

Effects of habitat loss on the plant–flower visitor network structure of a dune community

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Pollination is a valuable ecosystem service, and plant–pollinator interactions in particular are known to play a crucial role in conservation and ecosystem functioning. These mutualisms, like other ecological interactions, are currently threatened by different drivers of global change, mainly habitat loss, fragmentation, or modification of its quality. Most studies so far have focused on the impact of such disturbances on particular species interactions and we thus need more empirical evidence on the responses at a community-level. Here we evaluated how habitat loss influenced the pattern of interactions between plants and their flower visitors in a coastal dune marshland community. Using data from four years (2008–2011), we assessed the effect of a large disturbance in the area (occurring in 2010) that represented the loss of more than 50% of the vegetation cover. We found a considerable decrease in species richness and abundance of flower visitors, which resulted in a lower number of interactions after the disturbance. Not all functional groups, however, responded similarly. Contrary to the expected from previous findings, bees and wasps were less negatively influenced than beetles, flies and ants, possibly due to their higher movement capacity. Species interactions in the community were more specialized after habitat loss, resulting in a lower level of network nestedness and a higher modularity. At a species level, the number of flower visitors per plant decreased after the disturbance, and plants were visited by less abundant flower visitors. Our findings lead us to predict that the overall plant–flower visitor network became less robust and resilient to future perturbations. However, the fact that each functional group responds distinctly to disturbances makes it more difficult to foresee the final consequences on community composition and ecosystem functioning.

The interactions between plants and their pollinators play a crucial role in biodiversity, conservation and ecosystem functioning. Habitat loss, fragmentation and changes in habitat quality, and in landscape structure in general, represent major threats to such interactions and thus to both plant and pollinator species persistence in the communities. Studies examining such threats at a community level, however, are still few and we thus have rather little empirical evidence on the final consequences of such habitat and landscape changes for the functioning of this important ecosystem service (Klein et al. 2007, Hagen et al. 2012, Ferreira et al. 2013, Nielsen and Totland 2014). Previous work has shown that a reduction in habitat quality and landscape heterogeneity cause species losses and leads to changes in the pattern of interactions among species, i.e. in the interaction network structure (Tylianakis et al. 2007, González et al. 2011). By reducing pollinator availability and diversity due to decreased floral resource supplies as well as nesting sites, habitat modifications can influence the levels of cross-pollination and, ultimately, fruit and seed production (Aguilar et al. 2006, Winfree et al. 2011, Hagen et al. 2012, Viana et al. 2012, Ferreira et al. 2013, Vanbergen et al. 2014). Likewise, variation in conspecific plant densities may affect plant reproductive success by changing the pollinator-mediated

connectivity between individuals in a plant population at different spatial scales (Hegland et al. 2014, Vanbergen et al. 2014). This indicates that, by altering interspecific interactions at a plant community-level, habitat disturbance can cascade down affecting the patterns of gene flow across levels of biological organization and potentially driving evolutionary changes (Eckert et al. 2010, Ferreira et al. 2013).

Rare and specialized interactions have shown to be the first to disappear after habitat reduction, and thus an increase in the frequency of generalist plants and/or pollinator species is usually observed (Ashworth et al. 2004, Aizen et al. 2012, Vanbergen et al. 2014). A decrease in network nestedness in disturbed habitats has been reported in several systems (Vanbergen et al. 2014, Moreira et al. 2015, Revilla et al. 2015), which has led authors to predict reductions in the number of coexisting species (Bastolla et al. 2009), and in the robustness and resilience of plant–pollinator networks to further perturbations (Bascompte 2009, Fortuna et al. 2013). The loss of species and their interactions in a disturbed network can also lead to the formation of isolated compartments within the network (Spiesman and Inouye 2013) which run a higher risk of disappearing after future disturbances than if species are connected in a cohesive network. Different models have shown that the distribution

of number of interactions becomes more skewed when moving from pristine to disturbed systems, and that mutualistic networks might collapse at critical habitat destruction thresholds (Keitt 2009, Kaiser-Bunbury et al. 2010, Viana et al. 2012, Fortuna et al. 2013).

Habitat degradation may also cause homogenization of the plant–pollinator networks by promoting higher link-diversity but lower link-turnover in disturbed sites compared to undisturbed ones (Nielsen and Totland 2014). Moreover, the particular species' network functional role can change notably along a disturbance gradient. Thus, a plant species can act as a hub (being at the network core) in one site but as a specialist (being at the network periphery) in another site (Campos-Navarrete et al. 2013, Nielsen and Totland 2014). Module and network hubs (i.e. species highly connected within their modules and with other species in other modules, respectively), together with connectors (species that link different modules), are considered keystone species for sustaining network structure and thus their removal due to a disturbance would have the strongest effects and might even collapse the network (Olesen et al. 2007, Kaiser-Bunbury et al. 2010, Fortuna et al. 2013).

Changes in pollinators' diversity are frequently reported mostly due to increased isolation of habitat patches and reduced landscape complexity caused by environmental simplification (Ferreira et al. 2013). However, not all pollinator species respond similarly to habitat changes. Social bees, for instance, are known to be sensitive to changes in the distribution of nesting and foraging habitats in the landscape (Williams et al. 2010, Carvell et al. 2012, Kennedy et al. 2013, Garibaldi et al. 2014); thus, land cover changes can directly affect individual survival probability, locally reducing species abundance (Ferreira et al. 2015). Solitary bees, however, may be more affected by habitat destruction as they are more specialized in food resources or nesting sites than social bees (Williams et al. 2010, Ferreira et al. 2015). By contrast, non-social insects with free-living progeny (e.g. dipterans, coleopterans) may be less affected by distance between resource patches, as they do not need to return to their brood cells repeatedly after foraging (Jauker et al. 2009, Parsche et al. 2011). Moreover, flower visitor abundance and species richness have been shown to increase with floral abundance (Hegland and Boeke 2006, Hagen and Kraemer 2010) and plant diversity (Potts et al. 2003, Ghazoul 2006, Blüthgen et al. 2007, Ebeling et al. 2008). In general, there is still scarce information on how different pollinator functional groups can respond to habitat disturbance (Burkle et al. 2013, Aguirre-Gutiérrez et al. 2015, Lázaro et al. 2016) and how they change their interaction patterns with plants in the community (e.g. their rewiring capacity within the network).

In this study, we aimed at evaluating the impact of habitat disturbance (habitat loss, in particular) on the patterns of plant–flower visitor interactions in a coastal dune marshland community at the north of Mallorca (Balearic Islands, western Mediterranean Sea). The plant–flower visitor network of this community was monitored for four consecutive years, from 2008 to 2011. After the flowering season of 2010, the study area was greatly disturbed due to the construction of a golf course that caused the loss of ca 50% of the vegetation cover, leaving the bare soil (Fig. 1). This provided an opportunity

to assess the extent to which substantial habitat loss altered the interactions between plants and their flower visitors. Our specific questions were the following: 1) did network structural properties change after habitat disturbance more than the expected from temporal changes in the previous years? 2) To what extent were floral resources and species richness and abundance of flower visitors affected by the disturbance? 3) At the species level, how consistent across years were degree (linkage level), contribution to nestedness, level of selectiveness, strength, and weighted closeness centrality, and did these parameters change notably after the disturbance? 4) Which flower visitors' functional groups and which plant species (regarding traits such as flower abundance and floral symmetry) experienced the greatest changes in species level parameters after the disturbance? 5) If networks had a modular structure, how consistent in time were species' roles regarding modularity, and did they change more after the disturbance relative to previous years?

Methods

Study site

The study was carried out in Son Bosc (39°46'28.11"N, 3°07'45.34"E), a diverse dune marshland in northern Mallorca, adjacent to S'Albufera Natural Park. The predominant vegetation consists of *Daucus carota* (Apiaceae), *Helichrysum stoechas* (Asteraceae), *Lotus corniculatus*

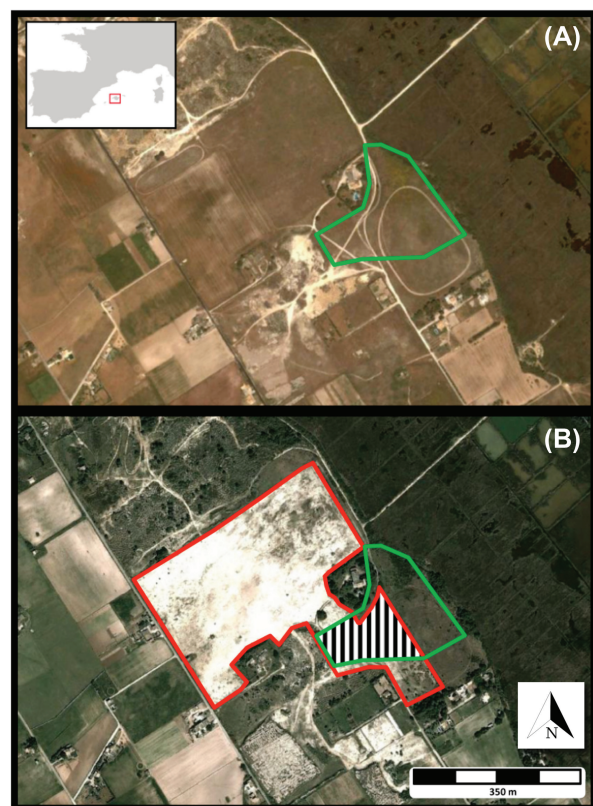


Figure 1. Aerial photograph showing the study area before (A) and after (B) the disturbance (soil removal for a golf course construction). The green line marks the study area, the red line the disturbed area and the vertical black and white pattern the study area damaged.

(Fabaceae), *Lotus cytisoides* (Fabaceae), *Scabiosa atropurpurea* (Dipsacaceae) and *Teucrium dunense* (Lamiaceae) and over 80 flowering species have been recorded in the area, mostly annual plants although also some shrubs like *Cistus salviifolius* (Cistaceae) and *Myoporum tenuifolium* (Myoporaceae). Such a high diversity of flowers allows maintaining an also high diversity of flower-visitors (ca 125 spp.), a good fraction of which nest in the sandy soils of this area. Specifically, this area bears the highest bee species richness of Mallorca Island (D. Baldock pers. comm.).

We performed censuses in Son Bosc during four consecutive years, from 2008 to 2011. During the summer of 2010, an area of ca 2.3 ha was disturbed due to the construction of a golf course, representing 52.3% of the total area covered in our study (ca 4.5 ha; delimited in green in Fig. 1). Given that the largest disturbance occurred when most plants had already flowered in 2010, we expected the highest impact on the plant–flower visitor network the following year. Thus, during 2011, we kept censusing all flowering plants in the remaining unaltered area including as well other plant species that were still present in the surroundings of the disturbed area (bare soil).

Sampling methods

All plants in bloom were monitored throughout the flowering season, from early April to the end of July. Once or twice per week, we made insect censuses on flowers from haphazardly selected individuals from all flowering plant species. Censuses were done from 10:00 a.m. to 17:00 p.m. on sunny and non-windy days. Insect visits to flowers were recorded from a distance of approximately 1 m to minimize interference with insect behavior. We recorded contacts of insect visitors to flowers during 3–5 min periods. Due to the small flower size of most species, insects nearly always touched the reproductive parts of the flower, although we did not record this or their behaviour. Hence, we use the term flower-visitation networks, regardless of the efficiency of each insect visitor in the pollination process. We must note, however, that considering such efficiency and distinguishing between true pollinators from those that act as cheaters might lead to a different network structure, e.g. the network might be more specialized (Alarcón 2010, Genini et al. 2010). During each census we recorded: 1) identity of flowering plant species; 2) number of open flowers of each individual plant observed; 3) identity of each flower visitor; 4) number of individuals of each species visiting flowers; and 5) number of flowers visited by each flower visitor. When flower visitors could not be identified in the field, these were collected (usually after finishing the census) for identification by taxonomists. We categorized flower visitor species into the following functional groups (as done in previous studies; Fenster et al. 2004): ants, bees, beetles, hoverflies, flies (mainly muscoid flies), butterflies, wasps and others (mostly hemiptera).

Time spent censusing flower visitors along the entire season was on average 36.3 h. Most intensive sampling was from 2009 to 2011, when we also estimated flower abundance fortnightly at each site. In each flower census, we recorded the number of all open flowers of each flowering plant encountered within permanent belt transects; we

surveyed 13 transects (50 × 2 m) in 2009 and 10 transects in 2010 and 2011, covering a total area of 1300 m² and 1000 m², respectively. Further details on sampling can be found in Castro-Urgal et al. (2012).

Network parameters

We built four quantitative interactions matrices (one for each year) using the number of visits per unit time as link weight. For each network, we calculated the most widely used quantitative descriptors of the structure of weighted ecological interaction networks (Tylianakis et al. 2010). At network level, these were: connectance (C), weighted nestedness (WNODF), complementary specialization H_2' , interaction evenness (IE) and quantitative modularity (Q). At species level, we obtained the following metrics both for each plant and flower visitor species in the networks: degree, strength, species selectiveness (d') (termed index of specialization in other studies; Blüthgen et al. 2006), weighted closeness centrality (wCC), contribution to nestedness ni (see Supplementary material Appendix 1 for definitions of each parameter), standardized connection ' c ' and participation values ' z '. We used the *bipartite* package ver. 1.18 (Dormann et al. 2009) run in *R* to obtain all these network metrics, except WNODF and contribution to nestedness which were obtained with the software NODF ver. 2.0 (<www.keib.umk.pl/nodf/>) (nestedness based on overlap and decreasing fill; Almeida-Neto and Ulrich 2011). The significance of WNODF values was assessed against 100 randomizations using the 'rc' and 'p' null models; the 'rc' model resamples with row/column weights fixed, while the 'p' model randomizes proportional to the respective marginal distribution (Almeida-Neto and Ulrich 2011).

Quantitative modularity (Q) was estimated using the QuanBIMo algorithm (Dormann and Strauss 2014), which is implemented in *R*. It consists of a recurrent Markov chain Monte Carlo (MCMC) algorithm to find the best division of nodes (species) into modules. A total of 10⁶ MCMC steps were used with a tolerance level of 10^{−10}. As Q values can vary among different runs, we repeated the calculations 100 times for each network – using the computeModules function – and selected the iteration with maximum likelihood as the best estimation of Q. To account for Q's dependence on network size and test the significance of modularity values, we calculated a z-score for each network by running the same algorithm in 100 random networks with identical marginal totals as the empirical network (using the null model 'r2d'; Guimerà and Amaral 2005) and comparing the modularity values between random and empirical networks. Such tests were done in the *bipartite* package (Dormann and Strauss 2014).

Following Guimerà and Amaral (2005), we identified species with important roles in the network by computing standardized connection and participation values (c and z , respectively). While c refers to the even distribution of links across modules, z refers to within-module degrees.

Statistical analysis

All analyses were conducted in *R* ver. 3.1.2 (<www.r-project.org>). To compare species richness of flower visitors among

years, we performed a generalized linear model (GLM) using a Poisson distribution and log as link function. In this analysis, year was included as a fixed categorical factor whereas the number of species in each flower visitor functional group as sampling units. The interannual variations in species level network parameters and abundances were analysed by means of generalized linear mixed models (GLMM, package *lme4*) that included species as a random factor to avoid pseudoreplication. We used separate models for plants and flower visitors, and for each network parameter. The models for plants only included year as fixed categorical predictor variable, whereas those for flower visitors also included functional group and its interaction with year. If the interaction was non-significant, we run the models with the fixed variables separately and chose the best model based on AIC. All functional groups were included in the models, except for the 'others' group owing to its low species number. Due to the nature of the data, we used: 1) Poisson distribution and log link functions for the degree analyses, after checking for the absence of overdispersed data (Zuur et al. 2009); 2) Gaussian distribution and log link function for the models of selectiveness; and 3) gamma distribution and log link function for the rest of the variables. The consistency among years in species roles within the network was also analysed by means of GLMMs, including c and z as response variables, year as fixed factor, and species as random factor. Plant species were the sampling units, and data were adjusted to a gamma distribution in each model.

As we found significant differences in both plant degree and selectiveness between 2011 and the average of the three previous years, we further assessed whether such differences were associated to changes in the prevalence of plant species with different flower symmetry and different flower abundances. For this, we performed two separate GLMs to analyse the after-disturbance change in degree and selectiveness (calculated as the difference between the degree/selectiveness in 2011 and the average degree/selectiveness in the previous years) as response variables, and flower symmetry (zygomorphic versus actinomorphic) and flower abundance (average from 2009–2011) as independent predictor variables. In both models, sampling units were the study plant species, and a Gaussian distribution was used given that the response variables fulfilled the assumptions of normality.

Post hoc analyses to test for differences among levels of a significant factor were conducted using Tukey a posteriori tests (package *multcomp* in R).

Data deposition

Data available from the Fileshare Repository: <<https://csicannatraveset.sharefile.com/d-sf34b761ef9a4607a>>. (Traveset et al. 2017).

Results

Overall community structure

The number of flower visitor species, number of links and weighted nestedness were much lower the year following

Table 1. Network parameters for each study year. WNODF: weighted nestedness, H_2' : index of specialization (selectiveness), IE: interaction evenness. For modularity, the z-score is given, as the Q observed is compared to that expected with a null model based on marginal totals (representing abundance distributions of plants and flower visitors; see Dormann and Strauss 2014 for further details).

	2008	2009	2010	2011
No. plants	56	68	67	52
No. flower visitors	120	110	123	86
No. links	347	390	494	248
Connectance	0.052	0.052	0.060	0.055
WNODF	7.698	8.67	9.412	5.456
H_2'	0.589	0.618	0.547	0.685
IE	0.532	0.529	0.514	0.497
Modularity (Q)	0.307	0.370	0.368	0.568
Number of modules	8	8	6	13
Modularity z-score	316.60	760.34	722.79	303.58

habitat disturbance (2011) than the three previous years (Table 1). The number of plant species was also reduced after the disturbance but to a lower extent than the number of flower visitors (Table 1). All networks showed a highly consistent connectance around 5%. The networks were significantly nested ($p < 0.001$), meaning that the partners of the most specialized species are a subset of those that interact with the most generalist species (Table 1). The lower nestedness in 2011 might thus result from the loss of some generalist species after the disturbance and/or from an increase in specialized interactions; the latter is actually supported by the higher H_2' value in 2011 (Table 1). Interaction evenness was moderate (ca 0.50) across the four years of the study (Table 1). Finally, the networks were significantly modular each year; however, while both modularity (Q) and the number of modules were higher in 2011 than the other years, this was not the case for z-scores (Table 1).

Overall, species richness of flower visitors was lower in 2011 (mean \pm SE: 10.75 ± 3.65) compared to the previous years (14.71 ± 2.23) ($\chi^2 = 8.25$, $df = 3$, $p = 0.046$). However, this difference was mostly due to a decrease in beetle and fly species richness (Table 2). The other groups barely changed across the four years of the study. Regarding flower visitor abundance, the best model showed that it varied significantly among all the study years, consistently among functional groups (year: $\chi^2 = 72.45$, $df = 3$, $p < 0.0001$). It was lowest in 2011 (visits min^{-1} : 0.09 ± 0.02), highest in 2010 and 2009 (1.10 ± 0.11 and 1.12 ± 0.004 , respectively), and intermediate in 2008 (0.18 ± 0.02).

Table 2. Species richness in each flower visitor group across the four study years. The groups in which species richness was considerably reduced after habitat disturbance are marked with an asterisk.

Flower visitor group	2008	2009	2010	2011
Ants	6	3	4	2
Bees	29	35	38	31
Beetles	25	24	29	18*
Butterflies	7	5	3	3
Flies	25	18	23	11*
Hoverflies	5	6	6	5
Wasps	13	13	14	15
Others	11	6	6	1

Table 3. Results of the generalized linear models comparing species level network parameters among the study years for plants and flower visitors. When the interaction between year and functional group was significant, the LRT for the interaction is given, but both factors were also included in the models.

Species-level network index	Plants Year	Flower visitors Year \times Flower visitor group
Degree	$\chi^2_3 = 55.14$, $p < 0.0001$	$\chi^2_{18} = 36.34$, $p = 0.006$
Strength	$\chi^2_3 = 5.14$, $p = 0.162$	$\chi^2_{18} = 36.40$, $p = 0.006$
Selectiveness (d')	$\chi^2_3 = 27.59$, $p < 0.0001$	$\chi^2_{18} = 64.09$, $p < 0.0001$
Weighted closeness centrality	$\chi^2_3 = 139.78$, $p < 0.0001$	$\chi^2_{18} = 51.78$, $p < 0.0001$
Contribution to nestedness	$\chi^2_3 = 15.4$, $p = 0.001$	$\chi^2_{18} = 51.79$, $p < 0.0001$
Standardized connection (c)	$\chi^2_3 = 10.55$, $p = 0.014$	$\chi^2_{18} = 34.99$, $p = 0.009$
Participation values (z)	$\chi^2_3 = 4.07$, $p = 0.25$	$\chi^2_{18} = 20.37$, $p = 0.31$

Species-level network properties

Plant species

At the species level, network parameters differed significantly among years, except plants' strength (Table 3). In 2011, plants' degree was significantly lower (Fig. 2A) and selectiveness was significantly higher (Fig. 2B) than the previous years; that is, the number of flower visitors per plant decreased after the disturbance, and plants were visited by less abundant flower visitors. Significant differences among years were also

observed in weighted closeness centrality and contribution to nestedness, but these did not seem to be related to the disturbance, as both parameters were significantly different between 2008 and the other years (Fig. 2C–D), whereas the values in 2011 did not differ significantly from those in other years (Fig. 2C–D).

Flower abundance positively influenced the after-disturbance change in plant species degree ($\chi^2 = 4.57$, $df = 1$, $p = 0.03$) but not in selectiveness ($\chi^2 = 0.60$, $df = 1$,

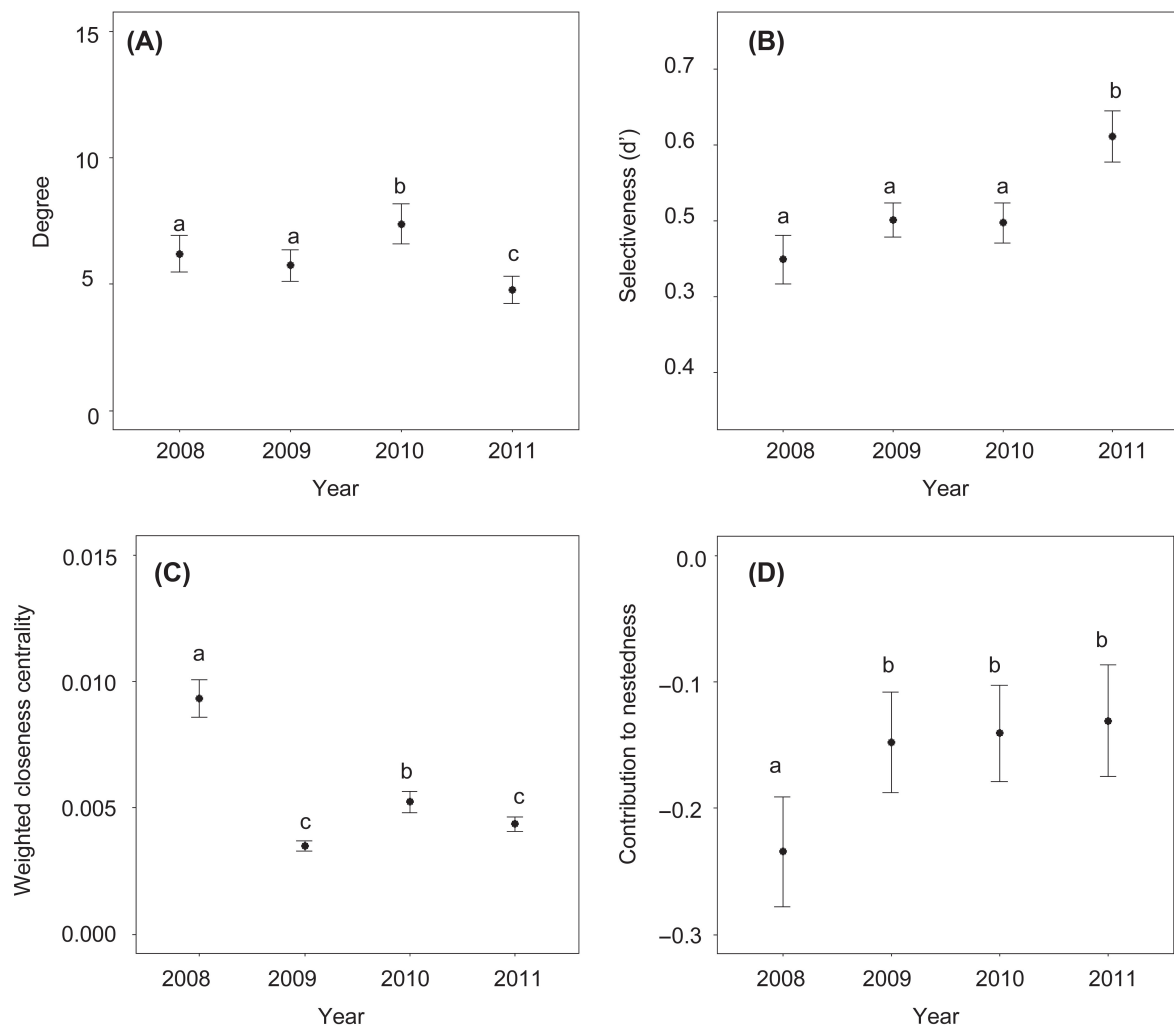


Figure 2. Mean (\pm SE) values of (A) degree; (B) selectiveness (d'); (C) weighted closeness centrality; and (D) contribution to nestedness for plants across the study years. Different letters indicate significant differences among years. Note that the higher the negative value, the more the species contributes to nestedness (following definition by Almeida-Neto and Ulrich 2011).

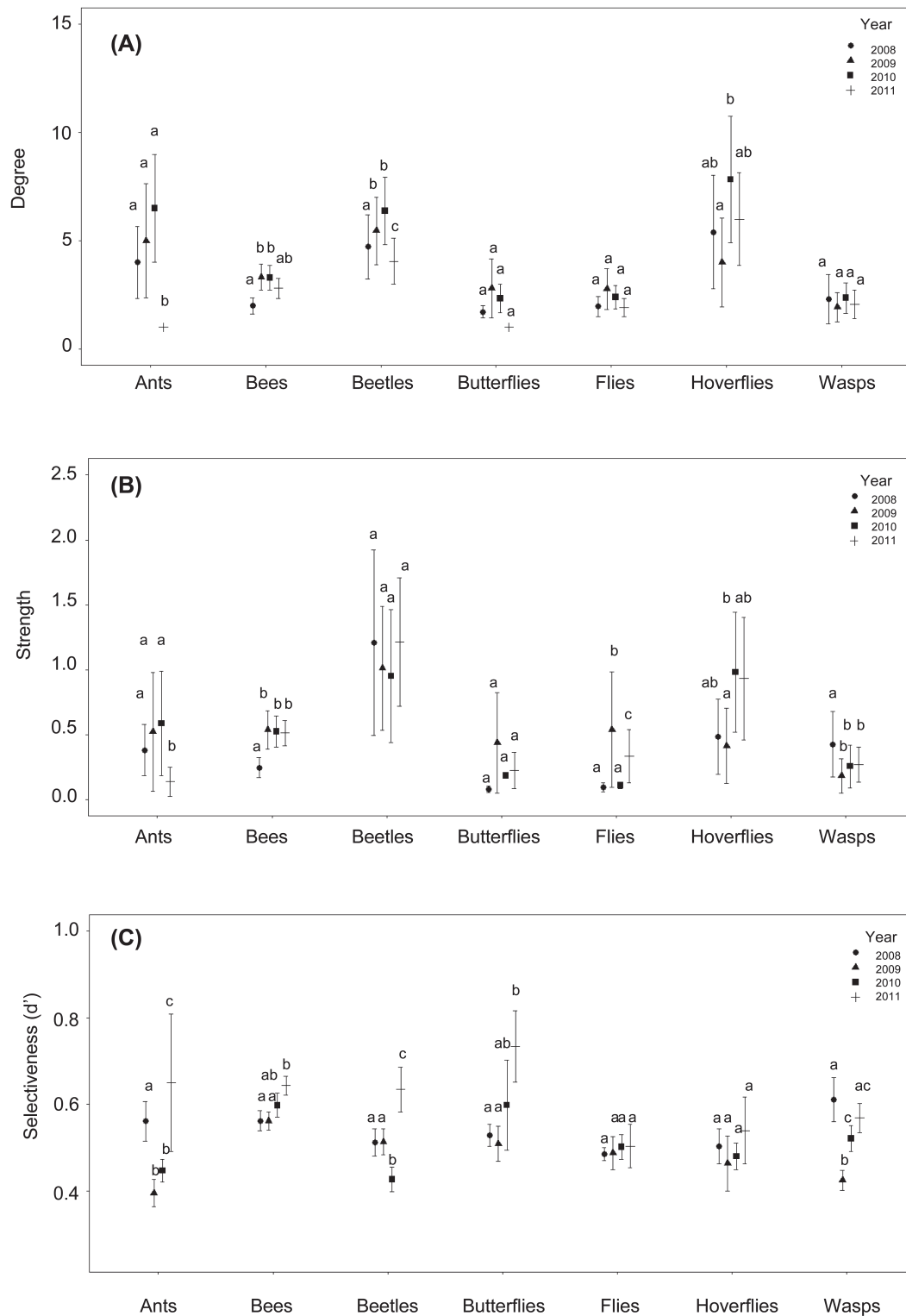


Figure 3. Mean (\pm SE) values of (A) degree, (B) strength, and (C) selectiveness (d') across years for each flower visitor group. In all cases, the interaction between year and flower visitor group was significant at $p < 0.05$. Different letters indicate significant differences among years within each functional group.

$p = 0.44$). In other words, those species producing more flowers were those most affected by the decrease in number of flower visitors after the disturbance, although they were not necessarily those showing a higher selectiveness. On the other hand, flower symmetry did not have a significant effect

on the after-disturbance change in either degree ($\chi^2 = 0.82$, $df = 1$, $p = 0.37$) or selectiveness ($\chi^2 = 0.81$, $df = 1$, $p = 0.37$), i.e. both actinomorphic and zygomorphic species responded similarly to the disturbance regarding these two metrics.

Flower visitor species

For all species level network parameters, a significant interaction was found between year and flower visitor functional group (Table 3), indicating that such groups do not vary consistently along time. Ants, beetles, and butterflies showed lower degrees in 2011 compared to the other years, whereas the rest of functional groups either showed no annual differences in their degree, or these were not due to the disturbance (Fig. 3A). Ants also showed a reduced strength in 2011 compared to the previous years (Fig. 3B), whereas the other groups showed either no variation among years or the variation was not related to the disturbance (Fig. 3B).

The loss of habitat led to a higher insect selectiveness, d' , in all functional groups, although only ants and beetles were significantly more selective after the disturbance than the previous years (Fig. 3C).

Regarding weighted closeness centrality, ants and butterflies showed lower values in 2011 than the previous years, although differences were significantly only for ants (Fig. 4A). The other flower visitor groups showed either an increase (bees, beetles and flies) or no interannual variations in this metric (Fig. 4A).

Lastly, flies and hoverflies tended to contribute more, but ants less, to nestedness in 2011 than the other years, though differences were not significant. The rest of groups showed interannual variations that were not related to the disturbance (Fig. 4B).

Species roles in the networks

Standardized connection, c , varied among years for plant species (Table 3), although such variation was unrelated to the disturbance (Fig. 5A). By contrast, the loss of habitat did influence c for flower visitors, although this was contingent upon the functional group (Table 3, Fig. 5B). Both ants and butterflies showed lower c in 2011 compared to the previous years whereas the other flower visitors showed either no significant variation across years or variation was not related to the disturbance (Fig. 5B).

On the contrary, participation values, z , showed low temporal variation for both plants (Table 3) and flower visitors (year: $\chi^2 = 2.92$, $df = 3$, $p = 0.40$; functional group: $\chi^2 = 5.11$, $df = 6$, $p = 0.53$), and there was not significant interaction year \times functional group; Table 3).

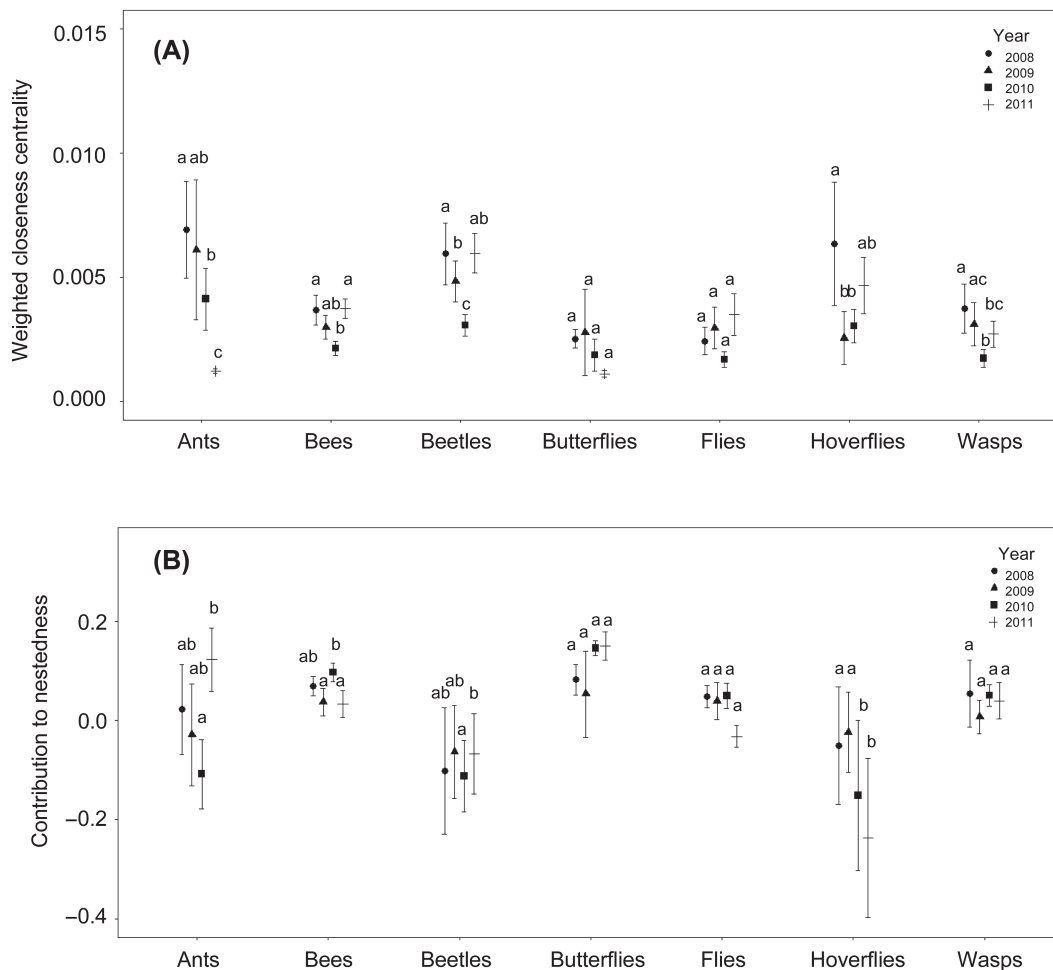


Figure 4. Mean (\pm SE) values of (A) weighted closeness centrality, and (B) contribution to nestedness across years for each flower visitor group. Note that, according to the definition of contribution to nestedness (Almeida-Neto and Ulrich 2011), a species with negative values contributes more than one with positive values. In all cases, the interaction between year and flower visitor group was significant at $p < 0.05$. Different letters indicate significant differences among years within each functional group.

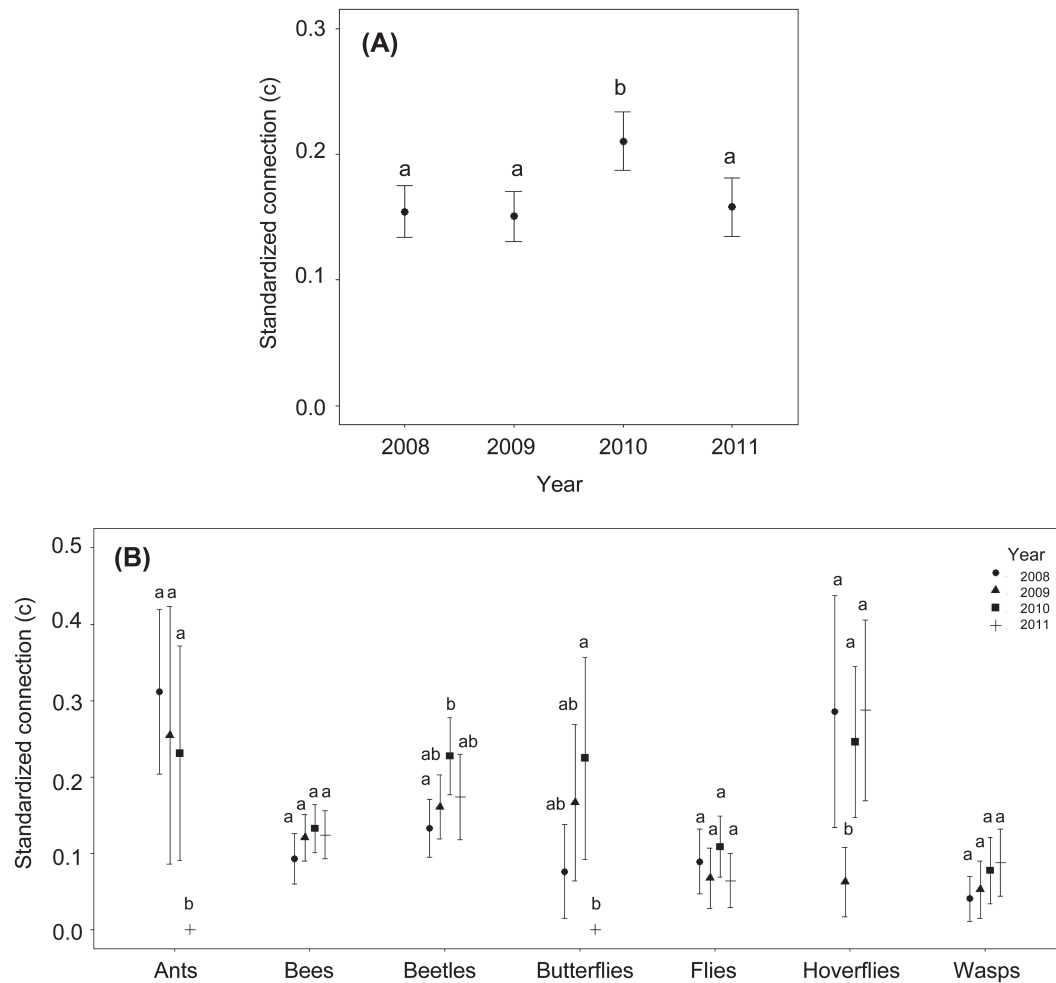


Figure 5. Mean (\pm SE) standardized connection, c , across years in (A) plant species, and (B) flower visitor functional groups. The interaction between year and functional group was significant at $p < 0.05$. Different letters indicate significant differences among years (A), or among years within each functional group (B).

Discussion

The habitat loss in our study area showed to notably impact some of the structural properties of the plant–flower visitor network. Although most metrics varied across years, the number of flower visitors and the number of links in the network decreased much more after the disturbance than the three previous years. This is concordant with results from other studies showing a reduction in pollinator availability and diversity attributed to a decrease in floral resource supplies as well as nesting sites after disturbance (Winfree et al. 2011, Hagen et al. 2012, Ferreira et al. 2013, Vanbergen et al. 2014). Despite this, network connectance was highly consistent in time, suggesting that the number of links changes with a similar proportion as the number of species does; this has also been reported in other studies that have examined temporal variation in the structure of pollination networks (Petanidou et al. 2008). Moreover, the nested pattern of interactions was weaker the year following the disturbance, which suggests that some generalist species (either plants or flower visitors) disappeared or were less abundant – and thus likely had fewer interactions – and/or that more specialized interactions appeared among the prevalent species in the community. The level of network specialization (H'_2)

in 2011 was in fact higher when compared to the previous years, what would support the lower nestedness values of that year. Other studies have also documented decreases in network nestedness in disturbed habitats (Vanbergen et al. 2014, Moreira et al. 2015, Revilla et al. 2015) though not always (Spiesman and Inouye 2013). A reduced nestedness is often associated with lower stability and resilience of plant–pollinator networks to perturbations (Bastolla et al. 2009, Fortuna et al. 2013), although there is controversy on this (James et al. 2012, Saavedra and Stouffer 2013, Rohr et al. 2014).

Greater modularity in disturbed habitats compared to undisturbed ones has also been reported (Spiesman and Inouye 2013). A more modular network is thought to reduce the opportunity for species to facilitate one another by sharing mutualistic partners and thus to have a destabilizing effect (Thébault and Fontaine 2010). Dormann and Strauss (2014) showed that quantitative modularity (Q) was positively related to complementary specialization H'_2 , using 22 quantitative pollination networks. We thus expected that an increase in H'_2 after habitat disturbance might result in a higher modularity. Both Q and the number of modules were actually higher in 2011 than the previous years, supporting the expectation. Nevertheless, when comparing the z -scores, the temporal differences disappeared.

At the species level, most network metrics varied across years. For plants, only strength was found to be consistent in time, indicating that the relative importance of a particular plant species for flower visitors was rather constant across the four study years, also after perturbation. This is indeed interesting as it suggests that despite some plants' traits can change over time (e.g. its abundance or its degree), the sum of dependencies of each flower visitor species on that plant is not modified. By contrast, the temporal changes observed in plant degree, weighted closeness centrality, and contribution to nestedness indicate that a plant's position in the network depend upon how generalist it is and on how generalists their flower visitors are in a particular year. Likewise, given the high temporal fluctuations in insect populations, the levels of plant selectiveness (d') are expected to be highly variable over time; the highest values observed in 2011 probably reflect that the lowest flower visitor abundances were found that year.

Regarding flower visitors, all species-level metrics varied across years, including species strength. In this case, the importance of a particular insect species for the entire plant community is likely to vary much depending upon its abundance and generalization level, which might be more variable than for plant species. In fact, we found large differences across years in flower visitor abundances, the year after habitat disturbance showing the lowest values. Disturbance did not only influence flower visitor abundance but also species richness, although this was contingent upon functional group. Species richness of beetles and flies were the most negatively affected, which might be because they are the most important functional groups in terms of percentage of pollinator visits, with 53.4% and 19.9%, respectively, (average for the four years). Moreover, ants, which represent a 4.7% of the total of visits, were the functional group most influenced by the disturbance regarding generalization level, strength, selectiveness, and closeness centrality. They also played a less important role as module connectors after the disturbance. This is most likely attributable to the shorter foraging range, compared to the other functional groups, specifically flying insects. It is unknown why the other groups, especially bees and wasps, which are also abundant in the area (14.5% and 3.8% of the visits, respectively), were not influenced to the same extent. One possible reason is that these groups depend upon nesting sites and food resources that were not a limiting factor, and despite flower visitor abundance was reduced the disturbance did not lead any species to local extinction. In addition, bees and wasps might have a greater mobility (Torné-Noguera et al. 2014) and thus are less influenced by local disturbances. We need more information on the rewiring capacity of different flower visitor functional groups in face of a habitat disturbance (Burkle et al. 2013, Aguirre-Gutiérrez et al. 2015, Lázaro et al. 2016) as well as on the ultimate consequences of such rewiring for plant reproductive success. From a conservation viewpoint, monitoring these changes in natural communities could be highly relevant to the proposal of effective conservation strategies (Campos-Navarrete et al. 2013).

In short, our findings showed that the large disturbance occurred in the study area altered to a large extent the structure of the plant–flower visitor network, making it more vulnerable to future perturbations. The lower floral

resources availability, together with a likely reduction in available nesting sites for some insect species, led to a reduction in species richness and abundance of floral visitors, which translated in turn to a less nested and more modular network composed of more specialized interactions. Not all flower-visitor functional groups were similarly affected; beetles, flies and ants were more negatively influenced by the disturbance than other groups such as bees and wasps, what we attribute to their overall lower mobility. These findings do not support, thus, the idea that non-social insects with free-living progeny are less influenced by habitat destruction than social bees (Jauker et al. 2009, Parsche et al. 2011). Future empirical studies from other systems are necessary to understand the mechanisms by which different functional groups of flower visitors respond to disturbances and to assess the consequences of such different responses on ecosystem functioning.

Acknowledgements – We thank Jaume Reus, Pep Mora, Joan Torrandell and Zeeba Khan for assistance in the field, and David Gibbs, David Baldock, Jordi Ribes, Marcos Báez, M. Carles-Tolrà, Paco Laroche, Pedro Oromí, Xavier Canyelles and Xavier Espadaler for insect identifications.

Funding – This study is framed within projects CGL2010-18759/BOS and CGL2013- 44386-P financed by the Spanish Ministry of Economy and Competitiveness. RCU was supported by a predoctoral grant from the Spanish Government (Ministry of Economy and Competitiveness and Ministry of Education, Culture and Sport), whereas AL was supported by a postdoctoral contract co-funded by the Regional Government of the Balearic Islands and the European Social Fund 2014–2020.

Permissions – The Servei de Protecció d'Espècies, Espais de Natura Balear (Conselleria de Agricultura, Medi Ambient and Territori) provided permissions to work at the study site.

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Supplementary material (available online as Appendix oik-04154 at <www.oikosjournal.org/appendix/oik-04154>). Appendix 1.