark beetle to complete two life cycles per season as opposed to one. In this case, the trees were particularly old, as fire had been suppressed to protect nearby property. The increased attack from the beetles caused most of the older susceptible trees to die, allowing grasses to establish. The grasses promoted increased fire frequency, which in turn prevented the forest from returning. Complexity in communities also means that true effects can take years to eventuate, and can differ substantially from immediate effects. In an experimental grassland, an increase in spring precipitation led to an increase in native nitrogen-fixing forbs in the first year, and stimulated grasses in the second year (Suttle *et al.* 2007). By the fifth year, the subsequent decrease in plant species richness led to a reduction in invertebrate richness and herbivore and predator abundance.

It is evident that an altered climate can affect species interactions, and seemingly minor changes can combine to exert important effects on entire communities (Tylianakis *et al.* 2008). The identification of interactions that will have important effects on an ecological community should they change, can form the foundations of a prediction about the effects of climate change. We can then use this information to formulate actions to mitigate the effects. Ideally, such interactions would best be recognised by using system-level studies that incorporate all interactions, provided methods are sensitive enough to detect changes. System-level studies also enable us to recognise community structure that leads to desirable function such as resistance to perturbation. Species participate in multiple interactions that link them to one or many other species that can be studied as complex networks (Bascompte and Jordano 2007; Memmott 1999). The topology of these networks plays an important role in the maintenance of biodiversity and the stability of ecosystem services (Bascompte and Jordano 2007). The preservation of network topology will, therefore, be important to mitigate the effects of climate change (Tylianakis *et al.* 2010).

Climatic extremes and community response

Climate extremes are predicted to increase in frequency and severity under climate change. While climatic averages have been explored most intensively, recent studies suggest that extreme events may have more pervasive effects on species interactions. These events are by their nature large, infrequent and stochastic, and can lead to changes in the structure, functioning and persistence of ecological communities. For example, increased rainfall variability has been shown to modify competitive interactions, species dominance and the composition of rodent, macropod and plant communities (Chesson *et al.* 2004; Thibault and Brown 2008), shift functional and numerical responses of predators to their prey (Pavey *et al.* 2008), decouple trophic linkages (Both *et al.* 2009; Brook 2009) and influence the occurrence of wildfires (Letnic and Dickman 2006).

Case Study: Flower-visitor interactions in the Simpson Desert

Building complex interaction networks

Flower-visitor interactions are an ideal system to study at a community scale. Insects are the most common flower visitors, but other invertebrates, birds, mammals and even reptiles also visit flowers. Such interactions involve hundreds of thousands of species across the globe, and depending on the species richness of any given area, can involve hundreds of species in any system (Olesen and Jordano 2002). Animals usually visit a flower to harvest nectar or pollen, but also to consume floral parts or even prey on other visitors (Pellmyr 2002). Flower visitation interactions are also the precursor to mutualistic pollination interactions, which is the transfer of pollen from the male to the female part of a flower by an animal in return for a reward, enabling the plant to reproduce. Pollination interactions are a vital ecosystem service required for the maintenance of natural plant and pollinator communities and agricultural productivity (Potts *et al.* 2010).

Flower-visitor interactions can be arranged into networks, just as predatory interactions can be arranged into food webs. A network illustrates all the visitation interactions that were recorded in the community in a defined area and period of time. Concepts from network theory underpin methods to quantify and statistically compare the network structure of different communities, or even the same community over time (Bascompte and Jordano 2007), a useful tool when looking at the effects of climate change. Network structure also has implications for the functioning of the network. For example, a network with nested structure, in which specialised species interact with a subset of the interaction partners of the more generalised species (Bascompte *et al.* 2003), is more tolerant to random species extinction (Memmott *et al.* 2004). This is partly because as species are lost from nested networks, only a small subset of species risk losing their last interacting partner species (Memmott *et al.* 2004).

Once the overall topology of a network is established, it is useful to characterise the type and strength of each interaction and examine how they vary over space and time, as changes to these parameters will provide a signal of climate driven changes. Firstly, flower visitors may be robbing nectar and pollen rewards, eating floral parts, or preying on other insects, and therefore it cannot be assumed that visitors are equivalent to pollinators (Pellmyr 2002). Quantifying the pollen carried on visitors' bodies by examining it under a microscope is a necessary but time-consuming initial step towards identifying potential pollinators. Secondly, elements of interaction strength can be crudely incorporated by recording the frequency of interaction over a given time period; ideally it would incorporate additional elements. The interaction strength between a plant species and its pollinator species will depend both on how dependent that plant is on a given pollinator species, and on the pollinator performance

of a given species which incorporates frequency and effectiveness of the pollination interaction (Ne'eman *et al.* 2010). Finally, conclusive evidence of the type and strength of interaction between a plant and its floral visitor requires manipulative experiments which ultimately follow these factors to determine the fitness effects for the plants and the invertebrate visitors. Few studies have achieved this level of detail to date for a single species, let alone whole networks, but progress is possible if the importance of the results is understood.

Temporal variation of interactions in an already variable environment

The arid zone constitutes 70% of the Australian continent, and is a highly unpredictable and extreme environment. Like other arid environments around the world, it is extreme in temperature and rainfall. The Simpson Desert in south-west Queensland is classified as a hot, dry desert with an average annual rainfall of about 150mm. Climatic averages are, however, a poor indicator of water availability in this environment. Compared to areas of similar average annual rainfall around the world, the climate of arid Australia is unusually unpredictable (Morton *et al.* 2011; Stafford Smith 2008). There are periods of very low rainfall (Figure 1), which, combined with high rates of evaporation, lead to prolonged periods of low water availability and even drought. Dry periods are periodically interrupted by large rainfall events (Figure 1), in which an amount in excess of the average annual rainfall can fall in a day, causing widespread flooding. Large rainfall events are the principal biological and physical drivers in the arid zone (Morton *et al.* 2011). They stimulate plant germination, growth and reproduction, with flow-on effects throughout the ecological community (Chesson *et al.* 2004), driving the classic 'boom-bust' pattern. This variable rainfall pattern is influenced by the phase of the El Niño Southern Oscillation, which is expected to intensify in magnitude due to climate change (IPCC 2007). We can therefore expect longer and drier droughts and rainfall events of greater magnitude.

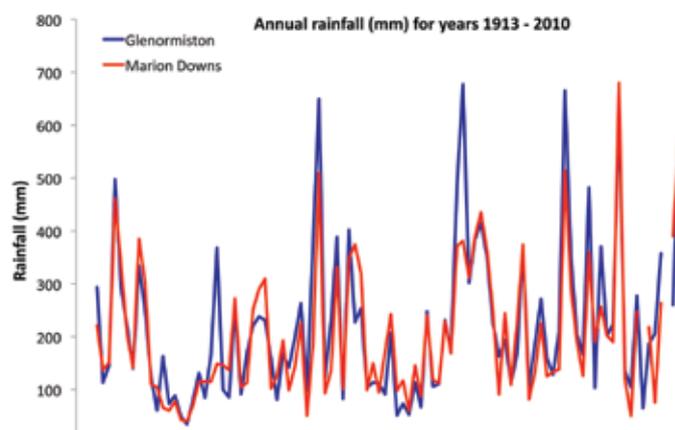


Figure 1. Yearly rainfall (mm) recorded for Glenormiston and Marion Downs stations for the period between 1913 to 2010. This illustrates the variability in annual rainfall on the edge of the Simpson Desert, SW Queensland (Source: BOM).

The timing of species interactions in arid Australia is fundamentally different to those in temperate or seasonal environments due to climatic unpredictability. Species in seasonal environments respond to environmental cues such as temperature and day length in precise ways, making them highly sensitive to climatic change (Walther 2010). Any variation in their phenology (timing of life

history events) could affect their interactions with other species, especially if their interacting partners respond asynchronously (Gilman *et al.* 2010; Walther 2010).

Plant phenological records from our study sites in the Simpson Desert, SW QLD (Popic *et al.* 2011 in review), show great temporal variation in plant flowering (Figure 2). Plant phenology was surveyed

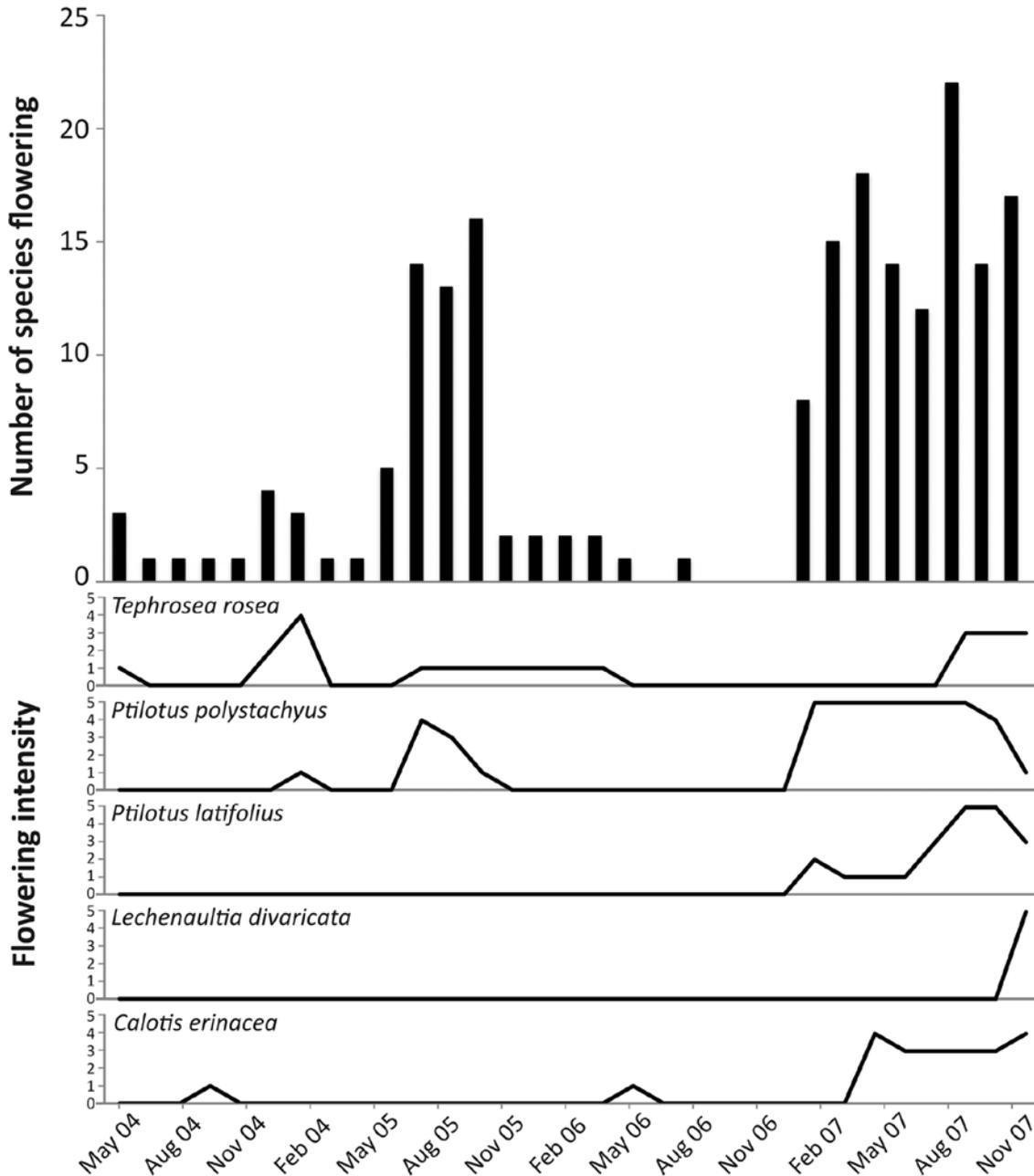


Figure 2. The number of plant species flowering (bars) and the flowering intensity of five plant species (F.Muell., (Guadich.) F.Muell. and Benth.). Intensity is on a scale of 0-5, where 0 indicates no flowering and 5 indicates abundant flowering. The boom-bust nature of the system is evident in the number of species flowering, however, the length and intensity of flowering varies among species.

at three sites at three-monthly intervals between May 2004 and November 2007. For each site, two one-hectare areas, each with 15 plots of 5m x 5m area were randomly placed along three 100m transects, across the crest, mid and swale dune zones respectively. In each plot, the abundance, and intensity of flowering and fruiting of each plant species was assessed. Figure 2 is a visual representation of the flowering phenology in terms of the number of plant species flowering and the flowering intensity of five representative plant species for one site of the three sites surveyed during this period. The temporal variation in flowering is driven by the amount and timing of rainfall. Over the 18 months prior to June 2005, 110mm of rain fell and little flowering occurred. Following the June 2005 and the January 2007 rainfall were periods of mass co-flowering. The species, intensity, duration and timing of flowering differed between the two boom periods due to rainfall: 100mm of rain over 9 days in June 2005 caused 16 species to flower in a boom lasting 6 months, whilst 220mm of rain over 12 days in January 2007 caused 22 species to flower in a boom lasting 12 months. Whether floral visitors respond to rain or resources (such as nectar and pollen) remains unclear, but their activity, like flowering, is also varied over time.

In this unpredictable and variable landscape, we can expect species interactions to be similarly highly variable in space and time. To assess this variability, visitation interactions were sampled in September and November of 2007, from several sites in the Simpson Desert by observing and collecting insects visiting flowers. A visitation was defined as any physical contact between the insect and a flower, and no *a priori* decisions were made about probable pollinators. To ensure an adequate sample of visitors was obtained, a stratified approach was used to select areas to sample: groups of plants within a one-metre square, or individual plants, with abundant flowering and additional samples were collected using transects in areas of sparse flowering. We used this combination of sampling methods in a stratified way to overcome the shortfalls and biases associated with each method (Gibson *et al.* 2011). Observations were made for 10 minute periods and any invertebrate floral visitors were caught using nets and plastic containers, and transferred into five millilitre vials for transportation. Nestedness was calculated using the Bipartite (Dormann *et al.* 2008) package implemented in the R statistical package (ver. 2.11.1, R Development Core Team 2010).

The interactions that were sampled from a single location during September and November 2007 are represented as networks in Figure 3. A relatively high turnover of species occurred between the two periods: in September there were 24 insect species and 9 plant species (Figure 3a) and in November there were 26 insect species and 14 plant species (Figure 3b), of which, 7 insect species and 6 plant species appeared in both networks. Species that occur in both networks and interact in one network do not necessarily interact in the other network. For instance *Calotis erinacea*

Steetz and *Lipotriches flavoviridis*, and *Ptilotus latifolius* R. Br. and *Lassioglossum immaculatum* interact in one network but not in the other. The position of species in the network also varied between the two periods. A 'linking species' within a network interacts with species from multiple groups. In the September 2007 survey, the insect species in blue (*Homalictus urbanus*) appears as a link. However, a few months later, in November, whilst *H. urbanus* remains as a link, two others (*L. flavoviridis* and *Amegilla chlorocyanea*) that were not linking species in September have become linking species. 'Hub species,' of which there are three in September (in red), interact with many other single interacting species. In November, however, these species cease to be hub species, and two other species assume that role. Network structure can also be expressed through concepts from network theory, such as nestedness, as explained earlier. The September network has a nestedness value of 0.60 (values range from 0 to 1, 1 indicating maximum nestedness) while November has a value of 0.86. This suggests that the network in November, being more nested than the September network, is more tolerant to random extinctions.

Whether we aim to preserve species, communities, the structure of interaction networks, or a combination of all three, knowing what 'state' to aim for or how much change is tolerable remains unclear. Spatio-temporal variation, a natural feature of ecological communities generally, is exemplified in the phenological variation and dynamic assemblages of plant and insect species in the Simpson Desert. Such variation is reflected in changes to the floral-visitor interaction network. Therefore, constructing dynamic networks, which also incorporate varying interaction strengths and account for varying mutualistic and negative interactions is an important next step. Quantifying temporal change in species interactions will help reveal the ecological mechanisms and processes that structure ecological communities and, therefore, help predict how they will respond to climate change.

Conclusions

Interactions between species are climate dependent. Even seemingly small changes between two species can have large cumulative effects through entire ecological communities. Therefore, predicting ecological responses to climate change will necessarily depend upon understanding how the full suite of species interactions function within the community. Current variation in species interactions, especially in highly variable and extreme environments, will inform us of mechanisms by which species and communities respond to change. An exciting opportunity exists to extend studies on the distribution and phenology of species to construct species interaction networks. Determining the fitness outcomes of species interactions in an entire network would allow us to track subtle changes. This level of detail would, however, involve considerably more time and effort.

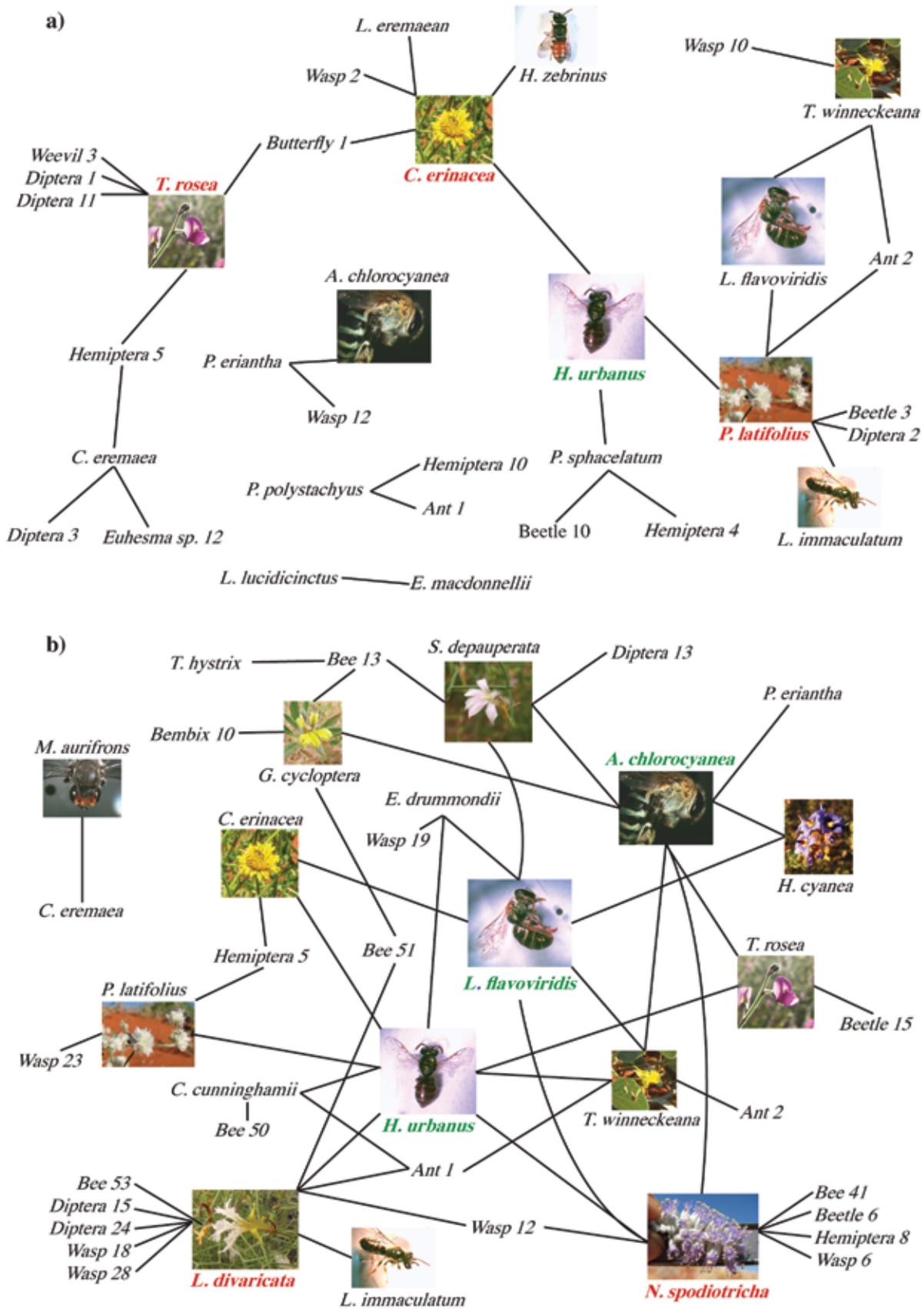


Figure 3. Two-mode interaction networks depicting floral-visitation interactions between plant and insect species at Carlo Station, Simpson Desert SW QLD, sampled during September (a) and November (b) 2007. A line between a plant and insect species denotes a visitation interaction. Plant species in red text refer to hub species in September, which then cease to be hubs in November, when two new hub plant species appear in the network. Visitor species in blue text denote link species in both September and November.

To successfully manage the effects of climate change, we must start by drastically reducing greenhouse gas emissions. This will limit the change we experience and reduce the likelihood of exceeding critical thresholds beyond which rapid and irreversible ecosystem state change occurs (Scheffer *et al.* 2001). Climate change is already underway, however, and its effects are being felt, rendering the immediate practice of robust management strategies important. Robust strategies are those that will allow ecological communities to persist without continuous human intervention and therefore continuous supply of money, and be able to persist through other environmental change should it occur. The success of strategies to conserve wildlife will depend on how they support the maintenance of the ecological and evolutionary processes that structure ecological communities. This involves three points of action: 1) continue mitigating known

threats such as pests, weeds and fire; 2) re-evaluate some actions such as translocations, the erection of fences and exotic species eradication; and 3) co-operation involving public and private partnerships at the local, regional and national level. The success of management strategies will rely on our flexibility and responsiveness to new information. We need to be aware that previous risk assessments of certain actions become less valid as climate change progresses, and we need to re-examine our assumptions of what we know about where species or communities are meant to be in the landscape. By considering the function and structure of ecosystems, rather than species lists, we may need to resign ourselves to the idea that some species will not be able to maintain wild populations in current locations, while other species, even exotics, will become important for the functioning and persistence of ecological communities.

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References

- Araujo M. B. & Rahbek C. 2006. How does climate change affect biodiversity? *Science*, **313**: 1396-7.
- Bascompte J. & Jordano P. 2007. Plant-animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology and Systematics*, **38**: 567-93.
- Bascompte J., Jordano P., Melian C. J. & Olesen J. M. 2003. The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, **100**: 9383-7.
- Bertin R. I. 2008. Plant phenology and distribution in relation to recent climate change. *Journal of the Torrey Botanical Society*, **135**: 126-46.
- Both C., Van Asch M., Bijlsma R. G., Van Den Burg A. B. & Visser M. E. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology*, **78**: 73-83.
- Brook B. W. 2009. Global warming tugs at trophic interactions. *Journal of Animal Ecology*, **78**: 1-3.
- Bruno J. E., Stachowicz J. J. & Bertness M. D. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, **18**: 119-25.
- Chesson P., Gebauer R. L. E., Schwinning S., Huntly N., Wiegand K., Ernest M. S. K., Sher A., Novoplansky A. & Weltzin J. F. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, **141**: 236-53.
- Dormann C. E., Gruber B. & Frund J. 2008. Introducing the bipartite Package: Analysing Ecological Networks. *R news*, **8**: 8-11.
- Elith J., H. Graham C., P. Anderson R., Dudík M., Ferrier S., Guisan A., J. Hijmans R., Huettmann F., R. Leathwick J., Lehmann A., Li J., G. Lohmann L., A. Loiselle B., Manion G., Moritz C., Nakamura M., Nakazawa Y., McC. M. Overton J., Townsend Peterson A., J. Phillips S., Richardson K., Scachetti-Pereira R., E. Schapire R., Soberón J., Williams S., S. Wisz M. & E. Zimmermann N. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**: 129-51.
- Gibson R. H., Knott B., Eberlein T. & Memmott J. 2011. Sampling method influences the structure of plant-pollinator networks. *Oikos*, **120**: 822-31.
- Gilman S. E., Urban M. C., Tewksbury J., Gilchrist G. W. & Holt R. D. 2010. A framework for community interactions under climate change. *Trends in Ecology & Evolution*, **25**: 325-31.
- Gotelli N. J., Graves G. R. & Rahbek C. 2010. Macroecological signals of species interactions in the Danish avifauna. *Proceedings of the National Academy of Sciences of the United States of America*, **107**: 5030-5.
- Hairton N. G., Smith F. E. & Slobodkin L. B. 1960. Community structure, population control, and competition. *American Naturalist*, **94**: 421-5.
- Hughes L. 2003. Climate change and Australia: Trends, projections and impacts. *Austral Ecology*, **28**: 423-43.
- Hughes L. 2011. Climate change and Australia: key vulnerable regions. *Regional Environmental Change*, **11**: S189-S95.
- IPCC. 2007. IPCC Fourth Assessment Report. Intergovernmental Panel on Climate Change, Geneva.
- Jentsch A., Kreyling J., Boettcher-Treschkow J. & Beierkuhnlein C. 2009. Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. *Global Change Biology*, **15**: 837-49.
- Kishi D., Murakami M., Nakano S. & Maekawa K. 2005. Water temperature determines strength of top-down control in a stream food web. *Freshwater Biology*, **50**: 1315-22.

- Kissling W. D., Field R., Korntheuer H., Heyder U. & Bohning-Gaese K. 2010. Woody plants and the prediction of climate-change impacts on bird diversity. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **365**: 2035-45.
- Kreyling J., Beierkuhnlein C., Ellis L. & Jentsch A. 2008. Invasibility of grassland and heath communities exposed to extreme weather events - additive effects of diversity resistance and fluctuating physical environment. *Oikos*, **117**: 1542-54.
- Letnic M. & Dickman C. R. 2006. Boom means bust: interactions between the El Niño/Southern Oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. *Biodiversity and Conservation*, **15**: 3847-80.
- Memmott J. 1999. The structure of a plant-pollinator food web. *Ecology Letters*, **2**: 276-80.
- Memmott J., Waser N. M. & Price M. V. 2004. Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London B-Biological Sciences*, **271**: 2605-11.
- Morton S. R., Stafford Smith D. M., Dickman C. R., Dunkerley D. L., Friedel M. H., McAllister R. R. J., Reid J. R. W., Roshier D. A., Smith M. A., Walsh F. J., Wardle G. M., Watson I. W. & Westoby M. 2011. A fresh framework for the ecology of arid Australia. *Journal of Arid Environments*, **75**: 313-29.
- Ne'eman G., Jurgens A., Newstrom-Lloyd L., Potts S. G. & Dafni A. 2010. A framework for comparing pollinator performance: effectiveness and efficiency. *Biological Reviews*, **85**: 435-51.
- Olesen J. M. & Jordano P. 2002. Geographic patterns in plant-pollinator mutualistic networks. *Ecology*, **83**: 2416-24.
- Pavey C. R., Eldridge S. R. & Heywood M. 2008. Population dynamics and prey selection of native and introduced predators during a rodent outbreak in arid Australia. *Journal of Mammalogy*, **89**: 674-83.
- Pellmyr O. 2002. Pollination by animals. In: *Plant-animal interactions: an evolutionary approach* (eds C. M. Herrera and O. Pellmyr) pp. 157-84. Blackwell Sciences Ltd, Oxford.
- Popic T. J., Wardle G. M. & Davila Y. C. 2011 in review. Flower-visitor networks only partially predict the function of pollen transport by bees. *Austral Ecology*.
- Potts S. G., Biesmeijer J. C., Kremen C., Neumann P., Schweiger O. & Kunin W. E. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, **25**: 345-53.
- Scheffer M., Carpenter S., Foley J. A., Folke C. & Walker B. 2001. Catastrophic shifts in ecosystems. *Nature*, **413**: 591-6.
- Stafford Smith D. M. 2008. The 'desert syndrome' - causally-linked factors that characterise outback Australia. *The Rangeland Journal*, **30**: 3-14.
- Suttle K. B., Thomsen M. A. & Power M. E. 2007. Species interactions reverse grassland responses to changing climate. *Science*, **315**: 640-2.
- Thibault K. M. & Brown J. H. 2008. Impact of an extreme climatic event on community assembly. *Proceedings of the National Academy of Sciences*, **105**: 3410-5.
- Tylianakis J. M., Didham R. K., Bascompte J. & Wardle D. A. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**: 1351-63.
- Tylianakis J. M., Laliberte E., Nielsen A. & Bascompte J. 2010. Conservation of species interaction networks. *Biological Conservation*, **143**: 2270-9.
- Walker B., Steffen W. & Langridge J. 1999. Interactive and integrated effects of global change on terrestrial ecosystems. In: *The terrestrial biosphere and global change: implications for natural and managed ecosystems* (eds B. Walker, W. Steffen, J. Canadell and J. Ingram) pp. 329-75. Cambridge University Press, Cambridge, UK.
- Walther G. R. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **365**: 2019-24.