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How to monitor ecological communities cost-efficiently: The example of plant–pollinator networks

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ABSTRACT

Conservation practitioners often lack tools to monitor functioning of communities because time and monetary constraints create a gap between the optimal monitoring methods and the practical needs in conservation. Interaction networks provide a framework that has proven useful in ecological research. However, they are considered time consuming and too expensive for conservation purposes. We investigate whether it is possible to sample interaction networks cost-efficiently and whether a compromise exists between data quality and amount of resources required to sample the data by using a highly resolved mutualistic plant–pollinator network sampled over two years in Norway. The dataset was resampled with decreasing sampling intensity to simulate decreasing monitoring costs and we investigated the cost-efficiency of these monitoring regimes. The success in monitoring community structure varied largely with sampling intensity and the descriptor investigated. One major result was that a large proportion of the functionally most important species in the community, both plants and insects, could be identified with relatively little sampling. For example, monitoring only in “peak-season”, which costs ca. 20% relative to full monitoring, resulted in recording of 70% (in 2003) or 85% (in 2004) of the top 20 most functionally important pollinator species. Also, peak-season monitoring resulted in relatively precise estimates of several network descriptors. We present a first estimation of the full cost (travel time, sampling time and taxonomic services) of constructing pollination networks with different sampling effort. We recommend monitoring plant–pollinator networks in temperate regions during peak-season to cost-efficiently collect data for practical habitat management of ecosystem functioning.

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1. Introduction

The aim of conservation ecology is to preserve the species composition and ecological structure of communities with the ultimate goal of maintaining or restoring the functioning of ecosystems (Ehrenfeld and Toth, 1997). If conservation practitioners, nature managers or ecological scientists seek to investigate or monitor both the ecological structure and function of ecosystems they need the proper tools and knowledge to accomplish such aims. Ecological interaction networks, or webs, could provide such a tool. They not only provide data on the architecture of the community, which species are present and who interacts with whom, but also provide data on functional aspects of ecosystems (Bascompte and Jordano, 2007; Forup et al., 2008; Gibson et al., 2006). For example, the information in such networks has implications for both plant

reproduction and for insect survival (Hegland et al., 2009a), although the approach is most valuable when paired with data on pollen flow or plant reproductive success (Memmott, 1999). The impact of biological invasions, habitat fragmentation, climate change and other perturbations on ecological communities all occur in the context of a network of species interactions (Bascompte, 2007; Hegland et al., 2009a). Hence, monitoring such networks is essential for understanding whether and how systems are changing due to perturbations, and whether management efforts are effective.

Conservation and restoration management requires setting priorities. For example one may focus management efforts on specific species for cost-efficiency purposes, although such targeting implies a ranking of species that often is controversial (Marris, 2007). Functionally important species may fulfill the criterion for target species, in particular when such species have facilitative interactions with many other species and therefore help increase local biodiversity (Brose et al., 2005; Bruno et al., 2003; Morris,

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2003). Re-establishing the role of facilitative species is often the key to restoring functions of the original system (Bruno et al., 2003). To determine the functional role of species within ecological communities we need to attain the best possible information on their interactions with other species.

Detailed characterization of ecological networks is time and labor intensive, and therefore conservation practitioners seldom collect data on such networks, resulting in a gap between ecological theory and conservation practice (Anonymous, 2007; McCann, 2007). What is needed is a better understanding of the trade off between data quality and the time taken to collect the data. Here we ask the pragmatic question of how much data we must sample from an ecological community to provide necessary information for efficient conservation through good management decisions, decisions which should be based on an understanding of community structure and community function. We do this by collecting data for a detailed plant–pollinator network and then resampling the network at decreasing sampling intensities. These data are used to explore how conservationists and scientists can identify key aspects of ecological structure and function in the most cost- and time-efficient way, for example to use the information to meet conservation and management goals.

The network we use in this paper characterizes the mutualistic interactions between plants and pollinators. Pollination networks have several advantages in terms of ecological functioning and economic efficiency. First, the interactions among flowering plants and flower-visiting insects are of great ecological and conservation importance as they reciprocally depend on each other for reproduction and survival (Ashman et al., 2004; Forup et al., 2008; Steffan-Dewenter and Schiele, 2008). Pollination is a valuable ecosystem service (Klein et al., 2007; Kremen et al., 2007), and mutualistic interactions play an important role in maintaining biodiversity at local to global scales (Bascompte and Jordano, 2007; Bastolla et al., 2009). Second, pollinator visitation to flowers is easily assessed by visual inspection enabling the relatively easy collection of extensive multi-species datasets on species' interactions (e.g., Hegland et al., 2009b) by conservation practitioners. Moreover, pollination can be inferred if quantitative data is available on visitation, with the most abundant visitors being the most likely pollinators (Vazquez et al., 2005; Sahli and Conner, 2007). The objectives of our work are to answer three primary questions: (1) how little can we sample and still reliably estimate network descriptors in comparison to the fully sampled network?; (2) how sensitive is the identification of functionally important species to monitoring effort?; (3) can a reasonable compromise be established between the quality of data collected and the time and money needed to collect the data? Related to earlier studies on sampling effort in ecological networks (e.g., Nielsen and Bascompte, 2007; Tylianakis et al., in press) we focus more on the practical considerations of sampling communities for use in management and science.

2. Methods

2.1. Field site and data collection

The data were collected in a temperate grassland in Kaupanger, western Norway (61°09'27N and 7°10'22E) during 2003 and 2004. The climate in the region is relatively warm and dry; the closest climate station (Lærdal-Moldo) had a mean July temperature of 17.3 °C and a July rainfall of 55 mm in 2003 and 14.5 °C and 53.8 mm, respectively, in 2004. An electric fence was used to mark out a plot ca. 50 × 50 m and to exclude sheep. The surrounding area was dominated by deciduous forest and contains several meadows of similar floral composition as the study site (see Heg-

land and Totland (2005) for more information on the local plant and pollinator community).

Three transects 50 m long were evenly distributed (ca. 13 m apart) along the horizontal axis of the study area. These transects were walked at a slow pace every 3–4 days in order to sample plant–pollinator interactions, in this community the plants being herbs and the pollinators being insects. The first insect observed visiting a flower within a 1.7 m swathe of vegetation (i.e., the length of the catching net and collector's arm) was caught with a net and both plant and insect was determined to species level immediately or collected for later determination. Most insects could not be classified to species level immediately and were sent to taxonomists (see Acknowledgements) or identified by the authors in the lab. This type of transect sampling is considered an efficient method for monitoring of plant–pollinator mutualisms (Westphal et al., 2008). We emphasize however, that the monitoring method must be adapted both to the practical situation and the complexity of study system, e.g., the specific transect method applied may not always be the best when monitoring in non-homogenous and/or very species rich areas. Sampling took place along the same transects in both years, and was performed between 0800 and 1700 h and from 26 May to 16 August in 2003 and from 27 May to 6 August in 2004. Walking pace was kept constant to ensure that all parts of transects were sampled with equal intensity. Transects were walked during periods with no rain and little wind. We walked transects in the same direction every time to avoid shading by the collector, which may affect capture rates of some types of insects.

2.2. Resampling data to determine relationship between monitoring intensity and data quality

Resampling the data was carried out with the aim of simulating monitoring regimes that would be realistic in the practical context of management-related monitoring. Thus our approach to resampling was to split the “full” dataset collected over two-years into subsets that would reflect practical applicable sampling schemes for monitoring from high to low sampling intensity. This led to eight different monitoring regimes (Table 1), ranging from the original full dataset collected over two-years to a “minimal” dataset sampled on three occasions during a single year. To investigate the success and cost-efficiency of the eight monitoring regimes in estimating structural and functional descriptors relative to the full dataset, we calculated three types of variables: (1) network descriptors, (2) species importance, and (3) cost estimation. Each of the variables within each monitoring regime was related to the full dataset simply by calculating their percentage relative to their value in the full dataset. The “2003” dataset and “2004” dataset allowed us to evaluate interannual temporal dynamics of the pollination network. We did this by comparing the species and links between years and by estimating the turnover in link composition (links and their frequency) between years by the means of the Bray–Curtis dissimilarity index (Legendre and Legendre, 1998).

2.3. Calculating network descriptors

Structural properties of mutualistic networks are important for their stability, as they may enhance the robustness of these systems to perturbations such as species extinctions, invasive species, habitat loss and/or fragmentation and climate change (Tylianakis et al., in press). However, the calculation of some network descriptors can be sensitive to sampling effort (Nielsen and Bascompte, 2007). It is therefore crucial to understand how much sampling is needed to identify the real structures found in the underlying network. We therefore, based on the recordings of insect species' visits to flowers and the frequency of visits from replicated

Table 1
Overview of the different monitoring regimes ordered according to declining cost declining cost.

Monitoring regime	Year	Description	Monitoring days	Monitoring period (weeks)	Transects	Hours ^a
Full dataset	2003 + 2004	Complete dataset, two-season monitoring	44	22	132	286
Annual 2003	2003	One years data (2003), monitoring twice a week	24	12	72	156 (55%)
Annual 2004	2004	One years data (2004), monitoring twice a week	20	10.5	60	130 (45%)
Weekly 2003	2003	Monitoring all three transect, once a week	13	12	39	84.5 (30%)
Single transect	2003	Monitor only one transect, all monitoring days	24	12	24	84 (29%)
Peak-season 2003	2003	Only data from July ^b 2003, monitoring all transects	9	4.5	27	58.5 (21%)
Peak-season 2004	2004	Only data from July 2004, monitoring all transects	8	4.5	24	52 (18%)
Minimal 2003	2003	Three monitoring events, 17 June, 15 July and 16 August	3	9	9	19.5 (7%)

^a The hours used per monitoring regime relative to the full monitoring are given as percentage in parentheses and correspond to numbers given in figures.

^b July was the month with highest abundance of pollinators and flowers per sampling day.

transect walks, calculated a set of network descriptors for each of the datasets/monitoring regimes representing different levels of sampling effort and compared our findings to the descriptors calculated on the full data set.

We calculated basic community descriptors such as the number of species of plants and pollinators, the number of unique plant–pollinator associations (i.e., links) and the total number of visits observed between plants and pollinators (i.e., interactions) in each network. To illustrate the heterogeneous distribution of links among the species within the network we also calculated cumulative link distribution, viz. the relationship between the number of links and the frequency of species having that particular number of links or more (Bascompte et al., 2006).

Moreover, we calculated four global community descriptors; connectance, quantitative link density, nestedness and the degree–strength relationship, network descriptors frequently used in studies of plant–pollinator networks when considering their robustness to environmental perturbations (Tylianakis et al., in press). Connectance of each network was estimated as the fraction of all possible trophic links that were realized, i.e., the number of links/(number of plant species × number of pollinator species); increasing connectance has been shown to increase a system's robustness to species loss (e.g., Dunne et al., 2002b) and is an indicator of the overall generalization level in a community (Jordano, 1987). Quantitative link density is a quantitative equivalent of connectance that incorporates the distribution of interaction strengths within the network (Bersier et al., 2002). Just as connectance it illustrates how connected the species within the network are, but it also captures variations in interaction strength that is hidden when analyzing only the presence/absence of links (Tylianakis et al., 2007). The degree of nestedness in the networks provides a measure of how ordered networks are with a higher nestedness value representing a more ordered network. Nested networks have been shown to be more robust to environmental disturbances (Bascompte et al., 2006; Fortuna and Bascompte, 2006; Memmott et al., 2004). Nestedness was calculated using the ANINHADO software freely available on internet (<http://www.guimaraes.bio.br/soft.html>; Guimarães and Guimarães, 2006). We used the NODF nestedness values (the 'N_Total' in ANINHADO) as an estimate of nestedness of the different networks. To evaluate whether the nestedness values were significantly higher than expected by chance we applied the recently developed NODF(Ce)-null model (Almeida-Neto et al., 2008) in ANINHADO. This null model is the best for cross-network comparisons as it allows significance testing irrespectively of matrix size and shape (Ulrich et al., 2009). We also analyzed the degree distribution and the degree–strength relationship for the species comprising the networks. These descriptors have been used to illustrate the heterogeneity of mutualistic networks. The degree distribution has been shown to follow a truncated power law indicating that most species only have a few links, while a few species have significantly more links than expected by chance while the degree–strength relationship shows

that the most connected species (with the highest number of links) also provides the strongest influence (strength) on the species they interact with (Bascompte et al., 2006). If the relationship between degree and strength is best illustrated by a model including a quadratic term the strength increases faster than the number of links. Such a relationship indicates that specialists tend to interact exclusively with the most generalist species, a heterogeneous property further stabilizing these networks (Bascompte et al., 2006).

2.4. Identifying functionally important species in the networks

We used an easy to apply and ecologically relevant approach to estimate the importance of species with the goal of targeting functionally important species within the study community (sensu Bruno et al., 2003). We consider a species to be functionally important when it has many interactions with other species. For example, pollinators usually contribute most strongly to plant reproductive success when they have a high interaction frequency (Vazquez et al., 2005). In addition, loss of species with many links has been shown in simulations to lead to more secondary extinctions than loss of those with few links in both food webs and pollination networks (Dunne et al., 2002b; Memmott et al., 2004; Kaiser-Bunbury et al., 2010). We ranked, in each data-subset, species according to the (1) number of species they visit or were visited by, often called degree, reflecting the interaction richness of species; and (2) total number of visits by or to species, often called interaction frequency. This ranking was done separately for plants and pollinators. By ranking the 10 plant species ("top-10 plants") and 20 pollinator species ("top-20 pollinators") with most links, we could quantitatively estimate the proportion of the most important species that were sampled in each data-subset related to the optimal monitoring of the full dataset.

2.5. Estimating the cost of monitoring regimes

To estimate the monetary cost for each monitoring regime we made the following assumptions. First, driving from the place of work to the field site took a half hour in each direction, and the total distance was set at 30 km. Second, sampling time per transect, including preparation time (getting equipment prepared) and supplementary work on the site (measuring floral abundance), was presumed to take one person one hour. Thus to sample all three transects in the community, including travel, will take four hours. Costs were based on sampling by one person and set at 20 €/h and transportation costs were set at 0.25 €/km. While costs are in Euros, the relative costs of each monitoring regime will be identical in any currency. Plant identification was assumed to be done in the field, whereas taxonomists were assumed to do insect determination at a set price of 0.25 Euros per individual insect. Furthermore, we estimated that managing and analyzing the data took 0.5 h per transect, i.e., 1.5 h for all three transects per monitoring day. The cost and time estimation should not be looked upon as a precise

budget for a specific monitoring protocol applicable in the real world, but rather as an approximation of their relative size of expenses associated with the different activities dependent on, for example, labor cost. The calculations were based on direct experience from field-work and we believe they provide a useful guide for estimating costs of future studies.

3. Results

3.1. Description of the plant–pollinator community

In total 39 plant species, 197 pollinator species and 657 links were recorded across 3844 plant–pollinator interactions, during the 2003 and 2004 pollination seasons in the meadow community in Kaupanger (Table 2). The main insect orders were Coleoptera (21 species), Diptera (133 species), Hymenoptera (20 species) and Lepidoptera (20 species). The dominant plant families were Asteraceae (5 species), Fabaceae (4 species), Rosaceae (9 species) and Rubiaceae (4 species).

Species and interaction richness increased from 2003 to 2004: in 2003, we recorded 31 plant species, 127 pollinator species and 350 links, whereas for 2004 these numbers were 38, 145 and 468, respectively (Table 2). The plant species recorded in 2004 were mainly the same as in 2003; only two species (7%) present in 2003

were not recorded in 2004 and six (19%) new plant species were recorded in 2004. The pollinator fauna had a much higher annual turnover and 47 (37%) of the insect species recorded in 2003 were not observed in 2004 whereas 76 (52%) new species were recorded in 2004 relative to 2003. Eighty (41%) of 197 pollinator species were recorded in both years. The changes in plant–pollinator associations over the two years indicated even greater temporal variability: 196 (56%) of the links in 2003 were not recorded in 2004 and 314 (67%) of the links in 2004 were novel compared to 2003. Only 154 (23%) of totally 657 links between plant and pollinator species were common for both years. However, when we weighted the plants' interactions with pollinators by their frequencies the interaction turnover was less pronounced as indicated by a 66% similarity (i.e., 34% dissimilarity) between years using the Bray–Curtis index.

3.2. Calculations of network descriptors

The number of species and total number of interactions and links decrease rapidly if we sample only part of the “full” network (Fig. 1). For example, only half of the links recorded in the full dataset were present in the “2003” dataset, whereas the “2004” dataset contains more species and scores relative better on links (>70% of full monitoring). The specific number of plant and pollinator species sampled did differ markedly across monitoring regimes: 42

Table 2
Species and interactions numbers including selected community descriptors of the different monitoring regimes of plant–pollinator networks.

Monitoring regime	Plant species	Pollinator species	Interactions	Links	Nestedness ^a	Quantitative link density	Connectance	Cost of monitoring ^b
Full dataset	39	197	3844	657	24.5 ^{**}	30.42	0.086	6131
Annual 2003	31	127	1477	350	25.1 ^{**}	23.63	0.085	3189
Annual 2004	38	145	2367	468	21.2 ^{**}	23.45	0.089	2942
Weekly 2003	29	93	775	227	18.3 ^{**}	16.99	0.103	1721
Single transect 2003	27	77	564	189	16.3 ^{**}	13.94	0.091	1521
Peak-season 2003	27	85	989	237	21.1 ^{**}	14.84	0.084	1305
Peak-season 2004	29	84	1247	275	18.3 ^{**}	17.81	0.112	1250
Minimal 2003	21	50	196	100	11.7 [*]	9.79	0.095	402

^a Significance of nestedness values.

^b Cost of monitoring in €.

* $P < 0.05$.

** $P < 0.01$.

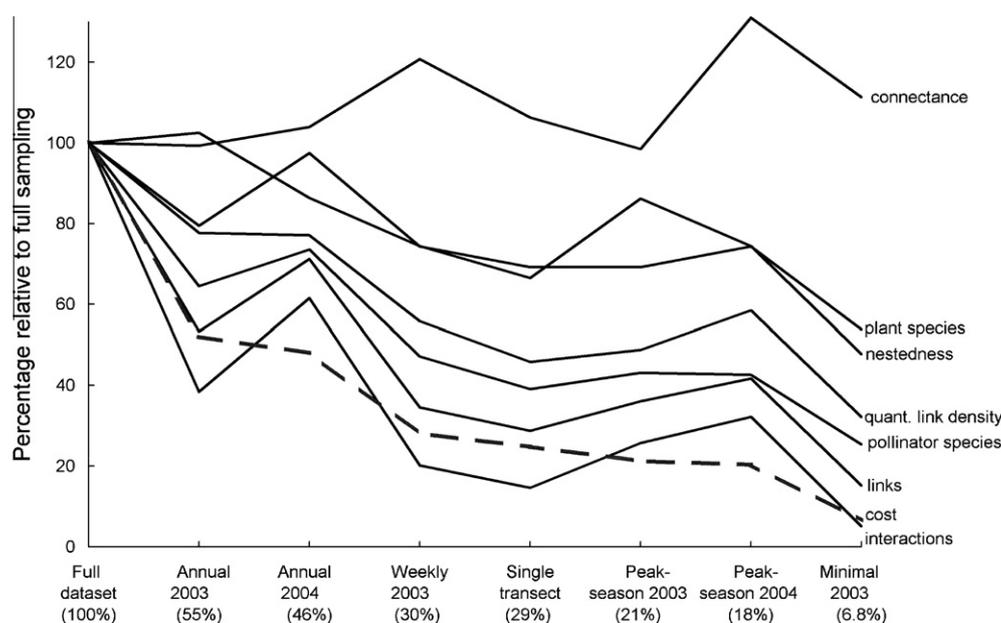


Fig. 1. The proportion of different community descriptors identified by different monitoring regimes relative to “full” monitoring. Sampling time, i.e., the percentage of hours used for sampling, determination and data management, relative to full monitoring is given within parentheses for each monitoring regime (x-axis) and the relative cost is represented by the cost line (dotted line).

species (18%), 19 (49%) plant species and 23 (12%) pollinator species were present in all monitoring regimes. Plant species were thus much more efficiently sampled than pollinator species, and the fraction of plant species sampled in any monitoring regime never fell below 50%, while discovery of 50% or more of pollinator species required a whole year of monitoring (2003 or 2004). In contrast, connectance estimates were relatively stable for all monitoring regimes. Connectance values, ranging from 8.3% to 11.2%, were higher for all regimes than in the full dataset except for the “peak-season 2003” dataset, for which it was slightly lower. Nestedness values, on the other hand, varied more among monitoring regimes (48–102% relative to the full monitoring), but all eight networks appear significantly nested (Table 2). The quantitative link density was sensitive to sampling effort, although it followed a pattern corresponding to several other descriptors and performed relatively well in the peak-season monitoring.

We found, by visual inspection, that the distribution of number of links, i.e., the cumulative degree distribution, followed a truncated power law in our study system (Appendix A for details and illustrations). We found that the best model describing the degree–strength relationship included a quadratic term in all our networks, regardless of sampling effort ($P < 0.01$ for the quadratic term in all models; Appendix B for details and illustrations).

3.3. Identification of functionally important species in the networks

We used two variables, degree and interaction frequency, to estimate functional importance for plants and pollinators and, although there was some variation in the identification of these, the results were consistent across monitoring regimes (Table 3). Looking at both variables, four (2.5%) out of 197 pollinator species were identified as functionally most important irrespectively of the importance descriptor we defined: the Diptera *Thricops cunctans*, the Hymenoptera *Bombus pascuorum* and *B. lucorum*, and the Coleoptera *Corymbia rubra*. An overview of the “top-3” most important pollinator species across both importance variables (Table 3) identifies consistently these four species in most cases. The Syrphids

Cheilosia longula, *Meliscaeva cinctella* and *Volucella pelluscens*, and the Coleoptera *Trichius faciatus* were also included among these top-3 pollinators for a few monitoring regimes.

Among plants, four (10%) of 39 plant species were identified as the functionally most important species across all monitoring regimes (Table 3): the Rosaceae *Potentilla erecta* and *Filipendula ulmaria* together with the Fabaceae *Trifolium pratense* and the Apiaceae *Carum carvi*. The overview of top-3 most important plant species also identified these species. *Carum carvi*, and four other plant species (*Centaurea jacea*, *Galium verum*, *Leucanthemum vulgare*, and *Pimpinella saxifraga*) were identified in \leq two cases each.

The proportion of important species identified by different monitoring regimes declined with decreasing sampling intensity (Fig. 2), but still remained at a relatively high level across monitoring regimes. Both the “top-10 plants” and “top-20 pollinators” were identified at minimum 70% and 55%, respectively, whereas all the ‘most links and visits’-descriptors dropped to less than 35% relative to full monitoring in the “minimal” monitoring regime.

3.4. Estimation of the cost-efficiency of monitoring regimes

The cost-efficiency of each regime can be evaluated by considering the difference between the trend line of a community descriptor (Fig. 1), or the proportion of functionally important species (Fig. 2) and the cost line in these figures. For example, relative to connectance and number of plant species, the cost-line decreases faster indicating a higher cost-efficiency for such variables when sampling less intensively (Fig. 1). The 2003 and 2004 peak-season datasets appears to be the most cost-efficient monitoring regimes because the distance between the cost line and other lines in Figs. 1 and 2 were larger than for all other monitoring regimes. These peak-season datasets had a much lower total cost than all other monitoring regimes, except the minimal dataset, and they take only ca. 20% of the total sampling hours and cost (Table 1). Monitoring only in peak season gave a comparable value for most variables than the whole annual datasets, 2003 and 2004. This was most evident for the peak-season 2004 dataset that, for example,

Table 3
Identity of “top-3” most important plant and pollinator species in the different monitoring regimes.

Monitoring regime	Most links to plant	Most visits to plant	Most links to pollinator	Most visits from pollinators
Full dataset	1. <i>Thricops cunctans</i> 2. <i>Meliscaeva cinctella</i> 3. <i>Chrysanthia viridissima</i>	1. <i>Thricops cunctans</i> 2. <i>Bombus pascuorum</i> 3. <i>Meliscaeva cinctella</i>	1. <i>Potentilla erecta</i> 2. <i>Carum carvi</i> 3. <i>Plantago lanceolata</i>	1. <i>Filipendula ulmaria</i> 2. <i>Potentilla erecta</i> 3. <i>Trifolium pratense</i>
Annual 2003	1. <i>Bombus pascuorum</i> 2. <i>Corymbia rubra</i> 3. <i>Thricops cunctans</i>	1. <i>Bombus pascuorum</i> 2. <i>Corymbia rubra</i> 3. <i>Bombus lucorum</i>	1. <i>Potentilla erecta</i> 2. <i>Filipendula ulmaria</i> 3. <i>Trifolium pratense</i>	1. <i>Potentilla erecta</i> 2. <i>Filipendula ulmaria</i> 3. <i>Trifolium pratense</i>
Annual 2004	1. <i>Thricops cunctans</i> 2. <i>Meliscaeva cinctella</i> 3. <i>Cheilosia longula</i>^a	1. <i>Thricops cunctans</i> 2. <i>Meliscaeva cinctella</i> 3. <i>Bombus pascuorum</i>	1. <i>Carum carvi</i> 2. <i>Potentilla erecta</i> 3. <i>Plantago lanceolata</i>	1. <i>Filipendula ulmaria</i> 2. <i>Carum carvi</i> 3. <i>Plantago lanceolata</i>
Weekly 2003	1. <i>Bombus pascuorum</i> 2. <i>Thricops cunctans</i> 3. <i>Bombus lucorum</i>	1. <i>Bombus pascuorum</i> 2. <i>Corymbia rubra</i> 3. <i>Bombus lucorum</i>	1. <i>Potentilla erecta</i> 2. <i>Filipendula ulmaria</i> 3. <i>Plantago lanceolata</i>	1. <i>Filipendula ulmaria</i> 2. <i>Trifolium pratense</i> 3. <i>Potentilla erecta</i>
Single transect	1. <i>Bombus lucorum</i> 2. <i>Bombus pascuorum</i> 3. <i>Corymbia rubra</i>	1. <i>Bombus pascuorum</i> 2. <i>Corymbia rubra</i> 3. <i>Bombus lucorum</i>	1. <i>Potentilla erecta</i> 2. <i>Leucanthemum vulgare</i> 3. <i>Filipendula ulmaria</i>	1. <i>Filipendula ulmaria</i> 2. <i>Potentilla erecta</i> 3. <i>Trifolium pratense</i>
Peak 2004	1. <i>Thricops cunctans</i> 2. <i>Cheilosia longula</i> 3. <i>Volucella pelluscens</i>	1. <i>Thricops cunctans</i> 2. <i>Bombus pascuorum</i> 3. <i>Trichius faciatus</i>	1. <i>Filipendula ulmaria</i> 2. <i>Centaurea jacea</i> 3. <i>Pimpinella saxifraga</i>	1. <i>Filipendula ulmaria</i> 2. <i>Centaurea jacea</i> 3. <i>Trifolium pratense</i>
Peak 2003	1. <i>Corymbia rubra</i> 2. <i>Thricops cunctans</i> 3. <i>Trichius faciatus</i>	1. <i>Bombus pascuorum</i> 2. <i>Corymbia rubra</i> 3. <i>Thricops cunctans</i>	1. <i>Potentilla erecta</i> 2. <i>Filipendula ulmaria</i> 3. <i>Galium verum</i>	1. <i>Filipendula ulmaria</i> 2. <i>Trifolium pratense</i> 3. <i>Potentilla erecta</i>
Minimal 2003	1. <i>Bombus pascuorum</i> 2. <i>Thricops cunctans</i> 3. <i>Chrysanthia viridissima</i>	1. <i>Bombus pascuorum</i> 2. <i>Corymbia rubra</i> 3. <i>Chrysanthia viridissima</i>	1. <i>Potentilla erecta</i> 2. <i>Filipendula ulmaria</i> 3. <i>Galium verum</i>	1. <i>Trifolium pratense</i> 2. <i>Filipendula ulmaria</i> 3. <i>Potentilla erecta</i>

^a Species identified as among the “top-3” most functional important species in \leq two monitoring regimes are in bolditalics.

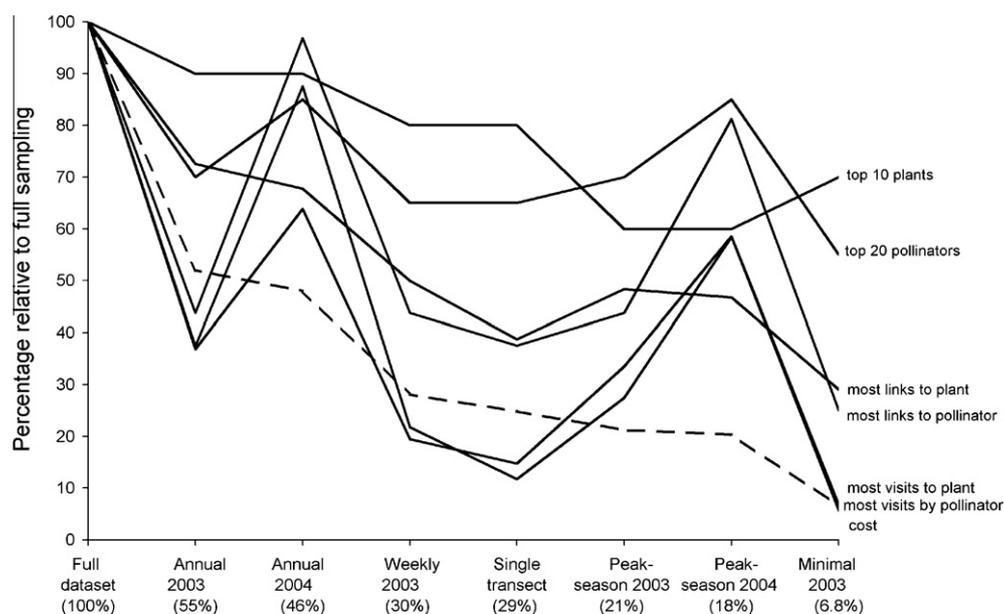


Fig. 2. The proportion of functionally important species identified by different monitoring regimes relative to “full” monitoring. Sampling time, i.e., the percentage of hours used for sampling, determination and data management, relative to “full monitoring is given within parentheses for each monitoring regime (x-axis) and the relative cost is represented by the cost line (dotted line).

identified the top-20 pollinators at similar proportion (85% relative to full monitoring; Fig. 2) than the annual 2004 dataset for less than half the price (Table 2).

4. Discussion

Our monitoring experiments revealed that it may be challenging to obtain some community descriptors when decreasing the sampling intensity. Connectance, nestedness and plant species richness were well represented even at lower sampling intensities (i.e., >70% relative to full monitoring), whereas pollinator species richness and the link and interaction frequencies were poorly estimated when sampling intensity decreased (Fig. 1). For practical monitoring and management considerations it may be more fruitful to focus on the important functional components of a community. The same handful of plants and pollinators (eight out of 236 species: 3.4%) were consistently returned as among the functionally most important species. Regardless of sampling intensity more than half of the top-10 plants and top-20 pollinators from the full monitoring were always identified.

Our limitations are several. First, we quantified pollinator visitation to flowering species and not pollination. Vazquez et al. (2005), however, elegantly showed that the most abundant pollinator is likely the most important pollinator as the most frequent animal mutualist usually contribute the most to plant reproduction regardless of their effectiveness on a per-interaction basis. Second, we base our analysis on only one field site that was sampled frequently across two full pollination seasons. When constructing networks there is a trade off between the detail of the network and the number of networks that can be constructed. Here, we needed the most detailed network possible because we wanted to find which components of the network were missed as sampling intensity decreased. Third, some of the network descriptors used in this study are easily applicable and probably will perform well for management use (see also Tyljanakis et al., in press). Lastly, we must emphasize that we have performed a single study in a species-rich but structurally homogenous temperate grassland and that this study, the methods and conclusion, may not be directly transferable to other systems without modification.

In the following sections we first discuss the challenges of using networks as practical tools for conservation managers and then consider some of the practical implications of our approach, i.e., how can the information gathered from the most cost effective monitoring protocol be used when making decisions on how to monitor?

4.1. Ecological networks: practical tools for practical people?

One obvious challenge when using networks for monitoring is that high temporal variability exists in species composition and plant–pollinator interactions within and between years. In particular the turnovers in pollinator species and plant–pollinator associations were large between years. Only 40% of pollinator species and no more than 23% of the plant–pollinator associations were recorded in both years, similar to numbers reported in other studies (Alarcón et al., 2008; Olesen et al., 2008; Petanidou et al., 2008). However, the turnover appears less dramatic when the interactions were weighted by frequency (66% similarity), which underlines the importance of focusing not only on interaction richness, but also interaction diversity (e.g., Dyer et al., 2010). The pattern emerges because many insect species are rare; in the full dataset more than 50% of insect species were singletons (data not shown), indicating that the major pollination role is played by a smaller fraction of the flower visitor community. However, for the structure, and consequently the robustness, of the system, the rare species are, of course, of utmost importance.

Only 12% of pollinator species were recorded across all eight monitoring regimes and such temporal dynamics emphasize the necessity for a compromise between sampling intensity and data quality. We had to sample a minimum of a whole year to estimate more than half of the pollinator species richness present in the full dataset (see Table 2 and Fig. 1). Thus monitoring the overall diversity of pollinating insects or their interactions with flowering plants as a measure of ecosystem functioning, and thus restoration or conservation success, is very cost and labor intensive. The only community property we obtained at a constantly high level, independent of our sampling intensity, was connectance, as has also been reported in most sampled versions of an endophytic grassland food web (Martinez et al., 1999) and in plant–pollinator networks of the

boreal forest (Tylianakis et al., in press). Thus the generalization level of the community is well-estimated throughout monitoring regimes. Its relative insensitivity to sampling intensity may, however, also pose a problem. Most studies find that higher values of these descriptors indicate higher robustness to perturbations (Dunne et al., 2002b; Memmott et al., 2004). We found that connectance was higher when monitoring, for example, once a week (the “weekly” dataset) compared to sampling more intensively (e.g., the 2003 and/or 2004 datasets). We also found that all networks were significantly nested. Until recently visitation frequency, i.e., quantitative information on interactions between species, was rarely included into calculations of network metrics. One reason may be that it requires higher sampling intensity (Tylianakis et al., in press) which reflects the result presented here: to obtain a comparable high value of link density as for the qualitative descriptors connectance and nestedness, we have to sample much more (Fig. 2). A more complete comparison of qualitative and quantitative network descriptors related to sampling intensity is required to conclude about their strength and weaknesses in ecological network monitoring (see Tylianakis et al. (in press) for a discussion).

Instead of searching for a network descriptor that is cost-effectively sampled, it may be more productive to focus analysis on the functional components of the community. We defined several easily computable variables indicating the functional importance of species and inspected these both qualitatively (Table 3) and quantitatively (Fig. 2) across monitoring regimes. Which species was identified as the most important differed slightly between the two importance variables and across monitoring regimes, but altogether only four plant species and four pollinator species were number one. Moreover, Table 3 shows that only three of these species in each group were repeatedly chosen in more than half of the top 3-lists. The possibility to target functionally important species for conservation efforts is important since it may enable us to preserve ecological functioning (e.g., Davic, 2003). The three target plant species (*Filipendula ulmaria*, *Potentilla erecta*, *Trifolium pratense*) identified in this study were among the most abundant and long-flowering flowering species in this study community (Hegland and Totland, 2005). Other authors have suggested that network analysis can serve as a useful proxy for identifying species with traits important for community function (Olesen et al., 2008). Our results may point to traits or characteristics of species, for example abundance or long-flowering, as aid to identify species that are important for community functioning. Moreover, the three plant species are all very common temperate herbs (e.g., Fitter and Peat, 1994) and applying a more traditional conservation view focused on preserving rare plant species would overlook the critical role of these more common taxa in preserving the diversity and functioning of the system (see also Dupont et al., 2003).

4.2. Monitoring recommendations

Our study shows that it is relatively expensive to monitor the functioning of a community by collecting data that will allow precise estimation of community descriptors such as species richness and abundance, the number of interactions, and to some extent network structure. When monitoring biodiversity for management or restoration purposes it is a challenge to know how little we can sample and still obtain sufficient information on ecological functioning and structure. We have presented one approach that we believe may be efficient, at least within the biological system studied here. For example, we were able to determine some of the functional most important taxa considering plant–pollinator mutualisms in a temperate grassland with a highly defined season. Within this type of season, based on the results from this study, we would recommend to focus the monitoring in the peak-season period. In terms of species it is still questionable whether a certain

monitoring scheme will indicate the single most important species in functional terms. For example, in the top 3-lists of the peak-season datasets, half of the plants and pollinators are not present in the full dataset. However, the top-10 plants and the top-20 pollinators approach to characterizing species importance appear promising. These importance descriptors include a larger proportion of the species in the community and Fig. 2 shows that the top-species are especially well identified in the peak-season dataset. Specifically, monitoring only in peak-season appears cost-efficient as it takes only 20% of time and money relative to full monitoring, but resulted in recording of 70% (in 2003) or 85% (in 2004) of the top-20 most functionally important pollinator species. As highlighted in the results also network descriptors are most efficiently obtained by the peak-season monitoring. Perhaps most important for practical management considerations is the fact that peak-season monitoring was much more cost-efficient than the other monitoring schemes. This is particularly important when sampling interactions among species at different trophic levels, as one can never sample all the species and their links (Nielsen and Bascompte, 2007).

Conservationists often hesitate to point out functionally important species due to associated uncertainty from lack of information (Marris, 2007). Here, we show that it is possible to cost-efficiently identify a set of functionally important species within a system based on limited monitoring of their interactions with other species. Future studies may approach data from other systems in similar ways to investigate whether this approach is limited to the community geographical region or ecological interaction of our study, or whether comparable success is achieved within other systems. It would also be interesting to know whether a few taxa, like the dipterans and hymenopterans in this study, generally appear to be of major ecological importance relative to other taxa.

Acknowledgements

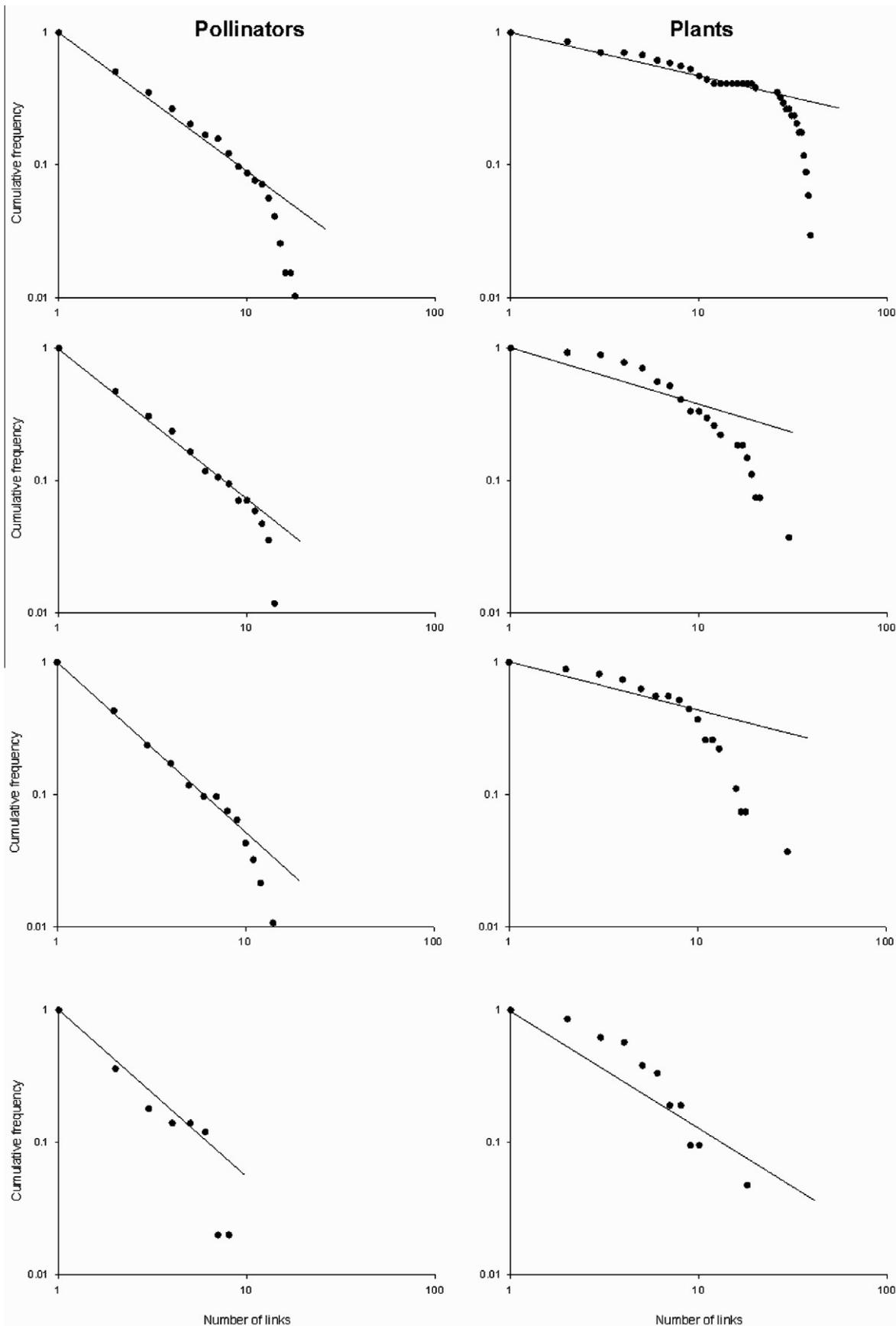
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Appendix A. Cumulative degree distribution

Previous studies have shown that there is a well-defined relationship between the shape of the connectivity (number of links) distribution and the robustness of the network to secondary extinctions (Albert and Barabasi, 2000; Tylianakis et al., in press). The cumulative distribution of links in mutualistic interaction networks has been shown to follow a truncated power law. This relationship illustrates the asymmetric distribution of links within the networks, viz. that most species have few interactions while a few species display a number of interactions significantly higher than what would be expected by chance. We found (illustrations below) that the relationship followed a truncated power law in our study system. The truncation, i.e., the departure from the straight line to the right in the graphs, illustrates the lack of fit of a power law. The graphs represents, from the top: 2003 + 2004, peak-season 2003, weekly 2003 and minimal 2003 for plants and pollinator separately. Though most obvious in the larger networks, this truncation

could also be seen in networks resulting from low sampling effort. In ecological terms this means that most species have few links

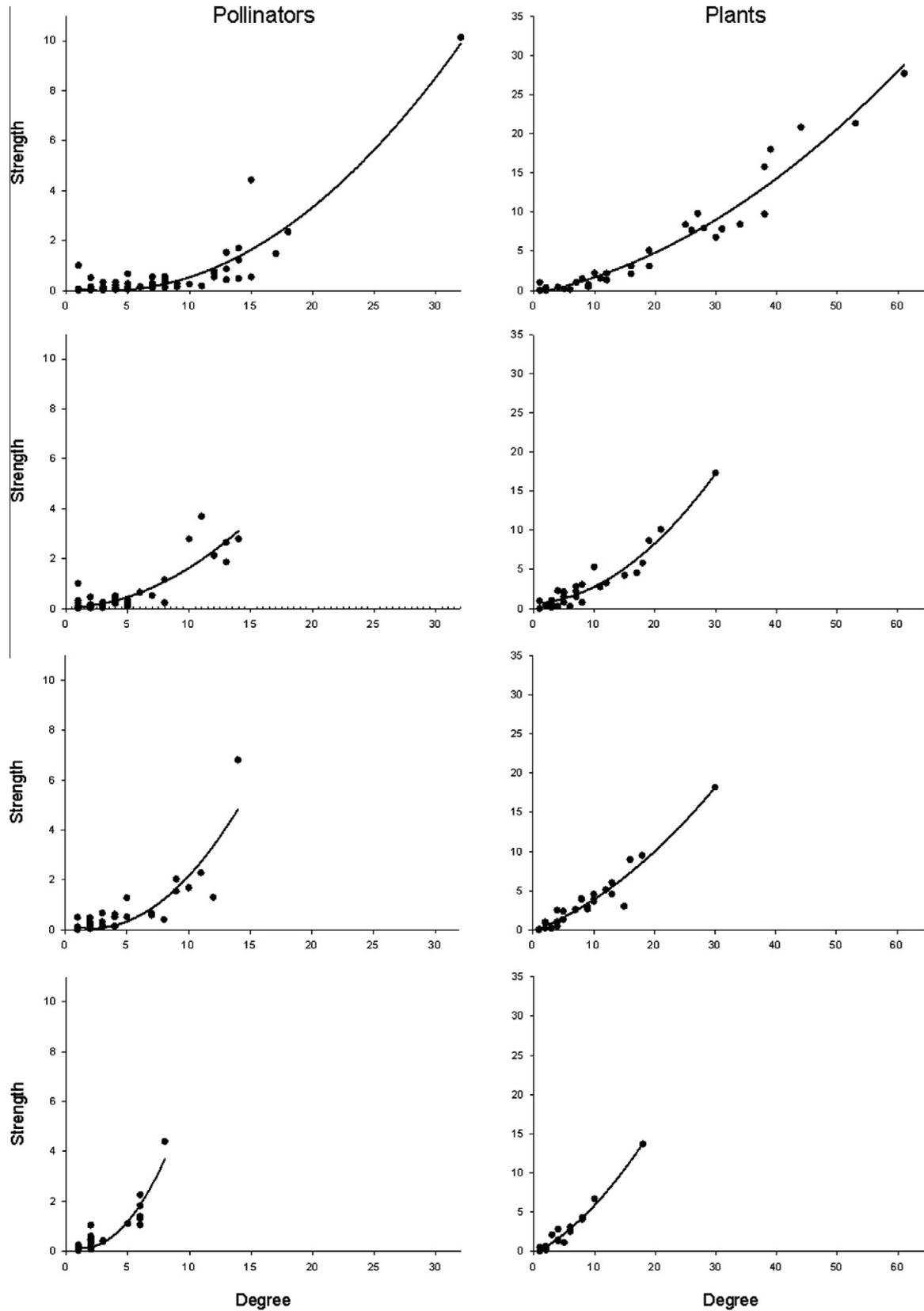
and some few have many links, and this pattern is found irrespectively of sampling intensity.



Appendix B. Degree–strength relationship

The relationship between a species degree (number of links) and strength (the summed importance of the focal species for all species it interacts with) has been showed to follow a quadratic,

nonlinear model. The nature of this relationship illustrates the high heterogeneity in species strength within mutualistic networks and the higher-than-expected strength of generalist species (Bascompte et al., 2006). We found that the best model describing the degree–strength relationship included a quadratic term in all our



networks, regardless of sampling effort ($P < 0.01$ for the quadratic term in all models; see also illustrations below), thus the asymmetric tendencies are present in all networks regardless of sampling effort. The graphs represent, from the top: “full” sampling (2003 + 2004), “peak-season 2003”, weekly 2003 and minimal 2003. Models for all monitoring regimes indicated.

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