Structural properties of mutualistic networks withstand habitat degradation while species functional roles might change

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Species diversity and interactions vary on a landscape scale and are sensitive to landscape alterations, such as landscape fragmentation and habitat degradation. At the same time, the species position within food webs or mutualistic networks (e.g. generalist or specialist, network hub or peripheral vertex) may affect their ability to persist after perturbations. This study was conducted in a heavily managed boreal forest landscape in southeastern Norway, using study plots situated in forest stands with contrasting disturbance history: old growth forest (least disturbed), young forest (intermediate) and clear cuts (most disturbed). By studying 12 pollination networks with contrasting disturbance history we found that important network descriptors were conserved after perturbation. Link-diversity was higher, both overall and per site, in the more disturbed communities while link-turnover was highest in the least disturbed community. We conclude that despite an increase in diversity in the more degraded habitat, the higher link-turnover in the least degraded, old growth forest, community indicates a homogenization of the plant–pollinator networks as a result of habitat degradation. Finally, we found that the degree (number of interacting partners) and network functional role for particular species changed along the disturbance gradient, though not in any systematic way. We conclude that structural properties of the pollination network are conserved after perturbations, but that particular species' network functional roles may change.

Human land use is a major driver of landscape degradation, and habitat fragmentation and modification is regarded a threat to biodiversity (Forman 1995, Kareiva and Wennergren 1995, Foley et al. 2005). Negative effects of landscape fragmentation are documented repeatedly for both population survival and persistence and for the composition and structure of ecological communities (Debinski and Holt 2000). Indeed, species composition and diversity vary on a landscape scale both due to natural processes (MacArthur 1965, Rosenzweig 1995) and to human induced landscape alterations (Foley et al. 2005). However, species do not function as isolated entities, but participate in a myriad of interactions with other species. Consequently, as the occurrence and abundance of species change, the occurrence and strength of species interactions will also change. In addition, the structure of species interaction networks might change as a response to landscape alterations, even without any change in species composition. Several studies have shown that species interactions respond to landscape variation (Steffan-Dewenter et al. 2002, van der Putten et al. 2004, Tscharntke et al. 2005, Fortuna and Bascompte 2006, Tylianakis et al. 2007). Multi-species interaction systems, such as food-webs or mutualistic interaction networks can be analysed using a network approach (Memmott

1999, Bascompte et al. 2003, Memmott et al. 2004, Tylianakis et al. 2010). The major advantage of network analysis is its ability to gain insights into properties of multi-species systems that is not possible to reveal when studying single species or single interactions (May 1983, Paine 1988, Cohen et al. 1990, Jordano et al. 2006). These studies discard all species-specific information leaving the possibility that the network structure can appear similar in networks comprised of totally different species. However, other studies have used network analyses to investigate the fate of particular species and links within the networks (Aizen et al. 2012, Dupont and Olesen 2009, Estes et al. 2011, Stouffer et al. 2012). Studies have shown that plant species degree of specialization, with respect to pollinators, is highly variable in space (Herrera 1988, 2005). This suggests that a plant species role within the pollination networks might change, e.g. from being a generalist placed in the core of the network (sensu Bascompte et al. 2003) in one location to being a relative specialist situated in the periphery of the network elsewhere. If such changes in species role within the network follow perturbations, an apparent stability in network properties along a disturbance gradient might hide significant changes in network composition at a species level (Vázquez et al.

2009, Mello et al. 2011, 2013), i.e. two networks might both be significantly nested while the species comprising the core of generalists might be totally different.

Tylianakis et al. (2010) list several structural attributes of ecological networks that may promote system stability and functional rates. First, all networks are connected by links and the connectance of a network can be calculated as the number of realized links per number of possible links. Quantitative link density is a quantitative counterpart of connectivity that also includes information on interaction strengths. Higher connectance indicates higher generalization levels and redundancy within the network and may increase the rate of ecosystem processes. Second, mutualistic networks typically display a nested structure, where a core of generalist species interact with each other and where specialists interact only with proper subsets of the species interacting with the more generalist species (Bascompte et al. 2003). This nested structure may give the networks more resilience to perturbations (Okuyama and Holland 2008) and maximise the number of coexisting species (Bastolla et al. 2009). This is mainly because, in nested networks, the species constituting the core of the network are highly connected among themselves, while highly specialized species are interacting with generalist species, thereby limiting the possibility for extinction cascades. Third, the interactions among plants and pollinators are highly asymmetric, meaning that if a plant is highly important to a pollinator (a high percentage of the pollinator's visits occur to this particular plant), this pollinator's importance for the plant is low (a low percentage of the visits received by the plant comes from this pollinator). This asymmetric nature of the interactions within a network may enhance long-term coexistence and facilitate biodiversity maintenance within ecosystems (Bascompte et al. 2006, Jordano et al. 2006, but see, Okuyama and Holland 2008). Fourth, plant–pollinator networks are very heterogenic, with the bulk of species having few interactions, while a few species have substantially more interactions than expected by chance. For scale-free abiotic networks such heterogenic patterns makes them sensitive to attack on the most connected nodes (Barabasi et al. 2000, Barabasi 2009). For mutualistic networks, on the other hand, the truncated power law nature of the cumulative degree distribution may confer higher robustness to the loss of keystone species that form the backbone of these webs (Jordano et al. 2003). Finally, mutualistic networks above a certain size are modular, i.e. they have weakly interlinked subsets of species which are internally strongly connected (Olesen et al. 2007). In modular networks, species might be regarded as more or less important depending on their functional role within the network. Species that are hubs, i.e. highly connected within their module, and connectors linking different modules are regarded as highly important for sustaining the network structure. If these key-stone species go extinct the network might break apart and extinction cascades might be initialized (Olesen et al. 2007).

Plant–pollinator networks are highly variable in space (Olesen and Jordano 2002, Potts et al. 2006, Vázquez and Aizen 2006, Trøjelsgaard and Olesen 2012) due to environmental variation in general (Dalsgaard et al. 2009) and to landscape degradation and fragmentation in particular

(Tscharntke et al. 2005, Fortuna and Bascompte 2006, Tylianakis et al. 2007, Hagen et al. 2012). In this study we investigate how the plant–pollinator system of a heavily managed boreal forest landscape responds to landscape degradation. Vast areas of the boreal forest are, and have been for centuries, subject to intensive forestry, which has resulted in a profound transformation and degradation of boreal forest ecosystems (Östlund et al. 1997). Biologically young spruce or pine stands composed of single-aged and even-sized trees established on former clear-cuts dominates the present-day forest. The result is a highly heterogeneous and partly artificial landscape matrix displaying a large variation in physical properties and resource availability. In particular, the removal of trees increase the light influx to the ground vegetation on the clear cuts, increasing the potential photosynthetic activity in the plants but also altering the water balance due to increased evaporation. By analysing plant–pollinator networks from three communities representing a real gradient of landscape degradation within a forest landscape we validate empirically whether the composition and structures of mutualistic networks are conserved after perturbations in a real ecosystem. We hypothesise that the plant–pollinator networks in all the studied areas, despite contrasting disturbance history, will display structural properties previously found in other mutualistic networks (Tylianakis et al. 2010). In particular we ask the following questions: 1) are network structural properties of plant–pollinator networks conserved along a gradient of disturbance? 2) Does the species' role within the plant–pollinator network change along the disturbance gradient?

Methods

Focal area and study plots

We established 12 study plots throughout a study area located ca 35 km north of Skien, in Telemark County, southeastern Norway (59°21′N, 9°45′E) between 444 and 528 m elevation. See Nielsen and Bascompte (2007) and Nielsen et al. (2007) for further details on the study area. The study plots were located within an area approximately 2.5×2.5 km, with a minimum distance to the nearest plot of 100 m, though most plots were separated by at least 800 m. The plots were, at least within the young and old growth forest, surrounded by forest habitat with limited availability of floral resources. Given that bumblebees can travel several kilometres in search for floral resources while many dipterans act as drifters and not central place foragers, the study plots cannot be considered spatially independent with respect to the pollinator community. However, a constrained correspondence analysis (CCA), with the pollinator species assemblages in each of the study plots as response variables and the X- and Y-coordinate of the plots as constraining variables revealed that physical placing did not explain the composition of the pollinator community ($p > 0.35$ for both spatial axis). We used three community types of contrasting forest maturity to represent three levels of habitat degradation. We placed our study plots within four forest stands from each of the three community types. The three different stages of maturity were: clear cuts with no trees

(most degraded), young forest with trees of age between 13–35 years (medium degraded) and old-growth forest, with trees older than 100 years (least degraded). In all stands but the clear cuts (with no trees per definition) Norway spruce *Picea abies* dominated the tree layer counting more than 90% of the trees. Scots pine *Pinus sylvestris*, Birch *Betula pubescens* and Aspen *Populus tremula* occurred in some of the study plots, but never in high densities. The insect pollinated goat willow *Salix caprea* is found in the area, but all insect observations were done after its flowering had ceased. All floral resources were located at the forest floor. Each study plot was a 20×20 m square, placed within the forest stand based on the presence of three plant species; *Cornus suecica*, *Melampyrum pratense* and *Vaccinium myrtillus*, in the forest floor vegetation. The abundance of the three species varied among the plots, but this criterion ensured at least some floral resource availability for pollinators and to some degree an ecological similarity among the plots.

Data sampling

We sampled flower visitors throughout the flowering season from 3 June to 24 August in 2004. The study plots were sampled by walking randomly around within the plot for 30 min, catching all insects observed within flowers inside the plot (variable transect walks sensu Westphal et al. 2008 and Nielsen et al. 2011). When an insect was caught and collected, the plant species it had visited was recorded. Due to the extensive number of interactions observed in the field we were not able to assess whether each flower visit resulted in pollination. The insects are therefore flower visitors, strictly speaking. We assume however, that most visits involve pollination to some degree and we therefore, for convenience, refer to all flower visitors as pollinators. We randomized the order the sampling plots were observed during each day of sampling, to ensure that all plots were observed at all times of day. Due to change in weather conditions during some of the days of sampling (afternoon rain) we were unable to sample all study plots all days. Each study plot was sampled from 29 to 34 times during the season (mean 31.33). Despite this slight variation in sampling effort we use the accumulative plant–pollinator interaction data for each plot, from the entire season, in our analysis. By use of individual based rarefaction we found that our networks were not adequately sampled, that is, if we had sampled longer and/or over a larger area we would have found more species and links (Supplementary material Appendix A1 Fig. A1). However, network metrics, e.g. nestedness and connectance, seem to stabilize within the sampling effort applied (Nielsen and Bascompte 2007). Flower abundance changed throughout the season in all study plots, making it difficult to provide a representative abundance index that described the availability of particular plant species in a particular site over the entire season. In addition, due to limitations in our sampling protocol we were unable to obtain good estimates of the abundance of important plant species. We acknowledge that variations in floral abundance can induce bias in our insect sampling, as the probability of finding additional pollinators will be higher in more abundant plant species.

We assume this bias to be similar in all study plots and have not made any corrections to our data prior to analysis.

Data structure

To quantify the plant–pollinator system within the study area we created both qualitative and quantitative data matrices based on observations of plant–pollinator interactions. We used the number of individuals of a particular pollinator species collected in flowers of a particular plant species as an estimate of the strength of their interaction in the quantitative matrices. We created matrices for each of the 12 study plots separately, for the three community types (by pooling the data obtained from the four study plots within each community type) and for the entire study system (by pooling all data from all 12 study plots).

Link diversity

We used the Shannon–Wiener index H (Eq. 1) to estimate link diversity. From H we calculated the diversity D as an expression of the 'effective number of links' in the community (following MacArthur 1965) (Eq. 2). D is the number of evenly distributed links that is needed to obtain a diversity index similar to the one estimated for the community under study. P_i for a particular interaction is the number of individuals of the pollinator species caught in that particular plant species divided by the total number of pollinator individuals caught in the entire focal network.

$$H = -\sum_{i=1}^{s} p_i \ln p_i \qquad (1)$$

$$D = \exp(H) \qquad (2)$$

$$D_\beta = D_\gamma/D_\alpha \qquad (3)$$

We calculated α-diversity as the average diversity of the four study plots within a forest type or three forest types within the study system. γ-diversity was calculated as the diversity of the matrix comprising the pooled network from all four study plots of a forest type or for the entire study system. To illustrate the variation in diversity (link turnover) among the three communities, and among the four replicate sampling plots within each community, we calculated β-diversity (D_β) (Eq. 3). See Jost (2006) for the mathematical proofs and a more detailed discussion of the calculations of α, γ and β-diversity.

We used jackknifing (Magurran 2004), to assess whether the γ-diversity of the community types were statistically significantly different. We calculated pseudo-values based on the Shannon–Wiener index for each community by generating four networks each containing observations from three out of the four study plots in the focal community type. The pseudo-values were then transformed to the effective number of species using Eq. 2 before we conducted pairwise t-tests between the three communities. p-values were Bonferroni corrected for multiple (3) comparisons.

To assess to what degree β-diversity reflected spatial species turnover and/or nestedness of assemblages we used the

partitioning procedures described in Baselga (2010). In particular this method disentangles the contribution of spatial turnover (species replacement) and nestedness (species loss) to the observed β-diversity pattern. The calculations were conducted by use of the R-script 'beta-multi.R' downloadable as supporting information of Baselga (2010).

To obtain standardized entities for direct comparisons of α-, β- and γ-diversity among the three community types we adopted the following, individual-based technique. First, we generated combinations of sampling plots where each clear cut plot was associated with a randomly selected plot from the young forest and old growth forest community type, giving a set of four combinations of plots from all three community types. We then identified which plot within each combination of three plots (one from each community type) that was containing the smallest plant-pollinator network (the network composed of the lowest number of sampled pollinator individuals). Finally we reduced the number of pollinators in the two largest networks so that their number of pollinators equalled the smallest one. The reduction was conducted by sampling pollinators form the original distribution with a probability equalling the proportion of pollinator individuals of that particular species occurring in a particular plant species, to the total number of pollinators collected in the original network. We generated 1000 replicate combinations of standardized plots, and calculated diversity measures on the resulting networks for each community type. p-values were Bonferroni corrected for multiple (3) comparisons.

Interaction diversity

We calculated the size of each network as the number of plants times the number of pollinators. To estimate interaction diversity we used connectance (fill) of each networks as the number of realized links divided by the size (Tylianakis et al. 2010). To also incorporate the quantitative component of each link (the interaction strengths) we calculated quantitative link density (LD_q) following Bersier et al. (2002) by weighing each species by their relative frequency.

Nestedness

To calculate nestedness we used the ANINHADO (ver. 3, Bangu) software by Guimarães and Guimarães (2006). We used the NODF metric (Almeida-Neto et al. 2008) as is less sensitive to the size and fill of the matrix than matrix temperature (Atmar and Patterson 1993). The significance of the NODF values was tested through null model analysis (null model Ce) against 1000 random networks. We used this more conservative null model as the nested pattern is not always to be expected and that it is not independent of network connectance (number of realized links in the network) (Fortuna et al. 2010, Ulrich and Gotelli 2013).

Species strength and interaction asymmetry

The strength of a pollinator species is defined as the sum of dependencies of the plants relying on the particular pollinator, and the strength of a plant is the sum of dependencies of the pollinators relying on the particular plant

species (Bascompte et al. 2006). We calculated the dependency of each pollinator to each plant by dividing the number of visits conducted by each pollinator species to the focal plant by the total number of visits recorded for the pollinator species. Conversely we calculated the dependency of each plant to each pollinator by dividing the number of visits by the pollinator species to the plant species by the total number of visits received by the plant species. The asymmetry value for a particular interaction was obtained by subtracting the lowest value from the largest, making the asymmetry value a positive number ranging from 0 (symmetric interaction) to 1 (highly asymmetric interaction).

Degree distribution

Degree for a pollinator species was calculated as the number of plant species it was recorded visiting and the degree for a plant species was calculated as the number of pollinator species recorded conducting visits to it. As the degree values for plants were much higher than for pollinators we present and analyse them separately. To illustrate the degree distribution in the three communities of contrasting disturbance we plotted the cumulative distribution against number of links (Jordano et al. 2003).

Generalization level

To assess whether plants and pollinator species were fulfilling similar roles along the specialist–generalist continuum in the different communities we conducted pair-wise correlation tests of the number of links (degree) of the species found in all three communities. High correlations would suggest that the species had similar roles in the two communities compared.

Modularity and species roles within the networks

We measured modularity with the index M in the software Netcarto (Guimerà and Amaral 2005). This network concept is based on a simulated annealing procedure that aims at finding the optimal modularity. M varies from 0 (no subgroups) to 1 (totally separated subgroups). The statistical significance of M was tested using a Monte Carlo procedure with 1000 randomizations. We calculated M, and its statistical significance, for each of the 12 networks separately and for each of the study communities by pooling all four replicate networks. To test whether M was affected by community type we used a linear model with community type as fixed factor and number of species in the network as covariate (Mello et al. 2013).

In addition we used Netcarto to calculate each species 'ecological functional role' within the networks, through an assessment of each species 'network functional role' (Guimerà and Amaral 2005). Based on each species within-module degree and participation coefficient they were assigned one of the following roles within each network: (R1) 'ultra-peripheral vertices' with all interactions within their module; (R2) 'peripheral vertices' with most interactions within their module; (R3) 'non-hub connector vertices' with many interactions to other modules; (R4)

'non-hub kinless vertices' with interactions evenly distributed among all modules; (R5) 'provincial hubs' with most interactions within their module; (R6) 'connector hubs' with many interactions to most of the other modules; and (R7) kinless hubs with interactions homogeneously distributed among all modules. Roles 5, 6 and 7 are very important because they define hubs, i.e. species that have a large number of interactions in the network. Plant species falling under one of these definitions represent generalist species providing floral resources to many pollinator species and conversely, pollinators defined as hubs pollinate numerous plant species. If these species are removed from the network they will affect a large number of mutualistic partners, as opposed to the more peripheral species interacting only with a limited number of species. In addition, the connectors (R3) are of particular importance as they bind together different parts of the networks. See Guimerà and Amaral 2005 for details on the simulated annealing algorithm and mathematical definitions of the different roles and Mello et al. (2013) for a practical implementation of the analyses. To test whether a particular species' functional role within the networks varied among the three community types we used a generalized linear mixed model approach using the nlme package in R ver. 3.0.1. Our goal was to assess whether the functional role of a species in one community could explain the same species functional role in another community. If this was the case we could argue that the species roles were to some degree conserved among the communities. In these analyses we used the three networks pooled over four study plots rather than the 12 separate networks as the number of species found in all 12 networks was small. While 41 species were found in all three pooled networks, only three species were found in all 12 separate networks, and only nine species in nine or more networks, reducing the strength of the analyses. We included the functional role in the focal community type as response variable, the functional role in the community of comparison as predictor variable, the abundance of the species as covariate and species as random factor. We also included the interaction between the functional role in the predictor community and the abundance in all models. Abundance was defined as the total number of visits conducted by a pollinator species and the total number of visits received by a plant species. Since the plant species in general were more dominant within the networks (having more important roles, i.e. higher role number) than the pollinators, we analysed the variation in network role separately for the two species groups. We also used linear regression to assess whether the functional role of a species within a community could be explained by the species abundance within that particular community. Plants and pollinators were also here analysed separately.

Results

The old growth forest community contained the lowest number of plant and pollinator species both on average per study plot and in total for each community type (Table 1). All three community types had a comparable fraction of unique species of both plants (18–25%) and pollinators

(31–34%). See supplementary material Appendix A1 Table A1, A2 and A3 for lists of important species within the system.

Link diversity

The young forest community had the highest link diversity (D_γ) for the entire community, also after corrections for unequal sample size (Table 2). The average link diversity contained within each of the study plots within each community (D_α) was also highest for the young forest community. The old growth forest had the lowest D_α and the clear cuts showed intermediate values. The old growth forest community type had a significantly higher link turnover (D_β), also after correcting for unequal sample size. The link turnover was lowest on the clear cuts, but the difference in relation to the young forest community was not statistically significant. Our β-diversity partitioning procedure (Baselga 2010) revealed that only a small fraction of our β-diversity values can be ascribed to a nested pattern of species distributions, indicating that our β-diversity values represents real estimates of species turnover (Table 2).

Interaction diversity

Connectance was highest in the networks of the old growth forest and lowest on the clear cuts (Table 1), though the difference was not statistical significant (Kruskal–Wallis test, p = 0.39). The average degree (number of interacting species) of the plant species was highest in the young forest (15.00) and lowest in the old growth forest (11.30) while the average degree of the pollinator species was highest in the clear cuts (2.00) and lowest in the old growth forest (1.61) (Supplementary material Appendix A1 Table A4). Pooled over all four study plots, quantitative link density (LD_q) was highest in the young forest community type (5.88), with the old growth forest community showing the lowest value (4.87), while the mean LD_q value was highest in the clear cut community (4.13) and lowest in the old growth forest (3.50) (Supplementary material Appendix A1 Table A5).

Nestedness

None of the networks in our 12 study plots were significantly nested when analysed separately. The three networks made from pooling all four study plots within each community and the network made from pooling the three communities were all nested, though the nestedness value of the network from the old growth forest only tended towards significance (Table 1). However, one half of the networks have previously been published as nested (Nielsen and Bascompte 2007), based on nestedness temperatures obtained from an earlier version of ANINHADO. This suggest that nestedness analysis are sensitive to the null model and algorithm used to assess its significance and that results from older analysis should be interpreted with caution. See Joppa et al. (2010) and Ulrich and Gotelli (2013) for a throughout discussion of nestedness metrics and null model analysis.

Table 1. Qualitative measures of the three plant–pollinator communities studied in southeastern Norway in 2004. Poll/Plant is the number of pollinator species per plant species. Size = plants × pollinator. Links are the number of realized links in the network matrix, and connectance (matrix fill) is the number of realized links / possible links. 'Clear cut', 'Young forest' and 'Old growth' represents the pooled plant–pollinator networks from four sample plots. 'Total' represents the pooled plant-pollinator network from the three communities. The p-value is related to the nestedness analysis and indicates whether the observed NODF value is higher than what would be expected by chance. NODF and null model Ce was used in the nestedness analyses. M is the modularity index calculated with the software Netcarto. An asterix (*) behind the M value indicates that the value is significantly higher than would be expected by chance.

Study site	Plants	Pollinators	Poll/Plant	Size	Links	Connectance	NODF	p-value	M
Clear cut 1	7	48	6.85	336	30	0.09	27.11	0.64	0.49
Clear cut 2	8	28	3.5	224	45	0.20	23.91	0.63	0.51
Clear cut 3	7	35	5	245	49	0.20	22.76	0.9	0.58*
Clear cut 4	9	33	3.66	297	59	0.20	25.19	0.77	0.49
Mean	7.75	36	4.75	275.5	45.75	0.17	24.74		
SD	0.96	8.52	1.55	50.68	12.04	0.06	1.61		
Unique species	3	27							
Young 1	8	39	4.88	312	63	0.20	23.02	0.5	0.51
Young 2	9	41	4.56	369	59	0.16	20.30	0.2	0.52
Young 3	8	41	5.13	328	61	0.19	23.39	0.31	0.53*
Young 4	5	35	7	175	47	0.27	28.96	0.96	0.57*
Mean	7.5	39	5.39	296	57.5	0.20	23.92		
SD	1.73	2.83	1.10	84.16	17.19	0.05	3.15		
Unique species	2	29							
Old 1	8	40	5	320	61	0.19	24.30	0.09	0.47
Old 2	3	18	6	54	20	0.37	31.72	1	0.60*
Old 3	6	32	5.33	192	43	0.22	27.20	0.89	0.54*
Old 4	3	15	5	45	12	0.27	34.38	0.95	0.53
Mean	5	26.25	5.33	152.75	34	0.26	29.40		
SD	2.45	11.79	0.47	130.22	22.29	0.08	3.91		
Unique species	2	22							
Community									
Clear cut	12	77	6.42	924	146	0.1580	22.25	<0.01	0.45
Young forest	11	86	7.82	946	165	0.1744	22.43	<0.01	0.45
Old growth	10	70	7	700	113	0.1614	20.90	0.16	0.50
Total	16	137	8.56	2192	313	0.1428	19.73	<0.001	0.41

Table 2. Link diversity measures on the three plant–pollinator communities sampled in southeastern Norway during the summer of 2004. D is the effective number of links. β indicates the effective number of distinct samples found within each community or among the three communities (Total). Note that for the three separate community types and the 'total' community D_β is not comparable. β_{SOR} is a measure of the total β-diversity, while β_{SIM} and β_{NES} are the partitions of the β-diversity stemming from species turnover and species loss (nestedness), respectively (Baselga 2010). The values corrected for unequal sample size are the average values obtained from 1000 permutations. p-values are corrected for multiple comparisons.

Community	$D\alpha$	$D\beta$	β_{SOR}	β_{SIM}	β_{NES}	$D\gamma$
Clear cut	24.8	1.71	0.982	0.908	0.074	42.5
Young	30.6	1.99	0.982	0.911	0.071	61.1
Old growth	12.4	3.12	0.984	0.916	0.067	39
Total	46.6	1.71	0.970	0.925	0.045	79.7
Corrected for unequal sample size						
Clear cut	20.8	1.83				38
Young	25.2	2.01				50.8
Old growth	15.7	2.43				38.3
Significance levels for pair-wise comparisons						
Clear – Young	0.018	0.12				0.006
Clear – Old	<0.003	<0.003				>0.5
Young – Old	<0.003	<0.003				<0.003

Species strength and asymmetry

A high proportion of the plant–pollinator interactions in our study were highly asymmetric, as shown by the clear peak in probability of high asymmetry values (>0.95) in Fig. 1. Supplementary material Appendix A1 Table A5 shows mean and median asymmetry values for the three community types and the study system as a whole.

There were significant positive relationships between species degree and species strength for plants and pollinators in the three community types and the entire study system (Fig. 2). A quadratic regression line is given where the quadratic term was significant, if not a linear model is given. In general the increase in strength is faster than the increase in degree, as shown by the high number of quadratic models explaining the relationships (7 out of 8).

Degree distribution

The cumulative degree distribution followed a truncated power law (Jordano et al. 2003) for plants and pollinators in all three community types and in the entire study community (Fig. 3). The deviation from linearity was clearest for
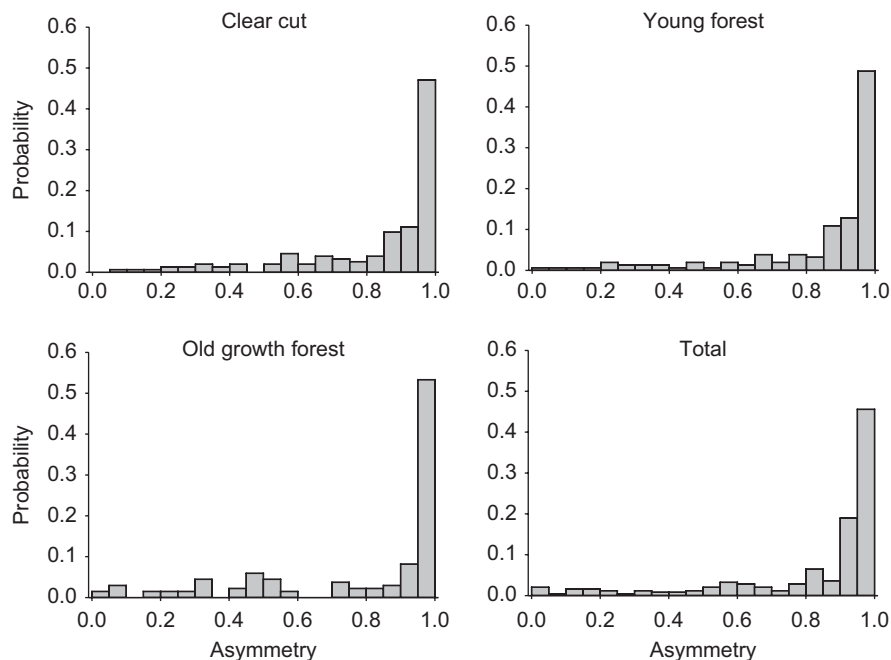
Figure 1. Probability distribution of asymmetry values of mutual dependencies among plants and pollinators collected in southeastern Norway in 2004. High values (close to 1) indicate strong asymmetry. Data is presented for the three community types and the total community separately.

plants due to the lower number of interaction partners found for the pollinators.

Generalization level

There was no pair-wise correlation ($p > 0.3$) in the degree (number of interacting partners) for particular plants species among the three community types, indicating a change in the particular species' number of links (i.e. degree) along the disturbance gradient. A negative correlation would have indicated a systematic change, but the lack of correlation suggests a more random pattern. For the pollinators all three pair-wise correlations were significant ($p < 0.05$) (Supplementary material Appendix A1 Table A6). When looking at the species participating in most interactions that are found in all three community types the same pattern emerge; the pollinators seem more stable, e.g. the hoverfly *Thricops cunctans* interacting with eight plant species in all three communities (Supplementary material Appendix A1 Table A1).

Modularity and species role within the network

In five of the 12 study plots we found the networks to be significantly modular (M not within 2 standard deviations from the average M based on 1000 Monte Carlo randomizations) (Table 1). Significantly modular networks were found in all three community types. Degree of modularity, M, did not differ among the community types when tested in a linear model with number of species in the network as a covariate ($F_{3,8} = 1.53$, $p = 0.28$). When generating networks by pooling data from all four study plots of each community type, none of the networks were significantly modular (Table 1).

No species in any of our networks were found to be 'kinless hubs' (R7) with interactions homogeneously distributed among all modules. When analysing the 12 study sites separately most species were identified as 'peripheral vertices' (R1 or R2), in clear cuts: 61%, in young forest: 83%, and in old growth forest: 87%. When analysing the networks pooled over all four sites of each community type the same pattern emerged in the clear cut community: 80%, in young forest: 77% and in old growth forest: 85% of the species were 'peripheral vertices'. In the 12 separate networks species acting as hubs (R5 or R6) were found among the plants and the pollinators, however, when analysing the pooled networks the species acting as hubs were all plant species. Here, the most important pollinator species were 'non-hub connector vertices' (R3 sensu Mello et al. 2013) (see Supplementary material Appendix A1 Table A2 for the 12 separate networks and Table A3 for the three pooled networks representing each community type). Among the plants, some species, e.g. *Calluna vulgaris, Melampyrum pratense, Rubus chamaemorus* and *Potentilla erecta*, appeared as network hubs in all community types, while others, e.g. *Solidago virgaurea* and *Vaccinium vitis-idaea* were network hubs in the young forest only. Also within each community type species being network hubs in some study plots played less important network roles in other plots. The one exception is *Potentilla erecta* in the young forest community being a 'connector hub' (R6) in all four study plots (Supplementary material Appendix A1 Table A3).Our linear mixed model analyses revealed that the most abundant species (viz. the plant species visited by most pollinator individuals and the pollinator species conducting most visits) had more important roles within the network, as the abundance of a species
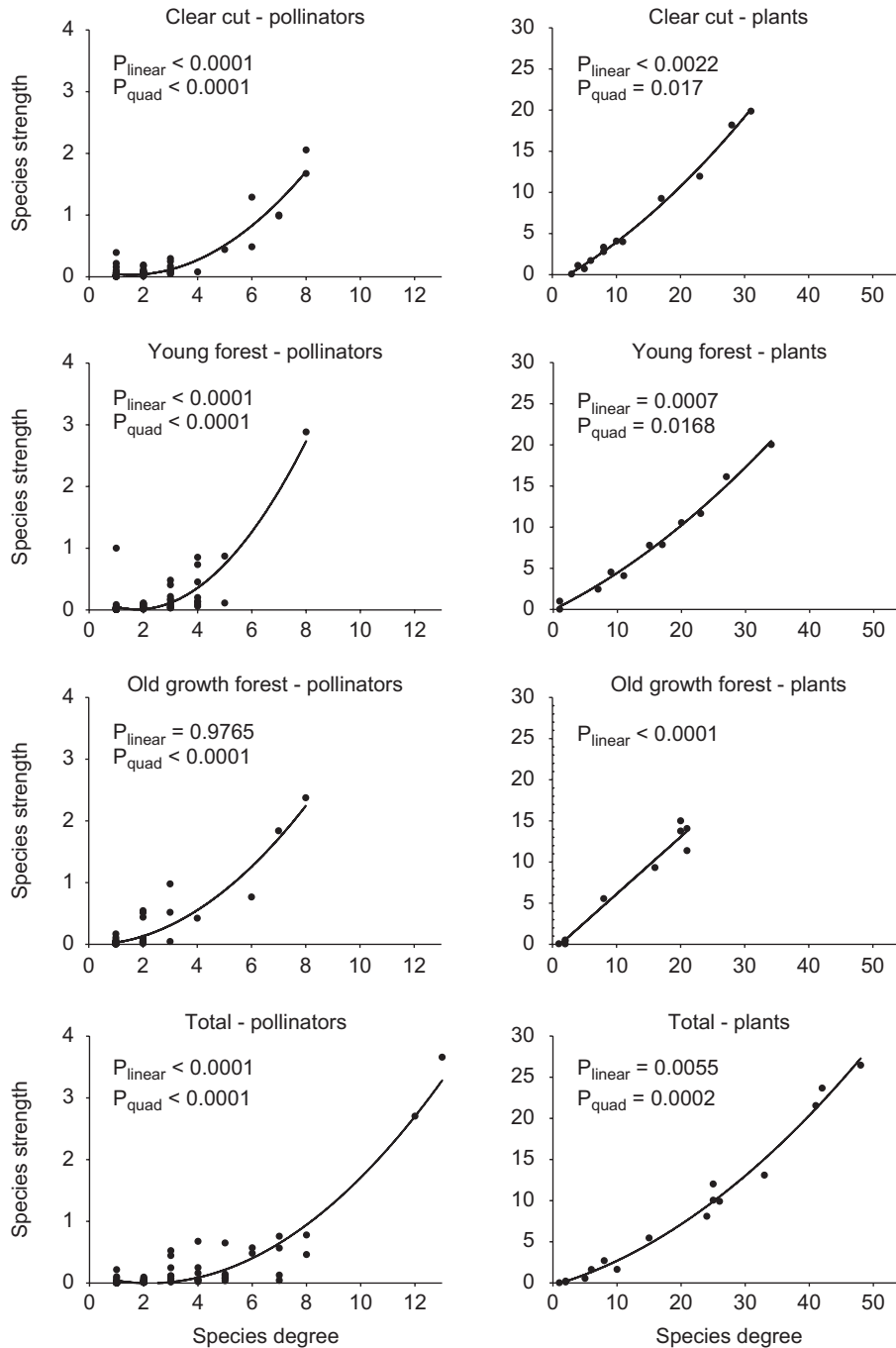
Figure 2. The relationship between species degree (number of interacting species) and species strength (the sum of dependencies of all species interacting with the focal species) for the plant–pollinator system studied in southeastern Norway in 2004. Data is given for each of the three communities and for the total community and plants and pollinators are presented separately. A quadratic model best fitted the relationships for all relationships except for the plants in the old growth forest community where a linear model provided the best fit ($p = 0.74$ for the quadratic term). P_{linear} and P_{quad} are the p-values for the linear and quadratic term of the regression model respectively.

within a community significantly explained its functional role within that particular community ($p < 0.05$ for all models except for pollinators in the young forest community where $p = 0.08$. On the other hand there was no consistency in network functional roles for particular species among the three community types, as the functional role in one community could not be explained by the functional role in another (Supplementary material Appendix A1 Table A7).

Discussion

Species composition and link diversity

The least disturbed old growth forest community contained a slightly smaller plant–pollinator network than the more disturbed young forest and clear cuts. Link diversity was also higher in the young forest and on the clear cuts, compared to the old growth forest. This pattern is a result of
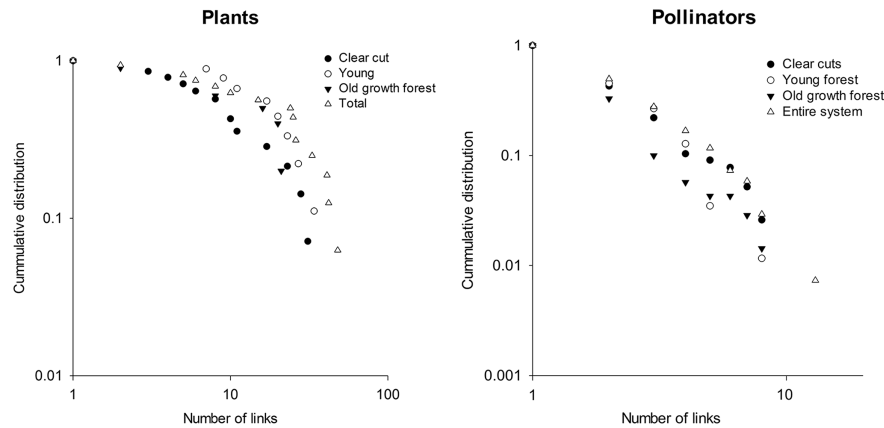
Figure 3. Cumulative degree distribution (i.e. the probability of interacting with one or more species, two or more species and so on) for the plants and pollinators in the three different communities and pooled over the entire study system studied in southeastern Norway in 2004.

higher number of species comprising these more disturbed networks and that these species are more generalized (Table 1, Supplementary material Appendix A1 Table A4). However, the number of unique species and species shared with the other communities were relatively similar for all three communities. β-diversity (link turnover) on the other hand, was highest in the old growth forest, indicating a higher variability in network composition among the sampling plots within the old growth forest community. Our β-diversity partitioning procedure clearly showed that this variation in link composition was due to link turnover rather than a nested distribution of link assemblages. Therefore, despite the visual impression of the plant–pollinator networks are flourishing on the clear cuts and in the young forest community (Nielsen unpubl.), the degradation of the forest landscape induces a homogenization of the plant–pollinator system, compared to the old growth forest community. However, the high fraction of unique species found in all three community types show that forest stands with contrasting disturbance history contain unique plant–pollinator systems with distinct species composition.

Network metrics

Despite large variation in disturbance history among the three communities, structural properties of their plant–pollinator networks were remarkably similar. This is in line with our assumption that structural properties of these networks make them robust to perturbations.

The networks of all three communities displayed relatively similar connectance values, indicating no significant reduction in average generalization of the species, with increasing level of disturbance. In addition, several network metrics suggest that the links within the networks were not randomly distributed and that these non-random patterns were similar in all three communities. Most species had few links, while a few species had significantly more links than would be expected by chance and most of the interactions were highly asymmetric. Some of the separate networks were modular but none of the networks pooled over four study sites, contradicting the suggestions put forward by Olesen et al. (2007); that modularity is more likely to be found in larger networks. On the other

hand, only the networks pooled over all four replicates within each community were significantly nested. This in line with Ulrich and Gotelli (2013) that found networks aggregated over a biogeographic scale more frequently nested than networks assembled at a local scale. The presence of these network structures, also in the heavily disturbed community, suggests that any loss of species, as a result of disturbance, has not lead to a cascade of secondary extinctions resulting in network collapse. A few studies have shown that these measures, previously argued to confer network robustness, are conserved in real networks exposed to perturbations (Tylianakis et al. 2007, 2010, Devoto et al. 2012). This suggest that the theoretical models on network resilience to habitat loss presented by Fortuna and Bascompte (2006) and the implications forwarded by Bascompte et al. (2003, 2006) and Jordano et al. (2006) about network structures and community persistence may reflect the nature of real mutualistic interaction systems. We believe this strengthens the argumentation for network structures as important determinant for community stability and ecosystem resilience to perturbations.

Species roles within the network

We have shown that despite similar network properties among the plant–pollinator systems of the three levels of habitat degradation, there was no correlation in linkage level for the plant species within the networks. This suggests that a plant species being generalist (visited by many pollinator species) in one habitat type might appear as a specialist (visited by one or a few pollinator species) in another. This is in accordance with the findings of Herrera (1988, 2005), who showed a large spatial variation in the generalisation level of *Lavandula latifolia*. Several studies have also documented that there is a large variation in generalization level of plants and pollinators also in time (Olesen et al. 2008, Petanidou et al. 2008, Lázaro et al. 2010). The temporal inconsistency of these systems suggests that one should be cautious when selecting the focal scale for studies of mutualistic networks, not only in space, but also in time. From the modularity analyses we assigned each species a particular role within the network. The plants played, in general, more important roles than the pollinators within the networks. Despite this, there was no

consistency in the species roles over the gradient of habitat disturbance; those acting as hubs did not necessarily so in all the networks. This means that the backbone of the networks change in space, though in no systematic way along the disturbance gradient. We believe this to be partly due to the spatial distribution pattern of the plant species. Highly abundant plant species may attract more visitors on a local scale, while the same species may appear less attractive to pollinators in another area where other plant species are more attractive due to their local dominance. Indeed, our analyses showed that the plants receiving more visits (and pollinators conducting more visits) played a more important role within the networks. In addition, our sampling protocol implies that more time is spent observing pollinators in the more abundant plant species potentially inducing a sampling bias towards the more abundant plant species. Unfortunately we have no good independent estimates of floral (or pollinator) abundance in the different study plots, so further studies are needed to corroborate these speculations.

Conclusion and implications

Historically, the boreal forest has been exposed to a complex disturbance regime composed of several factors enforcing impact with contrasting severity, frequency and spatial and temporal extent. Forest fires, wind throws and insect out-breaks are all key-determinants of the structure and function of boreal forest ecosystems (Bonan and Shugart 1989). In this sense, the introduction of even-aged forestry might to some degree resemble the historical disturbance regime experienced by the boreal forest biota. Our results do indeed suggest that the plant–pollinator system of the boreal forest ecosystem under study appear robust to the extreme habitat disturbance induced by even-aged forestry. The historical adaptation to severe disturbance events might make the plants and pollinators of the boreal forest especially resilient to perturbation. This might limit our result to this particular biome, or at least to biomes regularly experiencing large scale disturbance events. Future studies should focus on more stable communities and aim to quantify how ecological network structures might withstand disturbance processes, such as habitat degradation and fragmentation where large-scale disturbance is not a natural feature of the ecosystem. Our results also have implications for the conservation of plant-pollinator systems within the boreal forest. We have documented that the forest in three different stages of habitat degradation had unique species of both plants and pollinators. Consequently they also have unique interactions within their plant–pollinator networks. In addition, our diversity analysis indicates that a larger area is needed to conserve an equal proportion of the plant–pollinator network in the old growth forest compared to the two more degraded forest communities, as seen by the higher turnover in links within the old growth forest. The spatial variation in species roles within the networks further complicates the conservation of these systems. Even if the species interaction network is conserved sensu Tylianakis et al. (2010), important species might go extinct or change their functional role within the network in the more disturbed habitats. The high variation in the roles of particular species, also within each forest community type, highlights the importance of spatial heterogeneity in network composition, also in undisturbed habitats. We therefore suggest a mosaic approach to management, where a matrix of forest stands in contrasting stages of maturity is conserved. We also emphasize the importance of conserving a higher number of old growth forest stands if one aim at preserving a comparable proportion of the plant pollinator system.

By analysing the plant–pollinator system along a disturbance gradient we have shown that 1) network structural properties seem to be conserved after disturbance and that 2) species seem hold different roles within different networks but that this is not necessarily depending on the level of disturbance.

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