

Network size, structure and mutualism dependence affect the propensity for plant–pollinator extinction cascades

Adam J. Vanbergen^{*1}, Ben A. Woodcock², Matthew S. Heard² and Daniel S. Chapman¹

¹NERC Centre for Ecology and Hydrology, Bush Estate, Penicuik, Edinburgh EH26 0QB, UK; and ²NERC Centre for Ecology and Hydrology, Crowmarsh Gifford, Wallingford OX10 8BB, UK

Summary

1. Pollinator network structure arising from the extent and strength of interspecific mutualistic interactions can promote species persistence and community robustness. However, environmental change may re-organise network structure limiting capacity to absorb or resist shocks and increasing species extinctions.

2. We investigated if habitat disturbance and the level of mutualism dependence between species affected the robustness of insect–flower visitation networks. Following a recently developed Stochastic Co-extinction Model (SCM), we ran simulations to produce the number of extinction episodes (cascade degree), which we correlated with network structure in undisturbed and disturbed habitat. We also explicitly modelled whether a species' intrinsic dependence on mutualism affected the propensity for extinction cascades in the network.

3. Habitat disturbance generated a gradient in network structure with those from disturbed sites being less connected, but more speciose and so larger. Controlling for network size (z -score standardisation against the null model) revealed that disturbed networks had disproportionately low linkage density, high specialisation, fewer insect visitors per plant species (vulnerability) and lower nestedness (NODF).

4. This network structure gradient driven by disturbance increased and decreased different aspects of robustness to simulated plant extinction. Disturbance decreased the risk that an *initial* insect extinction would follow a plant species loss. Although, this effect disappeared when network size and connectance were standardised, suggesting the lower connectance of disturbed networks increased robustness to an initial secondary extinction.

5. However, if a secondary extinction occurred then networks from disturbed habitat were more prone to large co-extinction cascades, likely resulting from a greater chance of extinction in these larger, speciose networks. Conversely, when species mutualism dependency was explicit in the SCM simulations the disturbed networks were disproportionately more robust to very large co-extinction cascades, potentially caused by non-random patterns of interaction between species differing in dependence on mutualism.

6. Our results showed disturbance altered the size and the distribution of interspecific interactions in the networks to affect their robustness to co-extinction cascades. Controlling for effects due to network size and the interspecific variation in demographic dependence on mutualism can improve insight into properties conferring the structural robustness of networks to environmental changes.

Key-words: environmental disturbance, extinction cascade, mutualism, network structure, pollinator, stability, Stochastic Co-extinction Model, z -score

Introduction

Pollinators and pollination are threatened at a global scale by land-use change, conventional agricultural intensification, climate change, pollution, pathogens and invasive alien

species either separately or in combination (González-Varo *et al.* 2013; Vanbergen & the Insect Pollinators Initiative 2013; IPBES 2016). These multiple anthropogenic pressures are linked to long-term shifts in pollinator richness, distributions and abundance (Cameron *et al.* 2011; Carvalheiro *et al.* 2013; Kerr *et al.* 2015; Senapathi *et al.* 2015; IPBES 2016). However, the effect of these various sources of

*Correspondence author. E-mail: ajv@ceh.ac.uk

environmental stress often differs between pollinator species according to traits such as body size, sociality, phenology and diet breadth (Williams *et al.* 2010; Bommarco *et al.* 2011; Burkle, Marlin & Knight 2013). Such differential impacts among species lead to changes in pollinator community composition, re-organising interactions with plants and the structure of pollinator networks (Burkle, Marlin & Knight 2013; Nielsen & Totland 2014; Vanbergen *et al.* 2014; Weiner *et al.* 2014). Such re-organisation of network structure by anthropogenic perturbation of ecosystems may have implications for species persistence and community stability (Lever *et al.* 2014; Rohr, Saavedra & Bascompte 2014; Vieira & Almeida-Neto 2015).

Network topology, trait redundancy, behavioural plasticity and species abundance can all affect the robustness of assemblages of plant–pollinator interactions to species losses (Thebault & Fontaine 2010; Ramos-Jiliberto *et al.* 2012; Valdovinos *et al.* 2013; Winfree *et al.* 2014). High levels of connectance, modularity or nestedness are aspects of network topology thought to promote dynamic or structural stability in mutualistic networks (Bascompte *et al.* 2003; Olesen *et al.* 2007; Thebault & Fontaine 2010; Rohr, Saavedra & Bascompte 2014). Abundant generalist species often exhibit plasticity in foraging behaviour by switching to use different floral resources as they become more or less abundant. In this way, they can adopt feeding niches of extinct species thus maintaining network stability and community function (Ramos-Jiliberto *et al.* 2012; Valdovinos *et al.* 2013). Moreover, the most abundant pollinator species are key to network stability because they tend to be the least prone to extinction and the most connected via direct or indirect interactions to other species within the network (Aizen, Sabatino & Tylianakis 2012; Winfree *et al.* 2014; Fort, Vázquez & Lan 2016). Conversely, the risk of extinctions of species or their interactions with environmental change tends to be greater for more specialised plant–pollinator interactions or networks (Biesmeijer *et al.* 2006; Williams *et al.* 2010; Aizen, Sabatino & Tylianakis 2012; Burkle, Marlin & Knight 2013).

It is possible, however, that if environmental pressure attains a critical level, for example as a consequence of multiple sources of stress (González-Varo *et al.* 2013; Vanbergen 2013), then even the most generalised species in a network could be lost (Tylianakis & Coux 2014). Losses of such key species and their interactions have the potential to precipitate a cascade of secondary extinctions or potentially even sudden assemblage collapse (Kaiser-Bunbury *et al.* 2010; Lever *et al.* 2014; Tylianakis & Coux 2014).

The consequences of species extinctions for network robustness have mostly been evaluated using topological extinction cascade models (TCM) that assume the loss of an individual species in a mutualistic interaction requires the extinction of all its interaction partners (Memmott, Waser & Price 2004; Kaiser-Bunbury *et al.* 2010; Ramos-Jiliberto *et al.* 2012). However, this

approach is unable to distinguish the exact level of co-dependence between partners in a mutualism, which may have implications for the predicted impact of environmental changes on network stability. For instance, many insect-pollinated plants retain the capacity to self-fertilise to overcome pollination deficits (Eckert *et al.* 2010; Ollerton, Winfree & Tarrant 2011). In addition, many pollinators vary in their level of dependence on floral resources for nutrition. For example, while wild bees (Apidae) are dependent on floral resources for food throughout their life cycle, other pollinators, such as flies (Diptera), exploit other food resources (e.g. insect prey, animal dung or cadavers) (Laurence 1954; Potts *et al.* 2003; Vanbergen *et al.* 2014; Orford, Vaughan & Memmott 2015). Therefore, topological extinction models inevitably lack a degree of biological reality.

A recently developed Stochastic Co-extinction Model (SCM) (Vieira & Almeida-Neto 2015) explicitly accounts for the level of dependence between interacting species in mutualistic networks. It achieves this by specifying the variation in the mutual dependence between every species and each of its mutualistic partners. In doing so, this SCM relaxes the assumption that the co-extinction of a species requires the loss of all of its partners. This refinement allows the application of greater ecological realism to models that simulate extinction cascades and hence allow for more complex outcomes than under TCM modelling frameworks. For example, compared to topological modelling of a quantitative network data set, the SCM approach suggested that a high level of network connectance might actually increase the probability of an extinction cascade rather than provide stability (Vieira & Almeida-Neto 2015).

In a previous paper (Vanbergen *et al.* 2014), we showed how ecosystem disturbance modified the structure of replicated flower visitation networks. Networks from livestock disturbed woodlands were larger and more diverse, and controlling for network size, they were revealed as less nested than networks from undisturbed woodlands. While often debated, greater nestedness is thought to confer a level of stability on mutualistic networks (Thebault & Fontaine 2010; James, Pitchford & Plank 2012; Rohr, Saavedra & Bascompte 2014). Consequently, we use the network data from Vanbergen *et al.* (2014) within an SCM framework to test the prediction that less nested networks (typically from sites disturbed by grazing) would be most sensitive to species extinctions (i.e. less robust). Furthermore, species with lower dependence on mutualism should have lower extinction probabilities following local extinction of a partner in the mutualistic network, when compared to species with obligate dependence on pollinators or floral resources. Therefore, we also predicted that the degree of co-dependence between partners in these potentially mutualistic interactions would dictate the frequency of high-order co-extinction cascades.

Materials and methods

We tested whether gradients in the structure of observed insect–flower visitation networks, induced by habitat disturbance from grazing, affect network robustness to species loss. First, we quantified network structure using a range of standard metrics from disturbed and undisturbed sites. Then we ran simulations of the SCM (Vieira & Almeida-Neto 2015) to estimate network robustness. Finally, we tested correlations between the disturbance driven gradient in network structure and robustness.

STUDY SYSTEM

We used the flower visitation data from Vanbergen *et al.* (2014) and briefly summarise the details of their collection here. During 2009, we quantified insect visitation to flowering plants in nine birch (*Betula* spp.) dominated woods (five disturbed; four undisturbed). The birch wood sites were all located in the River Dee catchment of Aberdeenshire (between latitudes 57.0581 and 57.0367 and longitudes -2.9621 and -2.5124) and represent a widely distributed, semi-natural habitat with a long history of use for cattle farming (Woodcock, Leather & Watt 2003). Landowners confirmed that livestock had been absent for at least 70–100 years in undisturbed sites, while where livestock were present, cattle grazing was light to moderate (e.g. 2007: mean = 8.4 cattle per ha) and long term (mean = 33 years). The species identity and frequency of all insect–flower interactions was recorded in two transects (50 × 2 m; 15 m apart and at least 50 m from the woodland edge) randomly situated prior to the onset of flowering in the centre of each wood (20 site visits total from May–August). Species accumulation curves were used to assess the sampling completeness (Vanbergen *et al.* 2014).

VISITATION NETWORK STRUCTURE

A quantitative insect–plant network based on visitation frequency was created for each woodland site (Vanbergen *et al.* 2014). Parameters describing network structure predicted to affect assemblage robustness to extinction were derived using the ‘bipartite’ package in the R statistical environment (Dormann, Gruber & Frund 2008). In addition to the total number of pollinator and plant species and interactions, these network parameters were:

- (i) Connectance (C): The realised proportion of possible links in the network (see Dunne, Williams & Martinez 2002a), which is the sum of links divided by the number of possible links (equal to the number of pollinator species × flowering plant species).
- (ii) Linkage density (Lq): The quantitative diversity of interactions per species weighted by the marginal sum of interactions (see Bersier, Banašek-Richter & Cattin 2002).
- (iii) Vulnerability (Vqw): The mean number of insect visitors per plant species, weighted by their marginal totals (row sums) (see Bersier, Banašek-Richter & Cattin 2002; Tylianakis, Tscharrntke & Lewis 2007).
- (iv) Nestedness ($NODF$): In mutualistic networks, it reflects the tendency for specialist species to interact with generalists (Almeida-Neto *et al.* 2008). Values of 0 indicate non-nestedness, those of 100 perfect nesting.
- (v) Network specialisation ($H2'$): The extent to which observed interactions deviate from that predicted by the marginal totals of interactions per species. The more selective the species are the greater the value of $H2'$ for the web: 0 (no specialisation) and 1 (complete specialisation) (Blüthgen, Menzel & Blüthgen 2006).

Many of these descriptors of network architecture are sensitive to the size of the network, i.e. the parameter tends to vary with

the number of observed interactions (Bascompte *et al.* 2003; Nielsen & Bascompte 2007; Ulrich, Almeida-Neto & Gotelli 2009). Consequently, when analysing network structure, to control for the effects of network size across different sites, we standardised network parameters ($NODF$, Vqw , Lq , $H2'$) using z -scores ($z = [x - \mu]/\sigma$) against 10 000 random networks following the null model (vaznull) implemented in the bipartite R function (Vázquez *et al.* 2007). The resulting z -scores compare the observed network parameter to the distribution of simulated parameters (x = observed value, μ = mean, σ = standard deviation of the 10 000 values from the simulations) and therefore correct for network size (Almeida-Neto *et al.* 2008). The null model randomises the pattern of individual interactions in the network in such a way that the original values of connectance (i.e. number of interspecific connections), the species richness of both levels and the total number of interactions are preserved. Therefore, no z -score standardisation could be applied to connectance, species richness or interaction number. Positive values mean the observed metric is disproportionately high and negative values mean it is disproportionately low with departure from zero tested with one-sample t -tests at $P < 0.05$.

Because there was strong correlation between different network metrics, we used principal components analysis (PCA) to generate orthogonal multivariate gradients in network structure. We used a two-sample t -test (<0.05) to evaluate whether networks from disturbed and undisturbed sites differed in structure (PC axes). Normality of residuals was checked against a Shapiro–Wilk test ($\alpha = 0.05$).

ESTIMATION OF NETWORK STRUCTURAL ROBUSTNESS TO SPECIES LOSS

We estimated network robustness to species loss by applying, first, a ‘basic SCM’ where all species have equal dependence on the pollination mutualism, and second, a ‘dependence SCM’ reflecting each species’ relative intrinsic dependence on the pollination mutualism (Vieira & Almeida-Neto 2015). Each SCM simulation produced the number of extinction episodes (cascade degree), for which we analysed correlations (Pearson’s r) to the network structure gradient driven by disturbance.

In the SCM, the probability that a species i become extinct after extinction of a potential mutualist partner species j is:

$$P_{ij} = R_i d_{ij} \quad \text{eqn 1}$$

where d_{ij} is the dependence of species i on interactions with species j , and is defined as:

$$d_{ij} = \frac{v_{ij}}{\sum_k v_{ik}} \quad \text{eqn 2}$$

where v_{ij} is the number of observed interactions between i and j , and k indexes all currently surviving potential partner species of i in the network (i.e. all remaining plants if i is an insect, and vice versa).

R_i is an intrinsic demographic dependence on mutualism for species i . In the basic SCM, R is set to a value of 1 for all species, specifying equivalent dependence on mutualism. In the dependence SCM, species with lower intrinsic dependence are assigned lower values of R , which reduces their overall probability of extinction. For example, less-dependent species include plants that self-fertilise or reproduce clonally and insects able to feed on alternative plant, animal or other organic resources as adults (e.g. Vespidae, Muscidae, Coleoptera). In our model, species dependences were scored as ‘low’, ‘medium’ or ‘high’ ($R = 0, 0.5$ or 1 , respectively), based on known life histories (Appendix S1, Supporting Information). For plants, we primarily used information on normal modes of propagation from EcoFlora (Fitter & Peat 1994) (vegetative = low, seed and vegetative = medium,

seed = high). In a small number of cases, we also considered other attributes, such as anemophily (wind pollination) and apomixis (asexual reproduction), that reduce the dependence on pollination. For adult insects, obligate flower visitors were scored as high, those likely to use alternative food sources (e.g. dung, insect prey) in addition to pollen or nectar were scored as medium, and a small minority of insect species that rarely use floral resources, but were observed visiting flowers in this study, were scored as low (Appendix S1).

The algorithm for simulating the SCM is:

1. Initiate the SCM by choosing a plant species at random and making it extinct. The loss of plants before insects reflected the ecologically relevant assumption that in this data set the predominant influence on network structure, disturbance from grazing, affects the vegetation directly and insect pollinators only indirectly via change to floral resources.
2. For each remaining pair of species, calculate their current interaction dependences (d_{ij}) and extinction probability (P_{ij}).
3. Conduct Bernoulli trials (i.e. weighted coin tosses) with probabilities P_{ij} to randomly determine which species become extinct as a result of the loss of interactions with the species that has just gone extinct.
4. If the cascade has finished, i.e. no species went extinct in Step 3, stop the simulation. Otherwise go to Step 2.

For each network and model type, we ran 10 000 replicate simulations of the SCM. The output from each SCM simulation was the cascade degree, which is the number of extinction episodes, i.e. iterations of the SCM. For instance, a second order and fifth order cascade describe a simulation that includes two or five rounds of co-extinctions.

CORRECTION OF THE SCM FOR POLLINATION NETWORK SIZE

Simple comparison of SCM outputs between networks that differ in size is problematic because in a larger network there are more species, so each iteration of the SCM involves a greater number of Bernoulli trials. Consequently, there is a higher probability that at least one species becomes extinct, causing the cascade simulation to continue. For this reason, even if the larger networks are structurally equivalent to smaller networks (other than being more species rich) then the larger networks will yield higher cascade degrees and appear less robust to extinction than smaller networks. Systematic variation in network structure with size could negate or even reverse this relationship; consequently, it should be accounted for when comparing networks of different sizes.

Therefore, we applied z -score standardisations to the SCM outputs by repeating the whole simulation process for 10 000 null models (i.e. 10 000 SCM replicates were run for each of the 10 000 null model networks) generated randomly as above (Vázquez *et al.* 2007). Positive values mean the SCM resulted in disproportionately larger co-extinction cascades than would be expected for a network of that size, and negative values mean disproportionately smaller cascades were obtained. We tested the departure of the co-extinction cascade degree in the model simulations from the null model (expectation of zero) with one-sample t -tests ($P < 0.05$).

Results

GRADIENTS IN NETWORK STRUCTURE

The z -score standardisation of the metrics of network structure against the null model indicated non-random assembly

of the observed networks. For their sizes, they had disproportionately low linkage density (one-sample t -test, $t_7 = -4.112$, $P = 0.003$) and vulnerability ($t_7 = -4.549$, $P = 0.002$) and disproportionately high specialisation ($t_7 = 3.133$, $P = 0.014$). However, observed nestedness was similar to the null model ($t_7 = -1.850$, $P = 0.101$).

Network metrics were highly correlated and all were strongly associated with PC1 of a PCA on the network metrics, which explained the majority of the variance (PC1 = 80.6% vs. PC2 = 8.9%). Therefore, this represented the main gradient of network structure separating disturbed and undisturbed sites (Fig. 1). Networks from disturbed habitat had higher positive values of PC1 (two-sample t -test, $t_{6.72} = 3.861$, $P = 0.007$; Shapiro–Wilk normality test: $W = 0.920$, $P = 0.391$). Therefore, compared to the undisturbed situation the networks from disturbed sites tended to be more speciose (PC1 score: insect richness = 0.909; plant richness = 0.884) and consequently larger (number of interactions = 0.985), but less connected ($C = -0.705$). Controlling for their larger size and compared to the null model, the networks from disturbed sites had disproportionately low linkage density ($Lq = -0.978$), high specialisation of interactions ($H2' = 0.932$), lower nestedness (NODF = -0.788) and fewer insect partners per plant species ($Vqw = -0.961$) (Fig. 1). There was no comparable separation of networks from disturbed and undisturbed habitat along PC2 ($t_{6.02} = 0.030$, $P = 0.978$, Shapiro–Wilk normality test: $W = 0.910$, $P = 0.313$, Fig. 1).

SIMULATED CO-EXTINCTION CASCADES

The proportion of SCM simulations resulting in co-extinction cascades of at least degrees 2 (i.e. extinction of

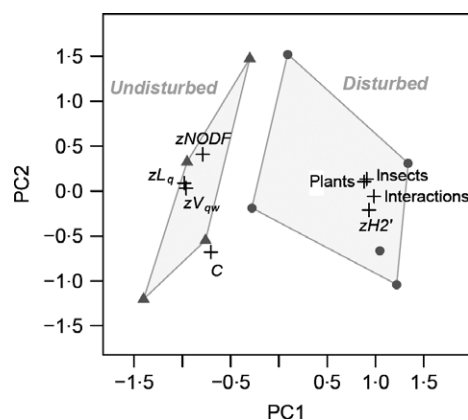


Fig. 1. Biplot of a principal components analysis (PCA) showing the two major gradients in the structure of nine plant–pollinator visitation networks driven by habitat disturbance from grazing livestock. Solid symbols show the scores of each disturbed (circles) or undisturbed (triangles) network. Crosses show the scores for the network structure metrics used to define the PCA. Network metrics were nestedness (NODF), linkage density (Lq), vulnerability (Vqw), connectance (C), network specialisation ($H2'$), and the total number of insect and plant species and interactions, with ' z ' signifying z -score standardisation of the metric to remove effects of network size.

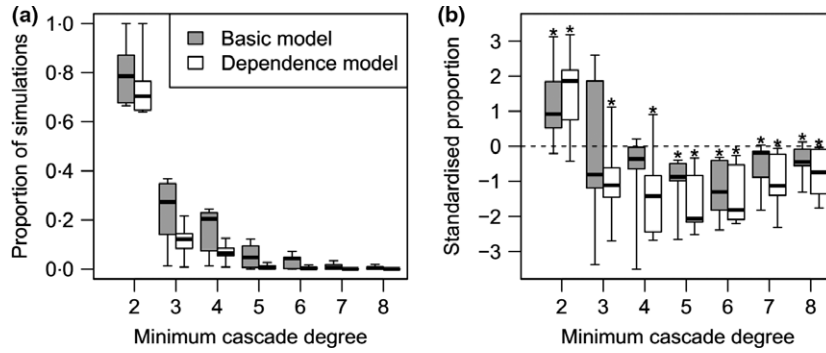


Fig. 2. (a) Boxplots showing the proportions of Stochastic Co-extinction Model (SCM) simulations in which co-extinction cascades of varying degrees were achieved for nine plant–pollinator visitation networks. Cascade degrees are the number of co-extinction rounds that occur during the model simulations. Results from both the basic SCM and the SCM with demographic dependence on the mutualism are shown. (b) Boxplots showing *z*-scores standardisation of the proportions in (a) against a null model, to account for the dependence of cascade degree on network size. Values greater than zero indicate disproportionately high proportions, values less than zero indicate disproportionately low proportions. Departures from zero were tested with one-sample *t*-tests and asterisks above the boxes indicate statistical significance at *P* < 0.05.

≥2 species) to degree 8, are summarised in Fig. 2 for the basic model and the model where the relative mutualism dependence (low, medium or high) of different species was explicit. By definition all co-extinction simulations achieved at least degree 1, since this resulted from the initial loss of a plant species. Large co-extinction cascades (high cascade degrees) occurred less frequently in the dependence model than in the basic model (Fig. 2a), resulting from lower extinction probabilities assigned to species with less dependence on mutualism. Standardisation of SCM outputs (*z*-scores) to account for differences in network size revealed that extinction cascades of at least two degrees were more common than expected in the observed networks than in the null models ($\bar{z} > 0$), but cascades of higher degree tended to be less common ($\bar{z} > 0$) (Fig. 2b).

EFFECT OF NETWORK STRUCTURE ON ROBUSTNESS

Correlations (Pearson’s *r*) between the network structure gradient (PC1) and the proportions of SCM simulations achieving co-extinction cascades of different degree sizes are shown in Figs 3 and 4. Low co-extinction cascade proportions indicate greater network robustness to species loss. Therefore, positive correlations indicate that networks with higher values of PC1, those from disturbed habitat, are less robust to species loss.

Considering the raw (not corrected for network size) frequencies of co-extinction cascades, networks from disturbed sites (higher values of PC1) were *more robust* to species loss in that there was a lower frequency of initial (low-degree) co-extinction cascades, but *less robust* in that they had more frequent large (high-degree) co-extinction

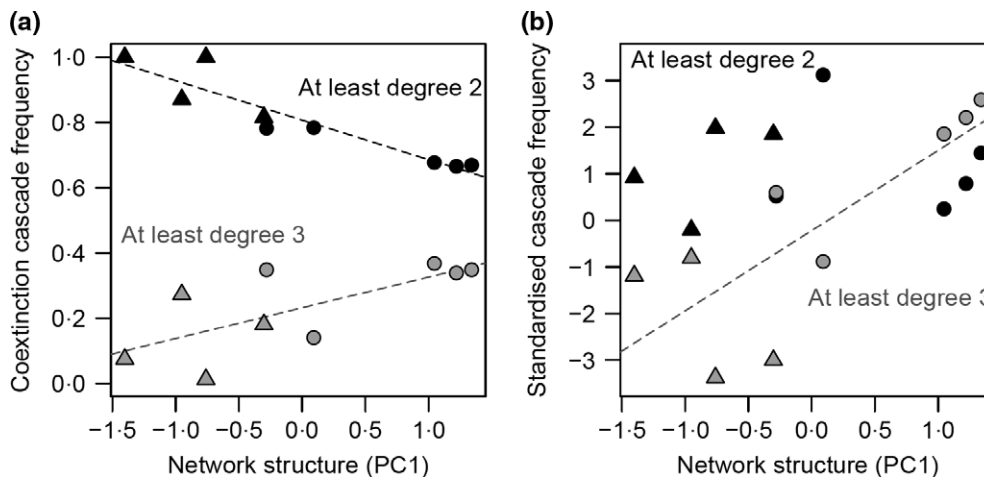


Fig. 3. Relationships between network structure (PC1) driven by disturbance and co-extinction cascade frequency as an inverse measure of robustness. Plots show the proportions of basic Stochastic Co-extinction Model (SCM) simulations in which co-extinction cascades of at least degree 2 or 3 occurred in plant–insect visitation networks. Both (a) raw and (b) network size-corrected (*z*-score standardised) proportions are plotted, along with statistically significant (*P* < 0.05) regression lines. Disturbed networks are circles and undisturbed networks are triangles.

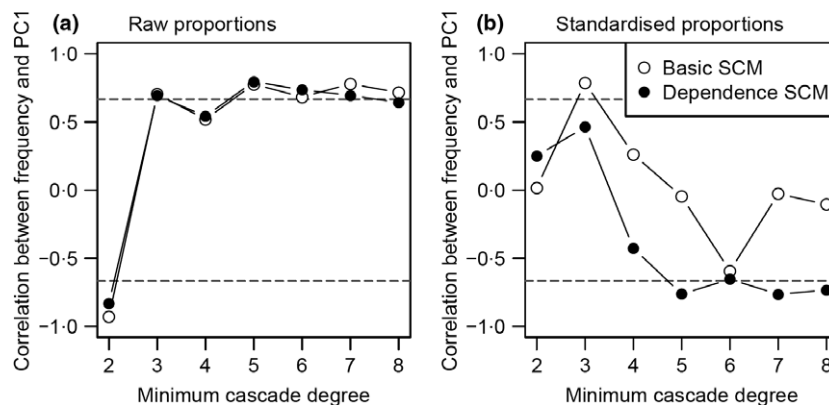


Fig. 4. Correlations between network structure (PC1 driven by habitat disturbance) and the proportions of Stochastic Co-extinction Model (SCM) simulations yielding co-extinction cascades of varying degree sizes (positive correlations indicate that disturbed sites have a higher frequency of extinction cascades - see Fig. 3). Results shown from both the basic SCM and an SCM with demographic dependence on the mutualism. Both (a) raw and (b) network size-corrected (z -score standardised) proportions are plotted, with dashed lines showing the critical value of Pearson's correlation coefficient r (d.f. = 7, $P = 0.05$).

cascades (Figs 3a and 4a). However, standardisation of cascade degree frequencies against SCM simulations on a null model altered these conclusions (Figs 3b and 4b). There was still evidence from the basic SCM that networks from disturbed sites (high values of PC1) were *less robust* to species loss, because they suffered disproportionately higher frequencies of degree-3 cascades (Fig. 3b). Conversely, the dependence SCM indicated that networks from disturbed sites were disproportionately *more robust* to very large cascades (\geq degree 5) following species loss (Fig. 4b).

Discussion

Earlier work in this forest ecosystem showed that the introduction of livestock shifted the plant community from a species-poor assemblage dominated by tussock grasses and bryophytes to a state of higher species richness dominated by forbs (Vanbergen *et al.* 2006). This habitat disturbance, particularly the increase in forb species richness, modified the flower visitation networks (Vanbergen *et al.* 2014). Overall, our current multivariate analysis revealed a pattern for greater selectivity of species interactions in disturbed habitat. We showed that networks assembled in the disturbed habitat were larger and more speciose but with lower connectance (i.e. number of realised interspecific interactions), confirming the inverse relationship between network size and connectance seen elsewhere (Thebault & Fontaine 2010). Furthermore, once network size was standardised, we found disturbed networks were characterised by lower linkage density, vulnerability (i.e. fewer insect visitors per plant species) and nestedness, but higher network specialisation. That various network parameters were sensitive to the size of the assemblage of interactions and can shape network responses to disturbance confirms earlier findings (Almeida-Neto *et al.* 2008; Ulrich, Almeida-Neto & Gotelli 2009; Thebault & Fontaine 2010; Vanbergen *et al.* 2014).

The consequences of the observed changes in network structure for robustness to species extinctions were complex

and depended on the effects of habitat disturbance on network size and connectance and the level of reliance on mutualism of the interacting species. The SCM simulations showed that initial insect extinction following random plant species loss was less common in the disturbed networks, as revealed by a strong negative correlation between the frequency of low-order (2 degree) co-extinction cascades and the gradient in network structure (PC1) due to habitat disturbance (Fig. 3a). This implies that networks from disturbed habitat were more robust to plant extinction. However, this pattern was removed when the effects of network size and connectance was controlled for, using z -scores standardisation of the SCM simulations against null networks (Vázquez *et al.* 2007). Therefore, the increase in robustness to plant extinction in disturbed networks appears to be driven by their larger size or lower connectance.

A likely explanation is that within the sparsely connected networks from disturbed sites, the loss of a single plant species will increase the extinction risk for a smaller number of insect species than would be the case in the more connected undisturbed networks. Therefore, in the disturbed situation, there was a greater likelihood of the extinction sequence terminating abruptly. This mirrors Vieira & Almeida-Neto (2015), who reported that increased connectance of mutualistic network structure increased the likelihood of co-extinction cascades, but departs from studies that identified connectance as a stabilising feature in the dynamic and structural stability of networks (e.g. Dunne, Williams & Martinez 2002b; Thebault & Fontaine 2010; Lever *et al.* 2014). Our results thus further contribute to the continuing debate over the importance of connectance for community stability (Thebault & Fontaine 2010; Heleno, Devoto & Pocock 2012; James, Pitchford & Plank 2012; Tylianakis & Coux 2014).

In contrast to the pattern described above, we also found that large co-extinction cascades tended to be more common in the disturbed networks, suggesting a lower robustness. However, standardisation of the *basic* SCM

outputs mainly eliminated the positive correlations between large co-extinction cascades and network structure (Fig. 4b). The probabilistic nature of the SCM algorithm means larger networks can inevitably support larger cascades, so the apparently lower robustness of disturbed networks to very large cascades likely arose solely from their larger size.

Results differed, however, when the SCM explicitly included interspecific variation in dependence on plant–insect mutualism. The standardised ‘dependence SCM’ revealed that the disturbed networks were disproportionately robust to very large co-extinction cascades (Fig. 4b). This difference between the ‘basic’ and ‘dependence’ SCMs may have arisen from non-random associations between insect species differing in their dependence on floral resources. For example, social bumblebee species have a total reliance on pollen and nectar foods throughout their life cycle, whereas syrphid hoverfly species, other Diptera fly species, and Lepidoptera exploit other sources of nutrition either at different life stages or as part of an omnivorous diet (Laurence 1954; Potts *et al.* 2003; Vanbergen *et al.* 2014; Orford, Vaughan & Memmott 2015). In this study system, networks in disturbed habitat saw a significant uplift in Dipteran species richness (Vanbergen *et al.* 2014), which could have imparted a degree of robustness. Generally, we suggest that interactions between species of different dependency on mutualism may stabilise networks against very high co-extinction cascades.

The difference we found between the standardised basic and dependence models (Fig. 4b) also demonstrates for the first time how accounting for interspecific variation in demographic dependence on mutualism can influence conclusions about network robustness to disturbance. The ability to reflect interspecific differences in mutualism dependence is therefore a key advantage of the SCMs in understanding network stability (Vieira & Almeida-Neto 2015) over previous topological approaches (Memmott, Waser & Price 2004; Kaiser-Bunbury *et al.* 2010; Ramos-Jiliberto *et al.* 2012). However, we also acknowledge that the way that mutualism dependence is described within the model is a simplification and somewhat arbitrary. More research is needed to more accurately quantify the mutualism dependence of different plant and insect species (Potts *et al.* 2003; Ollerton, Winfree & Tarrant 2011; Willmer 2011; Woodcock *et al.* 2013; De Palma *et al.* 2015). Molecular approaches (e.g. metabarcoding, metagenomics) scalable from individual to community scales are pointing the way toward an efficient, high-throughput sampling of ecological interactions via sequencing and distinguishing ‘host’ DNA from their gut contents or pollen loads (Arribas *et al.* 2016; Gill *et al.* 2016; Pornon *et al.* 2016). These molecular approaches have the potential to quantify trophic or mutualistic interactions at unparalleled resolution, which may reveal cryptic interactions or the extent of specialised interactions to advance our knowledge of mutualistic or trophic reliance in interspecific networks.

Beyond the structuring of interactions, how variable mutualism dependence influences the dynamic resilience of communities to environmental change and the delivery of sustained pollination function is not known (Vanbergen 2014; Gill *et al.* 2016). In this study, for example, relatively low mutualism dependence in these networks arose from the preponderance of flies in the community (Vanbergen *et al.* 2014). Such relatively weak interactions may have contributed to the degree of structural robustness to co-extinctions observed in our models. While beyond the scope of these data, a test of the dynamic stability of ‘mutualistic’ networks characterised by such weak connections would be an interesting future research question. Moreover, the efficacy of different pollinators (e.g. bees vs. flies) in delivering pollination services to plants is variable, debated and still in many cases to be well quantified (Garibaldi *et al.* 2013; Woodcock *et al.* 2013; Orford, Vaughan & Memmott 2015; Rader *et al.* 2015). Therefore, the functional merit of more structurally stable networks due to low levels of mutualism dependence, yet potentially less effective pollen transfer per visit, needs investigation in different environmental contexts. Another avenue of research must be the experimental validation of the rewiring patterns detected from simulation models (Ramos-Jiliberto *et al.* 2012; Valdovinos *et al.* 2013). For example, manipulating plant species extinctions to rewire and generate networks of variable size and complexity (Lopezaraiza-Mikel *et al.* 2007), which can subsequently be tested for robustness to extinctions and stability of pollination function.

A novel feature of this study is that the SCM outputs were subject to *z*-scores standardisation and compared against results from simulations on a null model appropriate for plant–insect visitation networks (Vázquez *et al.* 2007). Others have standardised network parameters to compare assemblages of interactions differing in size (Almeida-Neto *et al.* 2008; Ulrich, Almeida-Neto & Gotelli 2009; Vanbergen *et al.* 2014), and here we observed networks had disproportionately low linkage density and vulnerability and high specialisation when compared with standardised null networks. To our knowledge, however, equivalent standardisations of SCM outputs from multiple networks have not been done before. We argue that this standardisation is needed because the sizes of co-extinction cascades produced by the SCM have an intrinsic dependence on species richness. This is because each iteration of the SCM involves Bernoulli trials applied to each species in one of the network levels. The more species that are present, the greater the chance that one of the trials is ‘successful’, i.e. a species becomes extinct, which allows the SCM to progress to the next iteration. Therefore, all else being equal, we expect larger networks to yield higher frequencies of co-extinction cascades. In our data set, the ‘all else being equal’ condition was not met because other network parameters covaried with network size. Our standardisation used a null model that controlled for network size and connectivity, and therefore highlighted the role of these two

properties in driving some of the effects of disturbance on network robustness. Standardisation of SCM outputs is thus useful for both identifying the particular features of network structure that confer robustness and comparing this dimension of community stability among networks differing in size.

Conclusion

Habitat disturbance caused changes in plant–insect visitation network structure that may have both increased and decreased different aspects of robustness to plant species loss, according to the SCM. Co-extinction following plant loss was less likely in disturbed networks because of their lower connectance. However, networks from disturbed sites were more prone to undergo larger co-extinction cascades, probably resulting from their larger size. Accounting for interspecific variation in mutualism dependence affected the assessment of network robustness by the SCM. With mutualism dependence explicit, networks from disturbed habitat appeared more robust to very large co-extinction cascades. We suggest that this results from non-random interactions between species that differ in their dependence on mutualism. Our results demonstrate that SCM approaches coupled with null models of network assembly represent a powerful tool to compare the robustness of networks under different environmental contexts and understand better which properties of network structure confer stability.

Authors' contributions

A.J.V. led the original field study that produced the data; A.J.V. and D.S.C. jointly led the conception, analysis and preparation of this paper; D.S.C. carried out the modelling, and all authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

Data collection was co-funded by a British Ecological Society small grant (SEPG 1563/1968) and the NERC CEH Environmental Change Integrating Fund (NEC03463). A CEH national capability project (NEC5106) supported this paper. Thanks to the landowners for granting permission to carry out this research. Also to A. Gray for botany and R. Howells, N. Britton and C. Andrews for field and laboratory assistance in the original study (Vanbergen *et al.* (2014)).

Data accessibility

Plant–insect network data and metadata are lodged with and can be obtained from the NERC Environmental Information Data Centre (EIDC) (Vanbergen 2016) <https://doi.org/10.5285/4c058d1f-6166-4606-88a2-d2feaf036a2f>.

References

- Aizen, M.A., Sabatino, M. & Tylianakis, J.M. (2012) Specialization and rarity predict nonrandom loss of interactions from mutualist networks. *Science*, **335**, 1486–1489.
- Almeida-Neto, M., Guimaraes, P., Guimaraes, P.R. Jr, Loyola, R.D. & Ulrich, W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, **117**, 1227–1239.
- Arribas, P., Andújar, C., Hopkins, K., Shepherd, M. & Vogler, A.P. (2016) Metabarcoding and mitochondrial metagenomics of endogean arthropods to unveil the mesofauna of the soil. *Methods in Ecology and Evolution*, **7**, 1071–1081.
- Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003) The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, **100**, 9383–9387.
- Bersier, L.-F., Banašek-Richter, C. & Cattin, M.-F. (2002) Quantitative descriptors of food-web matrices. *Ecology*, **83**, 2394–2407.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M. *et al.* (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and The Netherlands. *Science*, **313**, 351–354.
- Blüthgen, N., Menzel, F. & Blüthgen, N. (2006) Measuring specialization in species interaction networks. *BMC Ecology*, **6**, 1–12.
- Bommarco, R., Lundin, O., Smith, H.G. & Rundlöf, M. (2011) Drastic historic shifts in bumble-bee community composition in Sweden. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 309–315.
- Burkle, L.A., Marlin, J.C. & Knight, T.M. (2013) Plant–pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science*, **339**, 1611–1615.
- Cameron, S.A., Lozier, J.D., Strange, J.P., Koch, J.B., Cordes, N., Solter, L.F. & Griswold, T.L. (2011) Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 662–667.
- Carvalho, L.G., Kunin, W.E., Keil, P. *et al.* (2013) Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. *Ecology Letters*, **16**, 870–878.
- De Palma, A., Kuhlmann, M., Roberts, S.P.M., Potts, S.G., Börger, L., Hudson, L.N., Lysenko, I., Newbold, T. & Purvis, A. (2015) Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes. *Journal of Applied Ecology*, **52**, 1567–1577.
- Dormann, C.F., Gruber, B. & Frund, J. (2008) Introducing the bipartite package: analysing ecological networks. *R News*, **8/2**, 8–11.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002a) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, **5**, 558–567.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002b) Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 12917–12922.
- Eckert, C.G., Kalisz, S., Geber, M.A. *et al.* (2010) Plant mating systems in a changing world. *Trends in Ecology & Evolution*, **25**, 35–43.
- Fitter, A.H. & Peat, H.J. (1994) The ecological flora database. *Journal of Ecology and Field Biology*, **82**, 415–425.
- Fort, H., Vázquez, D.P. & Lan, B.L. (2016) Abundance and generalisation in mutualistic networks: solving the chicken-and-egg dilemma. *Ecology Letters*, **19**, 4–11.
- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R. *et al.* (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, **339**, 1608–1611.
- Gill, R.J., Baldock, K.C.R., Brown, M.J.F. *et al.* (2016) Chapter four - protecting an ecosystem service: approaches to understanding and mitigating threats to wild insect pollinators. *Advances in Ecological Research* (eds G. Woodward & D.A. Bohan), Vol. **54**, pp. 135–206. Academic Press (Elsevier), Cambridge, MA, USA.
- González-Varo, J.P., Biesmeijer, J.C., Bommarco, R. *et al.* (2013) Combined effects of global change pressures on animal-mediated pollination. *Trends in Ecology & Evolution*, **28**, 524–534.
- Heleno, R., Devoto, M. & Pocock, M. (2012) Connectance of species interaction networks and conservation value: is it any good to be well connected? *Ecological Indicators*, **14**, 7–10.
- IPBES (2016) Summary for policymakers of the assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services on pollinators, pollination and food production (eds S.G. Potts, V.L. Imperatriz-Fonseca, H.T. Ngo *et al.*), pp. 36. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany.
- James, A., Pitchford, J.W. & Plank, M.J. (2012) Disentangling nestedness from models of ecological complexity. *Nature*, **487**, 227–230.
- Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Muller, C.B. & Calfisch, A. (2010) The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecology Letters*, **13**, 442–452.
- Kerr, J.T., Pindar, A., Galpern, P. *et al.* (2015) Climate change impacts on bumblebees converge across continents. *Science*, **349**, 177–180.

- Laurence, B.R. (1954) The larval inhabitants of cow pats. *Journal of Animal Ecology*, **23**, 234–260.
- Lever, J., van Nes, E.H., Scheffer, M. & Bascompte, J. (2014) The sudden collapse of pollinator communities. *Ecology Letters*, **17**, 350–359.
- Lopezaraiza-Mikel, M.E., Hayes, R.B., Whalley, M.R. & Memmott, J. (2007) The impact of an alien plant on a native plant-pollinator network: an experimental approach. *Ecology Letters*, **10**, 539–550.
- Memmott, J., Waser, N.M. & Price, M.V. (2004) Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 2605–2611.
- Nielsen, A. & Bascompte, J. (2007) Ecological networks, nestedness and sampling effort. *Journal of Ecology*, **95**, 1134–1141.
- Nielsen, A. & Totland, O. (2014) Structural properties of mutualistic networks withstand habitat degradation while species functional roles might change. *Oikos*, **123**, 323–333.
- Olesen, J.M., Bascompte, J., Dupont, Y.L. & Jordano, P. (2007) The modularity of pollination networks. *Proceedings of the National Academy of Sciences United States of America*, **104**, 19891–19896.
- Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos*, **120**, 321–326.
- Orford, K.A., Vaughan, I.P. & Memmott, J. (2015) The forgotten flies: the importance of non-syrphid diptera as pollinators. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **282**, 20142934. doi:10.1098/rspb.2014.2934
- Pornon, A., Escaravage, N., Burrus, M. *et al.* (2016) Using metabarcoding to reveal and quantify plant-pollinator interactions. *Scientific Reports*, **6**, 27282.
- Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G. & Willmer, P. (2003) Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology*, **84**, 2628–2642.
- Rader, R., Bartomeus, I., Garibaldi, L.A. *et al.* (2015) Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences of the United States of America*, **113**, 146–151.
- Ramos-Jiliberto, R., Valdovinos, F.S., Moisset de Espanés, P. & Flores, J.D. (2012) Topological plasticity increases robustness of mutualistic networks. *Journal of Animal Ecology*, **81**, 896–904.
- Rohr, R.P., Saavedra, S. & Bascompte, J. (2014) On the structural stability of mutualistic systems. *Science*, **345**, 1253497–9. doi:10.1126/science.1253497
- Senapathi, D., Carvalheiro, L.G., Biesmeijer, J.C. *et al.* (2015) *The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England*. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20150294. doi:10.1098/rspb.2015.0294
- Thebault, E. & Fontaine, C. (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, **329**, 853–856.
- Tylianakis, J.M. & Coux, C. (2014) Tipping points in ecological networks. *Trends in Plant Science*, **19**, 281–283.
- Tylianakis, J.M., Tschirntke, T. & Lewis, O.T. (2007) Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature*, **445**, 202–205.
- Ulrich, W., Almeida-Neto, M. & Gotelli, N.J. (2009) A consumer's guide to nestedness analysis. *Oikos*, **118**, 3–17.
- Valdovinos, F.S., Moisset de Espanés, P., Flores, J.D. & Ramos-Jiliberto, R. (2013) Adaptive foraging allows the maintenance of biodiversity of pollination networks. *Oikos*, **122**, 907–917.
- Vanbergen, A.J. & the Insect Pollinators Initiative (2013) Threats to an ecosystem service: pressures on pollinators. *Frontiers in Ecology and the Environment*, **11**, 251–259.
- Vanbergen, A.J. (2014) Landscape alteration and habitat modification: impacts on plant-pollinator systems. *Current Opinion in Insect Science*, **43**, 1–6.
- Vanbergen, A.J., Hails, R.S., Watt, A.D. & Jones, T.H. (2006) Consequences for host-parasitoid interactions of grazing-dependent habitat heterogeneity. *Journal of Animal Ecology*, **75**, 789–801.
- Vanbergen, A.J., Woodcock, B.A., Gray, A. *et al.* (2014) Grazing alters insect visitation networks and plant mating systems. *Functional Ecology*, **28**, 178–189.
- Vázquez, D.P., Melián, C.J., Williams, N.M., Blüthgen, N., Krasnov, B.R. & Poulin, R. (2007) Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, **116**, 1120–1127.
- Vieira, M.C. & Almeida-Neto, M. (2015) A simple stochastic model for complex coextinctions in mutualistic networks: robustness decreases with connectance. *Ecology Letters*, **18**, 144–152.
- Weiner, C.N., Werner, M., Linsenmair, K.E. & Blüthgen, N. (2014) Land-use impacts on plant-pollinator networks: interaction strength and specialization predict pollinator declines. *Ecology*, **95**, 466–474.
- Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L. & Potts, S.G. (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, **143**, 2280–2291.
- Willmer, P. (2011) *Pollination and Floral Ecology*. Princeton University Press, Princeton, NJ, USA.
- Winfree, R., Williams, N.M., Dushoff, J. & Kremen, C. (2014) Species abundance, not diet breadth, drives the persistence of the most linked pollinators as plant-pollinator networks disassemble. *American Naturalist*, **183**, 600–611.
- Woodcock, B.A., Leather, S.R. & Watt, A.D. (2003) Changing management in Scottish birch woodlands: a potential threat to local invertebrate biodiversity. *Bulletin of Entomological Research*, **93**, 159–167.
- Woodcock, B.A., Edwards, M., Redhead, J., Meek, W.R., Nuttall, P., Falk, S., Nowakowski, M. & Pywell, R.F. (2013) Crop flower visitation by honeybees, bumblebees and solitary bees: behavioural differences and diversity responses to landscape. *Agriculture, Ecosystems & Environment*, **171**, 1–8.

Received 4 July 2016; accepted 16 November 2016

Handling Editor: Alison Brody

Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. List of the insect and plant taxon, species or recognisable taxonomic unit (RTU) comprising the networks in this study.