Ecological Entomology

Ecological Entomology (2016), **41**, 400–412 DOI: 10.1111/een.12310

Effects of grazing intensity on pollinator abundance and diversity, and on pollination services

AMPARO LÁZARO,[1,2] THOMAS TSCHEULIN,[1] JELLE DEVALEZ,[1] GEORGIOS NAKAS[1] and THEODORA PETANIDOU[1] [1]Laboratory of Biogeography and Ecology, Department of Geography, University of the Aegean, University Hill, GR-81100, Mytilene, Greece and [2]Department of Biodiversity and Conservation, Mediterranean Institute for Advanced Studies (UIB-CSIC), C/ Miquel Marquès 21, 07190, Esporles, Balearic Islands, Spain

Abstract. 1. Pollinating insects provide important ecosystem services and are influenced by the intensity of grazing. Based on the Intermediate Disturbance Hypothesis (IDH), pollinator diversity is expected to peak at intermediate grazing intensities. However, this hump-shaped relationship is rarely found.

2. The effect of grazing intensity was tested on flower cover, on the abundance and richness of bees, hoverflies and bee flies, and on pollination services to early-flowering bee-pollinated *Asphodelus ramosus* L. For that, we used data on 11 plant–pollinator phryganic communities from Lesvos Island (Greece) widely differing in grazing intensities.

3. Flower abundance and richness showed hump-shaped relationships with grazing intensity. Grazing affected the abundance and richness of bees and hoverflies directly and also indirectly, through changes in the flower community. Grazing influenced directly the richness but not the abundance of bee flies. Overall, pollinator abundance and richness showed hump-shaped relationships with grazing intensity, but variations in strength (hoverfly abundance) and direction (bee community) of the effect appeared along the season. Early in the season, grazing increased bee abundance but decreased richness, resulting in increased pollen limitation in *A. ramosus*.

4. The effects of grazing on pollinators vary with the intensity of the disturbance, generally supporting the IDH, and the timing of land-use activities may influence pollination services. Management strategies should include moderate grazing levels to preserve overall diversity in this area, however, the conservation of particular early bee or bee-pollinated species may benefit from reduced grazing in early spring.

Key words. bee flies, bees, hoverflies, Intermediate Disturbance Hypothesis, Mediterranean phryganic communities, pollen limitation, species richness.

Introduction

Pollinating insects provide important services to ecosystems and are responsible for the maintenance of ecosystem biodiversity and function (Klein *et al*., 2007; Kremen *et al*., 2007), but they are vulnerable to anthropogenic disturbances and the intensive management of agroecosystems (Tscharntke *et al*., 2005; Winfree *et al*., 2009). Livestock grazing, through consumption of plants, trampling and excreta, modifies the plant community (Pykälä, 2004; Navarro *et al*., 2006), and influences the structure and dynamics of the entire plant–pollinator community (Potts *et al.,* 2003; Vanbergen *et al*., 2014). As a consequence, pollinating insects are influenced by the extent, intensity, and type of grazing (Carvell, 2002; Kruess & Tscharntke, 2002a; Sjödin, 2007). The largest effects of grazing on pollinators have been related to its effects on the amount and composition of floral resources (Mayer *et al*., 2006; Roulston & Goodell, 2011). This is because grazing alters the population density of entomophilous plants, thus flower cover and diversity (Vazquez & Simberloff, 2004; Mayer *et al*., 2006; Xie *et al*., 2008), and the floral community has been reported as the best predictor of

Correspondence: Amparo Lázaro, Mediterranean Institute for Advanced Studies (UIB-CSIC), C/ Miquel Marquès 21, 07190, Esporles, Balearic Islands, Spain. E-mail: amparo.lazaro@imedea.uib-csic.es

pollinator abundance in pastures (Carvell, 2002; Sjödin, 2007; Kearns & Olivera, 2009). In addition, grazing may influence the abundance and diversity of insects in other ways not related to floral resources. For instance, grazing may directly affect the pollinators' survival rate by killing them or destroying their nests through animal trampling (Sjödin, 2007), or indirectly, by decreasing the availability of pollinator shelters in the vegetation (Potts *et al*., 2009). However, grazing can also influence the amount of nesting resources by creating areas of bare soil, which constitute desired nesting sites for ground-dwelling wild pollinators (Petanidou & Ellis, 1993; Potts *et al*., 2003; Vulliamy *et al*., 2006; Murray *et al*., 2012), or by altering the availability of water, essential for the construction of nests (Gess & Gess, 1993).

The Intermediate Disturbance Hypothesis (IDH) states that species diversity may be highest at intermediate levels of environmental stress because of offsetting effects of abiotic limitation and competitive exclusion (Grime, 1973; Conell, 1978; Svensson *et al.,* 2012). A recent review has shown that IDH can successfully predict disturbance–plant diversity relationships in medium-to-high productive habitats (Kershaw & Mallik, 2013). Therefore, it might be likely that grazing pressure influences plant and pollinator diversity in accordance with the IDH. This means that plant and pollinator diversity would increase until a peak at intermediate levels of grazing, and decrease henceforth as the intensity of grazing increases to high levels. Previous studies on the effect of grazing intensity on the abundance and diversity of pollinating insects, however, have mostly found linear relationships (e.g. Vulliamy *et al*., 2006; Xie *et al*., 2008; Kimoto *et al*., 2012; but see Kearns & Olivera, 2009) with contrasting effects (i.e. positive or negative) and strengths (i.e. steepness of the relationship), depending on the pollinator group examined (e.g. Sjödin *et al*., 2008; Kimoto *et al*., 2012; Murray *et al*., 2012). Such contrasting effects of grazing on pollinator abundance and diversity may be related to species-specific differences in foraging and nesting requirements (e.g. Goulson, 2003), but they also could be related to the limited range of grazing intensities examined, as the effect of grazing may vary from positive to negative depending on intensity (Grime, 1973; Conell, 1978).

By changing the abundance and diversity of pollinators, grazers may disrupt pollination services and directly affect the reproduction of plant species. However, indirect effects of grazing on plant reproduction may also occur through the modification of plant display, i.e. the size and abundance of individuals (Hegland *et al*., 2005), and plant density (Vazquez & Simberloff, 2004), or through changes in resource availability for the plants (Ågren *et al*., 2006). The studies on the effects of grazing on the reproduction of particular plant species have reported conflicting results, with some plant species being negatively affected by grazing (Mayer, 2004; Vazquez & Simberloff, 2004; Hegland *et al*., 2005), whereas others are positively influenced (Ågren *et al*., 2006; Vanbergen *et al*., 2014). The relationship between grazing intensity in a community and pollinator services to plant species may not be straightforward because of the pollinator and intensity dependence in the effects of grazing (see above), and because the outcome of multiple interactions should depend on their respective strengths and on their additivity (Herrera, 2000; Gómez, 2003). However, understanding the cascading effects of grazing on pollination services is necessary to build up adequate management measures for biodiversity conservation.

The high pollinator diversity in the Mediterranean Basin (e.g. Michener, 1979; Petanidou & Ellis, 1993, 1996; Nielsen *et al*., 2011) is related to the high floral diversity and the availability of bare soil in the area (Petanidou & Ellis, 1996; Potts *et al*., 2003), and benefited from the traditional Mediterranean land management (Potts *et al*., 2006), such as extensive grazing (Petanidou & Ellis, 1996). Unfortunately, with the abandonment of traditional land practices, the number of grazing animals has considerably increased, leading to widespread overgrazing (Petanidou & Ellis, 1996; Petanidou *et al*., 2008; Kizos *et al*., 2010). However, only a few studies have directly linked grazing animals to pollinator communities in the Mediterranean (Petanidou & Ellis, 1996; Potts *et al*., 2003; Vulliamy *et al*., 2006), and the effects of grazing intensity on plant–pollinator communities are still unclear.

In this study, we used data from 11 communities on Lesvos Island (Greece) to investigate how grazing intensity influences the abundance and diversity of flowering plants, and the abundance and diversity of three main pollinator groups in the area (bees, hoverflies, and bee flies: Petanidou & Ellis, 1993, 1996; Potts *et al.*, 2006; Nielsen *et al*., 2011). We also assessed the effects of grazing intensity on pollination services to the common Mediterranean species *Asphodelus ramosus* L. We consider this plant species as a good model plant for our study, not only because it is dependent on pollinators for seed set (Ne'eman *et al*., 2000), but also because it occurs frequently in grazed Mediterranean habitats, especially those intensely grazed (Pantis & Margaris, 1988; Noy-Meir, 1990; Hajar, 1993). Based on the IDH, our main hypothesis was that moderately grazed systems may support higher pollinator abundance and diversity, as well as pollination services. Our specific questions were: (i) Are plant abundance and diversity highest at intermediate grazing intensities? (ii) Are pollinator abundance and diversity highest at intermediate grazing intensities? (iii) Are the responses to grazing pollinator-group specific? (iv) Is the effect of grazing on pollinator abundance and diversity exclusively related to floral resources? (v) Are pollination services to *A. ramosus* highest at intermediate grazing intensities?

Material and methods

Study sites

We conducted this study on Lesvos Island in the northeastern Aegean Sea, in Greece (39°10′N, 26°20′E). Observations and experiments were carried out in three survey rounds during the main pollinator activity period, from late March to early June of 2012. Eleven sites were selected in the south-western part of the island, six of them located close to the village of Sigri, three close to the village of Eressos and two close to the village of Vatousa (see Table 1 for coordinates; Fig. 1). All these sites correspond to phrygana, the main semi-natural habitat in the East Mediterranean, equivalent to the West Mediterranean garrigue. Phryganic habitats, dominated by low entomophilous shrubby or geophyte species, such as *Cistus*

Table 1. Study sites, their coordinates, and mean grazing intensity (see text for details).

Site	Latitude	Longitude	Mean grazing intensity (%)
Eressos 1	39.1771	25.946	42.3
Eressos 2	39.172	25.919	47.4
Eressos 3	39.1458	25.9211	43.2
Sigri 1	39.2274	25.8584	4.4
Sigri 2	39.2046	25.8533	4.8
Sigri 3	39.2069	25.9023	3.4
Sigri 4	39.229	25.928	65.9
Sigri 5	39.2292	25.9516	44.2
Sigri 6	39.2258	25.961	33.6
Vatousa 1	39.2368	26.0305	38.8
Vatousa 2	39.2463	26.0484	46.9

salvifolius L., *C. creticus* L., *Origanum onites* L., *Thymbra capitata* L., *Sarcopoterium spinosum* Spach, *Centaurea spinosa* L., and *A. ramosus*, are especially rich in bees (Hymenoptera: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, and Melittidae), bee flies (Diptera: Bombilidae), and hoverflies (Diptera: Syrphidae) (Petanidou & Ellis, 1993; Potts *et al*., 2006; Nielsen *et al*., 2011). Grazing in this area is mostly conducted by sheep, and, to a lesser degree, by goats, and occurs throughout the year, although it is considerably stronger during spring. We selected our study sites on the basis of prior observations, which suggested large among-site variability in the intensity of grazing, whereas other characteristics such as elevation, aspect, and habitat type remained relatively constant.

To estimate pollination services, we selected *A. ramosus* as a model species, as it was the only plant species present in the majority of our study sites. Apart from being a common Mediterranean species, *A. ramosus* is a geophyte whose presence is enhanced by intense animal grazing (Pantis & Margaris, 1988; Noy-Meir, 1990; Hajar, 1993). This plant species has numerous white flowers that bloom from late February–March to April in the study areas. *Asphodelus ramosus* is self-incompatible (Ne'eman *et al*., 2000), highly visited by bees (Petanidou, 1991; Díaz Lifante, 1996; Ne'eman *et al*., 2000; Terzo & Rasmont, 2003) and its fruits are small round capsules with a maximum of six seeds per fruit.

Grazing intensity

To estimate grazing intensity, we used a novel approach in pollination studies that consisted of comparing plant biomass inside and outside exclosures (2 m × 2 m wide; 1 m high) set up in each site ca. 2 months before the first insect surveys were carried out, i.e. in January 2012. Samplings were conducted in the central 1 m × 1 m square of the exclosure, and at least 3 m away from the fence (for the sample outside the exclosure), to avoid any potential bias in grazing behaviour in the proximity of the exclosure (Stohlgren *et al.*, 1999).

During each insect survey round (see below), two squares (0.5 m × 0.5 m) were randomly selected at every site, one inside (E) and one outside (O) the exclosure. All above-ground plant biomass within the squares was collected, dried, and weighed (± 0.01 g) in order to compare biomass and calculate the grazing intensity. Collected squares were marked in order to avoid future resampling. Grazing intensity (%) was estimated at each site and each sampling round as $(1 - (O/E)) \times 100$, where O is the biomass of plants outside the exclosure and E is the biomass of plants inside the exclosure.

Insect sampling: bees, hoverflies, and bee flies

At each site, we sampled three times (rounds) in 2012, with successive samplings separated by ca. 1 month: in late March–early April (round 1), late April–early May (round 2), and late May–early June (round 3). We used both pan-traps and hand-netting for insect collection because prior studies in the area suggested that the combination of these two techniques may be the best to assess bee richness (Nielsen *et al.*, 2011). Samplings were carried out under good weather conditions: temperature >15 °C, sunshine, and no wind (<4 m/s). In order to address the problem of low species coverage experienced in one of our previous studies using pan-traps (Nielsen *et al.*, 2011), we used double the quantity of pan-traps per study site (10 in this study vs. 5 in the previous one). We arranged pan-traps in triplet units, each triplet comprising three pan-traps of a different UV-bright colour: white, blue, and yellow. These colours account for different colour preferences among pollinating insects (Westphal *et al*., 2008). The 10 triplets were set up on the ground, with any two triplets being separated by ca. 15 m. Pan-traps were filled up to two-thirds (350 ml) with water + 1 drop of aroma-free kitchen detergent and left for 48 h in each site and round, thus covering the entire flight activity period of diurnal and nocturnal pollinators. The hand-netting survey consisted of a 120-min random walk during which we collected (or recorded in case of easily identifiable species) any insect observed on the flowers of any plant species in the community, stopping the timer any time the attention was distracted from the flowers (e.g. while transferring caught insects into vials). Surveys were conducted between 10.00 and 16.30 hours. Time allocated to each plant species was proportional to its abundance.

Insects collected by both pan-traps and hand-net were transferred to small plastic zip lock bags and to vials, respectively, and refrigerated if they were to be processed within 24 h, otherwise deep frozen until pinning. After processing in the laboratory, the specimens were identified to the species level (when necessary with the help of European specialists), and inputted in the database of the Melissotheque of the Aegean (Petanidou & Lamborn, 2005).

We pooled the data from the pan-traps and hand-netting surveys to calculate insect abundance (as the number of insects collected and recorded per site and round), and insect richness (as the number of species collected and recorded per site and round). We chose species richness as a diversity measurement, first, because it is the simplest measurement allowing comparison with the majority of other studies, and second, because a recent meta-analysis (Svensson *et al*., 2012) showed that IDH is supported when biodiversity is measured as species richness, whereas evenness tended to increase with increasing disturbance, and, therefore, the use of species richness is

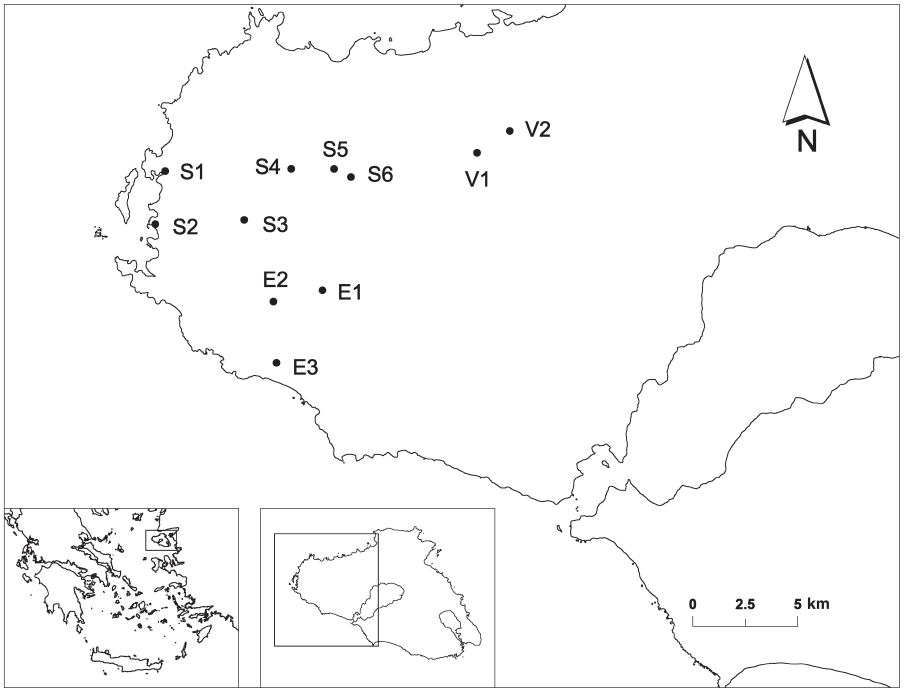

Fig. 1. Map of Lesvos Island (Greece) in NE Aegean, with the location of the 11 study sites. S1: Sigri 1; S2: Sigri 2; S3: Sigri 3; S4: Sigri 4; S5: Sigri 5; S6: Sigri 6; E1: Eressos 1; E2: Eressos 2; E3: Eressos 3; V1: Vatousa 1; V2: Vatousa 2.

recommended (instead of diversity indices based on abundances) when testing the IDH.

Flower cover

Flower cover measurements were conducted on 25 1 m × 1 m squares selected at random at every round and site, within the area where insects were collected. The total number of functional reproductive units, i.e. flowers or inflorescences depending on the species ('flowers' hereafter) for each plant species was counted within these squares. Per site and round, we calculated flower abundance as the average number of flowers/m^2, and flower richness as the total number of flowering species recorded. Plant specimens were deposited in the Herbarium of the Laboratory of Biogeography and Ecology.

Pollination services to A. ramosus

To evaluate pollination services to *A. ramosus*, we calculated pollen limitation indices at 10 of the 11 study sites (the species was not present in Sigri 3). For that, we randomly selected 30 *A. ramosus* individuals within each site (except for Sigri 2 and 4 where we selected all available plants which were less than 30), and two flowers within each individual. One of these flowers was assigned to be supplementary hand-pollinated (S), whereas the other was left unmanipulated for natural pollination (U). Supplemental cross-pollination was performed by carefully rubbing freshly-dehisced anthers from an individual separated by 2–5 m from the recipient. These supplemental hand-pollinations were conducted in round 1 in all sites except in Sigri 4, where they were conducted in round 2, as a result of the delayed flowering peak of *A. ramosus* in this population. Fruits were collected when mature and kept in individual paper bags to be later dissected in the lab and their seeds counted. We considered fully developed seeds as fertile and shrunk undeveloped flake-like ones, usually with a lighter colour, as aborted.

Pollen limitation indices were calculated for each site as 1 – (U/S), where U is the number of fertile seeds in the unmanipulated flowers and S the number of fertile seeds in the supplementary pollinated flowers (Larson & Barrett, 2000). As many plants did not produce seeds either in the unmanipulated or the hand-pollinated flowers, we calculated one index per site by aggregating the data of all studied plants.

Statistical analysis

All the statistical analyses reported here were conducted in R 2.15.3 (R Development Core Team, 2008). To study the effect of grazing intensity on the abundance and richness of plants and pollinators, we used generalised linear mixed models (GLMM, library lme4), with site as a categorical random variable to avoid pseudoreplication, grazing intensity as continuous fixed and round as a categorical fixed variable. Models on the abundance and richness of pollinators were conducted separately for each group and included also the abundance of flowers and flower richness. An additional predictor variable in the models of pollinator richness was the log-transformed pollinator group's abundance because GAMMs (library mgvc, Zuur *et al*., 2009)

indicated logarithmic relationships between these two variables, and abundances naturally vary in time and space. This approach also allowed testing whether there was a direct effect of grazing on pollinator richness independent of the effect on pollinator abundance. As some pan-traps (24 out of 990 individual traps within triplets) were lost, we included the number of intact pan-traps (log-transformed) as an offset in the models, to control for the effects of these small changes in sampling effort on the results (Zuur *et al*., 2009), the results, however, did not change when including or excluding this offset. We were specifically interested in testing the Intermediate Disturbance Hypothesis (Grime, 1973; Conell, 1978), and therefore, we included in the analysis the variable 'grazing intensity' both as linear and quadratic terms. To avoid collinearity between these two terms, we first standardised the variable 'grazing intensity' to $\bar{x} = 0$ and $\sigma = 1$ and then we calculated its quadratic term (Quinn & Keough, 2002). Prior to analyses, we ran variation inflation factor (VIF) analyses to identify collinear predictor variables that should be removed from further analyses (Zuur *et al*., 2009). VIF values were smaller than 3 for all variables, so none of the predictors needed to be removed (Zuur *et al.*, 2009). Before the analyses we also used Moran´s I (library ncf; Bjørnstad & Falck, 2001) to check for any spatial correlation in the data or in the residuals of the models (with no random factor), neither the data nor the residuals showed any spatial correlation, indicating that our approach with mixed models was appropriate. Owing to the nature of the data, we used: (i) Gaussian distribution and log link function for the analysis of flower abundance, (ii) Poisson distributions and log link functions for the analyses of flower and insect diversity, and for the analysis of hoverfly abundance, and (iii) Negative binomial distributions and log link functions for the analyses of bee and bee fly abundances, as in these cases data were overdispersed (Zuur *et al*., 2009). We used AICc, i.e. corrected AIC for small sample sizes (library sme; Hurvich & Tsai, 1989; Burnham & Anderson, 2004), to select best models among the set of combinations of predictor variables (including the interaction between grazing intensity and round), and to test whether model fit was better when including random intercept, random slope or both (in all cases best models included only random intercept). The best model is described in the results section, and the best five competing models for each analysis are given in Tables S1–S4 (Supporting information).

To analyse the pollinator services to *A. ramosus*, we used general linear models (library lme), because data fulfilled the assumptions of normality. In these models, the response variable was the "pollen limitation index". The best model was selected based on AICc among all the possible simple regression models on the predictors explained above (but measured during *A. ramosus* flowering period, i.e in round 1 except for Sigri 4 where they were measured in round 2) and *A. ramosus* density and its number of visits. Only simple regression models were compared because sample size ($n = 10$) did not allow multiple regressions. The best five competing models explaining pollen limitation in *A. ramosus* are shown in Table S5 (Supporting information). The best model based on AICc was the only model showing any significant relationship.

Results

Grazing intensity

Grazing intensity, calculated for each site and round, varied from 0.0% to 76.9%. Average grazing intensity values per site varied from 3.4% to 65.9% (Table 1).

Effects of grazing on the plant community

The best model showed that the effect of grazing on flower abundance varied among rounds (Grazing intensity^2 × Round: $\chi_2{}^2 = 23.84$, $P < 0.0001$): flower abundance in round 1 and 3 showed a hump-shaped relationship with grazing intensity,

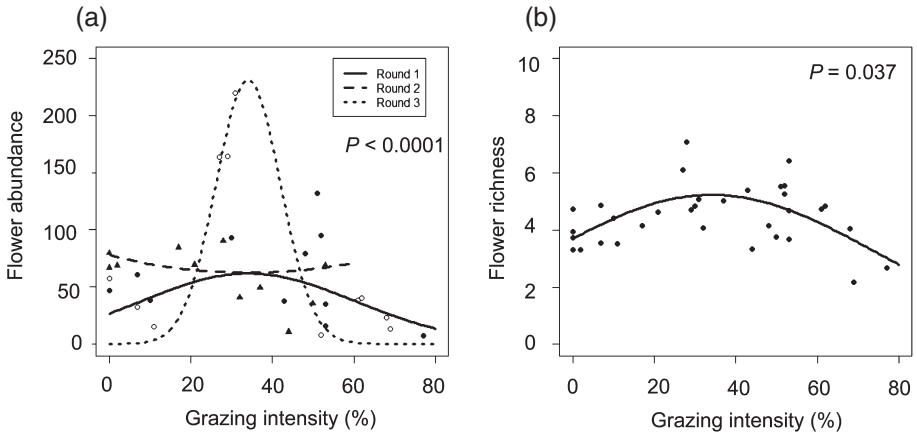

Fig. 2. Flower abundance and richness. Partial residual plots showing the relationship between grazing intensity and (a) flower abundance and (b) flower richness in the community. The results of the best models are shown. Lines represent the estimates of the best models and symbols represent partial residuals of the models. When the best model showed a significant effect of grazing intensity consistent across rounds, the line represent the overall effect of grazing; when there was a significant interaction, different lines represent the estimates for each round. Round 1: early in the season, round 2: in the middle of the season, round 3: late in the season.

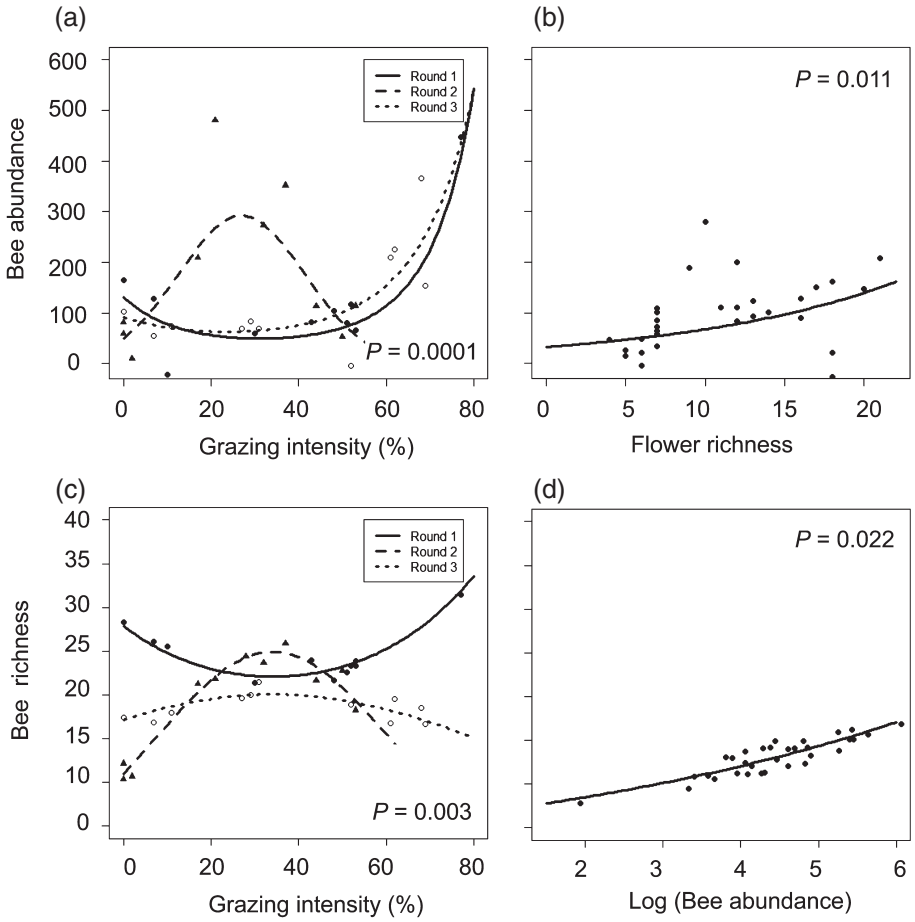

Fig. 3. Bee abundance and richness. Partial residual plots showing the relationship between (a) bee abundance and grazing intensity, (b) bee abundance and flower richness, (c) bee richness and grazing intensity, and (d) bee richness and bee abundance. The results of the best models are shown. Lines represent the estimates of the best models and symbols represent partial residuals. As in these cases the best models showed significant interactions between grazing intensity and round, different lines represent the estimates for each round. Round 1: early in the season, round 2: in the middle of the season, round 3: late in the season.

whereas there was no relationship between these two variables measured in round 2 (Fig. 2a). In contrast, the best model for the effect of grazing on flower richness was consistent across the rounds. Flower richness peaked at intermediate grazing intensities (Grazing intensity^2: $\chi_1{}^2 = 4.35$, $P = 0.037$; Fig. 2b) and significantly decreased along the season ($\chi_2{}^2 = 37.23$, $P < 0.0001$).

Effects of grazing on pollinator abundance and richness

In total, we collected or recorded 4925 insect individuals belonging to the three target groups: 4639 bees (168 species, 28 genera), 149 hoverflies (20 species, 12 genera), and 285 bee flies (25 species, 13 genera).

Bee abundance and richness. The best model showed that the effect of grazing intensity on bee abundance depended on the round (Grazing intensity^2 × Round: $\chi_3{}^2 = 18.78$, $P = 0.0003$). While bee abundance increased with grazing intensity in round 1 and round 3, it peaked at intermediate grazing levels in round 2 (Fig. 3a). Bee abundance also increased significantly with plant species richness ($\chi_1{}^2 = 4.87$, $P = 0.010$; Fig. 3b). Same as for bee abundance, the effect of grazing intensity on bee richness depended on the round (Grazing intensity^2 × Round: $\chi_2{}^2 = 11.65$, $P = 0.003$), as shown in the best model. Bee richness mostly decreased with grazing intensity in round 1 (although it showed a second peak at very high grazing intensities), peaked at intermediate grazing intensities in round 2, and showed no clear relationship with grazing in round 3 (Fig. 3c). Bee richness also increased with bee abundance ($\chi_1{}^2 = 5.23$, $P = 0.022$; Fig. 3d).

Hoverfly abundance and richness. The best model for hoverfly abundance showed a peak at intermediate grazing intensities, but the strength of the effect varied among rounds (Grazing intensity × Round: $\chi_2{}^2 = 25.32$, $P < 0.0001$, Grazing intensity^2 × Round: $\chi_2{}^2 = 20.80$, $P < 0.0001$, Fig. 4a). Hoverfly

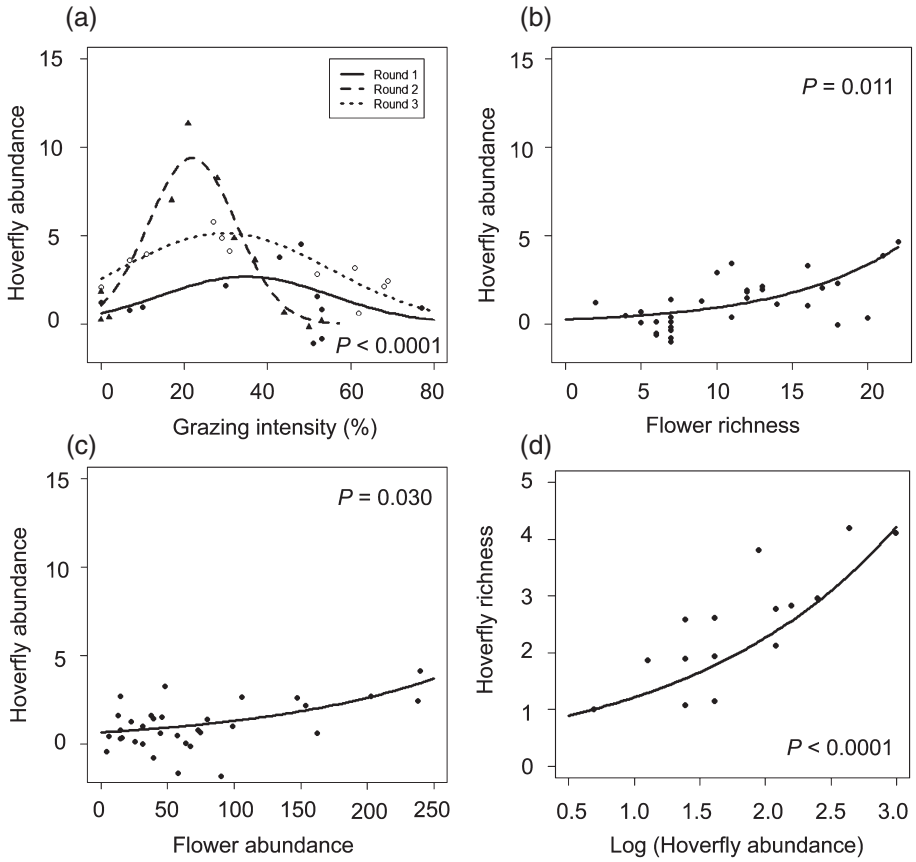

Fig. 4. Hoverfly abundance and richness. Partial residual plots showing the relationship between (a) hoverfly abundance and grazing intensity, (b) hoverfly abundance and flower richness, (c) hoverfly abundance and flower abundance, and (d) hoverfly richness and hoverfly abundance. The results of the best models are shown. Lines represent the estimates of the best models and symbols represent partial residuals of the models. For hoverfly abundance, the best model showed a significant interaction between grazing intensity and round, and therefore, different lines represent the estimates for each round. Round 1: early in the season, round 2: in the middle of the season, round 3: late in the season.

abundance increased also with flower richness ($\chi_1^2 = 6.41$, $P = 0.011$, Fig. 4b) and flower abundance ($\chi_1^2 = 4.71$, $P = 0.030$, Fig. 4c). The best model for hoverfly richness showed an increase with hoverfly abundance ($\chi_1^2 = 23.52$, $P < 0.0001$, Fig. 4d).

Bee fly abundance and richness. The best model showed that bee fly abundance significantly increased at the end of the season ($\chi_2^2 = 15.50$, $P = 0.0004$), no other predictor variable appeared in the best model of bee fly abundance. However, the best model for bee fly richness showed a hump-shaped relationship with grazing intensity consistently across rounds (Grazing intensity^2: $\chi_2^2 = 5.11$, $P = 0.024$), with richness peaking at intermediate levels of grazing intensity (Fig. 5a). Bee fly richness also increased with bee fly abundance ($\chi_1^2 = 34.55$, $P < 0.0001$; Fig. 5b).

Pollination services to A. ramosus

During the hand-netting transects, we recorded (i.e. collected or observed) on *A. ramosus* 208 insects belonging to 20 species, which consisted of 17 bee species, one species of Coleoptera, one species of Lepidoptera, and one species of Diptera. The most common insects collected on this plant species were all generalists. The main visitor was the honeybee, *Apis mellifera* L., which corresponded to 73.1% of individuals recorded on the plant, followed by the scarabaeid beetle *Tropinota hirta* (Poda) (10.1% of individuals), the solitary ground nesting bee *Anthophora dalmatica* Pérez (2.9% of the individuals), the syrphid *Eupeodes corollae* (Fabricius) (2.4% of the individuals), and the solitary ground nesting bee *Anthophora plumipes* (Pallas) (1.4% of the individuals). The other 14 species of bees and one Lepidoptera species represented together the remaining 10.1% of individuals recorded.

Pollen limitation in *A. ramosus* increased linearly with grazing intensity during its blooming period ($\chi_1^2 = 9.04$, $P = 0.003$, Fig. 6).

Discussion

Grazing affected the pollinators through effects on the flower community (mainly flower richness), but also directly and

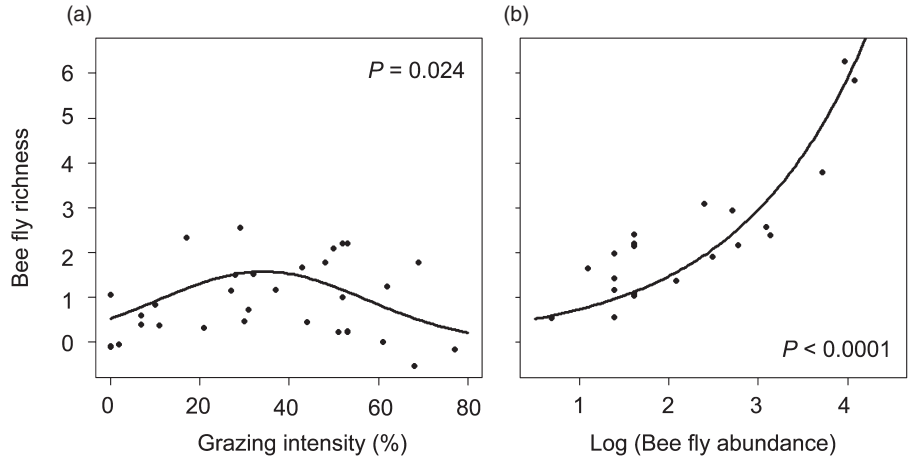

Fig. 5. Bee fly richness. Partial residual plots showing the relationship between bee fly richness and (a) grazing intensity and (b) bee fly abundance. The results of the best model are shown. Lines represent the estimates of the best model and symbols represent partial residuals of the model. In this case, the best model showed a consistent effect of grazing across the rounds.

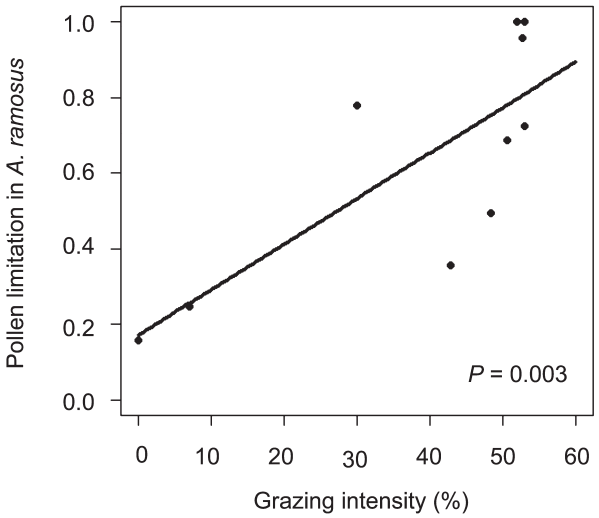

Fig. 6. Pollination services to *Asphodelus ramosus*. Partial residual plot showing the relationship between pollen limitation index in *A. ramosus* and grazing intensity. Line represents the estimate of the best model and symbols represent partial residuals of the model.

independently of its effects on flower cover. We found some support for the Intermediate Disturbance Hypothesis, but the effects of grazing intensity depended on the round and the pollinator group analysed. Hoverfly abundance and bee fly richness peaked at intermediate grazing, although the strength of the effect depended on the round for the former. However, the effect of grazing on bees, the main pollinator group, depended on the round. In the middle of the season, both the abundance and diversity of bees were highest at intermediate grazing intensities. However, later in the season, grazing intensity enhanced bee abundances, whereas, early in the season, grazing increased bee abundance but decreased bee richness, probably because it favoured some dominant species. Pollen limitation in *A. ramosus* (an early-flowering, bee-visited plant species) increased with grazing intensity, probably as a result of the decrease in bee richness with grazing intensity early in the season.

Effects of grazing intensity on the plant community

Grazing at moderate levels may be important in preserving diverse floral communities because plant species richness is often higher in grazed grasslands compared with mown and unmanaged grasslands (e.g. Hoiss *et al*., 2013; Vanbergen *et al*., 2014; but see Sjödin *et al*., 2008). Based on the IDH (Grime, 1973; Conell, 1978), we expected plant richness to peak at intermediate grazing intensities. Our results showed that both the abundance and diversity of flowers were highest at intermediate levels of grazing. However, the effect of grazing on plant abundance differed among sampling rounds. We found a hump-shaped relationship between grazing intensity and flower abundance early and late in the season, but no relationship between these two variables was detected in the middle of spring (round 2). This absence of relationship may be attributed to the much higher floral resources available during this period (81.3 ± 6.9 flowers/m^2 vs. 67.4 ± 6.9 and 66.1 ± 26.1 in early and late spring, respectively; see also Petanidou *et al*., 1995), in which floral abundance may be too high to be affected by grazing. However, we cannot discard that other factors, such as the identity of plant species flowering during middle spring, could also have influenced this relationship. The hump-shaped effect of grazing on flower richness was, however, consistent across the season. Despite several concerns related to the IDH (e.g. Mackey & Currie, 2001; Fox, 2013), higher plant diversity at intermediate grazing levels have been reported in many studies (e.g. Naveh & Whittaker, 1979; Bowers, 1993; Vulliamy *et al*., 2006; Hegland *et al*., 2013; but see Collins *et al*., 1995; Scohier & Dumont, 2012). Increases in flower richness at intermediate grazing intensities may occur because with moderate grazing the abundance of dominant species (which would normally outcompete the less dominant ones) is reduced, whereas when grazing intensity is too high, most of the species cannot

survive and, therefore, richness declines. The floral community has been reported as the best predictor of pollinator abundance in pastures (Carvell, 2002; Sjödin, 2007; Kearns & Olivera, 2009), and, therefore, the relationships between grazing intensity and plant abundance and richness shown here are extremely relevant to understand also the effects of grazing on the abundance and diversity of pollinators.

Effects of grazing intensity on pollinator abundance and richness

We found different effects of grazing depending on the pollinator group examined, as shown also in several previous studies (Sjödin *et al*., 2008; Kimoto *et al*., 2012; Murray *et al*., 2012). Differences in sensitivity to grazing may be driven by differences in insect life history traits and nesting requirements (e.g. Goulson, 2003) and by differential effects of grazing on the floral resources used by the pollinators (Carvell, 2002; Mayer *et al*., 2006; Sjödin *et al*., 2008; Kimoto *et al*., 2012). While both the abundance and richness of bee and hoverfly responded directly or indirectly to grazing, only the richness (but not the abundance) of bee flies was affected directly by grazing intensity. Interestingly, bee flies were not either influenced by the overall abundance and richness of flowers in the community, as the other groups were. Unfortunately, we are not aware of any other study examining the grazing effect on bee flies to compare our results with.

As for flower richness, we expected hump-shaped relationships between grazing intensity and pollinator richness (Grime, 1973; Conell, 1978). Previous studies have compared grazed with ungrazed sites or have mostly found linear relationships between grazing intensity and pollinator abundance and diversity (but see Kearns & Olivera, 2009, for an indication of IDH). In several of these studies, increased grazing was associated with a decrease in insect abundance or diversity (e.g. Kruess & Tscharntke, 2002b; Hatfield & LeBuhn, 2007; Wallis De Vries *et al*., 2007; Franzén & Nilsson, 2008; Xie *et al*., 2008; Preston *et al*., 2012; Scohier & Dumont, 2012; Minckley, 2014), whereas in others grazing had a positive effect on the abundance and/or diversity of insects (Carvell, 2002; Vulliamy *et al*., 2006; Morandin *et al*., 2007; Yoshihara *et al*., 2008). Focusing on the pollinator groups examined here, the only study we know on hover flies (Sjödin *et al*., 2008) indicated a negative effect of grazing on these insects; whereas the numerous studies on bees also showed contrasting responses to grazing (negative response: e.g. Hatfield & LeBuhn, 2007; Franzén & Nilsson, 2008; Xie *et al*., 2008; Minckley, 2014; positive response: e.g. Carvell, 2002; Vulliamy *et al*., 2006; Morandin *et al*., 2007). We hypothesised that these contrasting responses to grazing might be (at least partly) the result of the particular range of intensities examined. To avoid this potential pitfall, we used a wide range of grazing intensities varying from 0% to almost 80% and found hump-shaped relationships between grazing intensity and pollinator abundance and richness. First, as often shown in other studies (Potts *et al*., 2003, 2009; Vulliamy *et al*., 2006), the abundance and richness of pollinators increased with flower richness and abundance. This implies that grazing intensity may have a cascading indirect hump-shaped effect on the abundance and richness of pollinators because the effect of grazing on the plant community is hump-shaped. In addition, we found other hump-shaped effects of grazing unrelated to the floral resources. These effects could be associated with the increase in the amount or diversity of nesting substrates (Potts *et al*., 2003; Vulliamy *et al*., 2006; Murray *et al*., 2012), or the increase of ecological niches as a result of the spatial habitat heterogeneity caused by grazing (e.g. Dahlin *et al*., 2014; Jerrentrup *et al*., 2014).

The IDH is a controversial hypothesis that has led to active discussions (e.g. Mackey & Currie, 2000, 2001; Fox, 2013; Sheil & Burslem, 2013; Huston, 2014). Mackey & Currie (2000, 2001) questioned the validity of IDH because hump-shaped relationships do not seem to be the general response to stress, and when they occur, this response is weak. Also, Fox (2013) argued that the three major mechanisms thought to produce hump-shaped diversity-disturbance relationships are logically invalid, whereas Sheil and Burslem (2013) and Huston (2014) criticised that questioning. At any rate, all previous studies conducted in Mediterranean ecosystems on different organisms – such as plants (Koniak & Noy-Meir, 2009), carabid beetles (Kaltsas *et al*., 2013), grasshoppers (Kati *et al*., 2012), mammals (Goncalves *et al*., 2012) and birds (Malavasi *et al*., 2009) – have supported the IDH. This suggests that intermediate grazing might have positive effects on the diversity of organisms at least in the Mediterranean area characterised by at least an 8000 year-long history of livestock management and grazing (Le Houerou, 1981; Marathianou *et al*., 2000). In agreement, we found general support for the IDH in our system on Lesvos Island, however, hump-shaped relationships appeared only within some rounds (with the exception of flower and bee fly richness), probably because other factors, such as changes in community composition along the season, have stronger effects on richness and abundance. Differences across time in the effect of grazing are often shown (e.g. Yoshihara *et al*., 2008; Kimoto *et al*., 2012), and are not surprising taking into account the phenological changes that occur in the plant–pollinator community. In the case of hoverfly abundance, changes along the season were exclusively related to the strength of the effect, which was strongest in the middle of the season. The largest change in the effect of grazing across the season was related to the bee community, probably as a result of the natural large variation in the composition of bee communities over the spring months in these sites (Theodora Petanidou, unpublished data). As expected, in the middle of the season both the abundance and richness of bees were highest at intermediate grazing intensities. Later and earlier in the season, however, bee abundance was positively associated with grazing intensity. An increase in bee abundance with grazing intensity has been found in previous studies on bees (Carvell, 2002; Vulliamy *et al*., 2006; Morandin *et al*., 2007) and has been related to an increased amount of nesting resources (Vulliamy *et al*., 2006). Interestingly, despite the positive relationship between grazing intensity and bee abundance, grazing negatively affected bee richness early in the season, suggesting that grazing may enhance the abundance of particular species that outcompete the rest of the community early in the spring.

Pollination services to A. ramosus

Our study showed that *A. ramosus* was highly visited by bees, confirming the results of previous studies (Petanidou, 1991; Díaz Lifante, 1996; Ne'eman *et al*., 2000; Terzo & Rasmont, 2003). Our hypothesis that pollination services to *A. ramosus* might be highest at intermediate grazing levels owing to increased abundance and diversity of pollinators at these intensities was not corroborated. Instead, we found that *A. ramosus* pollen limitation increased linearly with grazing intensity, indicating that very high grazing intensity may reduce pollination services in this common Mediterranean species. A high grazing intensity is often related to low nutrient availability, especially in asphodel deserts (Pantis & Margaris, 1988), and, therefore, it could lead to a low seed set as a result of poor soil conditions. Because our seed set results were standardised (we used pollination limitation as a measure of pollination services, which controls for any effect of nutrient resource availability), the measured grazing effect is directly related to pollination. Previous studies have shown that plant reproductive responses to grazing are highly species-specific, with some species responding to grazing intensity positively and others negatively. For instance, higher overall outcrossing rates and more pollen donors were found in *Cirsium palustre* (L.) in the grazed compared with the ungrazed habitat, probably because of the higher attraction of flies to richer habitats (Vanbergen *et al*., 2014). Also, Ågren *et al*. (2006) found that grazing indirectly favoured seed production in *Primula farinosa* L. mainly because the removal of surrounding vegetation increased resource availability for those plants that escaped damage. In contrast, some other studies have shown a negative effect of grazing on the fecundity of plants, just as in the present study (Mayer, 2004; Vazquez & Simberloff, 2004; Hegland *et al*., 2005). Vazquez and Simberloff (2004) found that by directly reducing the population density of *Alstroemeria aurea* L., cattle indirectly reduced the reproduction of this plant species. Although several studies have found that *A. ramosus* presence is enhanced by intense animal grazing (Pantis & Margaris, 1988; Noy-Meir, 1990; Hajar, 1993), we did not find any relationship between grazing intensity and *A. ramosus* flower density ($N = 10$, $F_{1,8} = 1.13$, $P = 0.32$). Instead, the increase in pollen limitation with grazing intensity in this species may be related to the decrease in bee richness with grazing intensity early in the season, when *A. ramosus* flowered (round 1, Fig. 3c), given that this species is mostly visited (and most probably also pollinated) by bees. Note that although bee richness peaks again at very high grazing intensities early in the season (Fig. 3c), pollen limitation was not measured in the population with the highest grazing intensity, because *A. ramosus* was absent there. It seems that a rich bee community is important for *A. ramosus* pollination. Indeed, this plant species is visited by 17 species of bees, some of them of a large size, such as several species of *Anthophora*, *Xylocopa*, and *Bombus*. Although *A. mellifera* is the most common visitor, honeybees are inefficient compared to other large-sized bees such as *Anthophora* or *Xylocopa* (Díaz Lifante, 1996), and their presence is not affected by grazing intensity ($N = 10$, $F_{1,8} = 0.74$; $P = 0.41$), probably because this insect species is completely managed in the study area. Therefore, our results suggest that a decrease in bee richness is related to an increase in pollen limitation in *A. ramosus*. However, detailed studies on the efficiency of different pollinators and their impact on the reproduction of *A. ramosus*, would be needed to confirm this. Studying other plant species with a different flowering period could lead to different results and would be necessary to assess the overall effect of grazing on pollination services in the area. In any case, our results suggest that when the targets of conservation are individual species, detailed specific studies should be conducted, because overall trends may not fit all species.

Conclusions

Analysing data on 11 plant–pollinator communities and a wide range of grazing intensities in western Lesvos, we conclude that intermediate grazing intensities increase the overall abundance and richness of plants and pollinators. The effect of grazing on pollinators was expressed both through effects on the flower community (mainly richness), but also by direct effects unrelated to floral resources. However, the responses to grazing were pollinator-group specific, and often varied in strength and/or direction along the season. Although overall management strategies should maintain moderate grazing levels in this area, strategies related to the conservation of particular early bee species or early bee-pollinated plant species may benefit from the reduction of grazing intensity in early spring.

Acknowledgements

The research has been co-financed by the European Union (European Social Fund – ESF) and Greek national funds through the Operational Program 'Education and Lifelong Learning' of the National Strategic Reference Framework (NSRF) – Research Funding Program: THALES. Investing in knowledge society through the European Social Fund. We would like to thank H. Dathe, J Dils, A. Ebmer, D. Michez, A. Müller, A. Pauly, S. Patiny, C. Praz, M. Quaranta, S. Risch, W. Schedl, E. Scheuchl, M. Schwarz, and A. Vujic for insect identification; A. Stefanaki and E. Hanlidou for plant identification; and G. Tataris for the map used in the paper. We also thank the board of directors of The Natural History Museum of the Lesvos Petrified Forest for letting us install two of our sites (Sigri 2 and 3) in their parks.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12310

Table S1. AICc values obtained for the five best-competing models explaining flower abundance and richness.

Table S2. AICc values obtained for the five best-competing models explaining bee abundance and richness.

Table S3. AICc values obtained for the five best-competing models explaining hoverfly abundance and richness.

Table S4. AICc values obtained for the five best-competing models explaining bee fly abundance and richness.

Table S5. AICc values for all single regression models explaining pollen limitation in *Asphodelus ramosus*.

References

Ågren, J., Fortunel, C. & Ehrlén, J. (2006) Selection on floral display in insect-pollinated *Primula farinosa*: effects of vegetation height and litter accumulation. *Oecologia*, **150**, 225–232.

Bjørnstad, O.N. & Falck, W. (2001) Non-parametric spatial covariance functions: estimation and testing. *Environmental and Ecological Statistics*, **8**, 53–70.

Bowers, M.A. (1993) Influence of herbivorous mammals on an old-field plant community: years 1–4 after disturbance. *Oikos*, **67**, 129–141.

Burnham, K.P. & Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research*, **33**, 261–304.

Carvell, C. (2002) Habitat use and conservation of bumblebees (*Bombus spp.*) under different grassland management regimes. *Biological Conservation*, **103**, 33–49.

Collins, S.L., Glenn, S.M. & Gibson, D.J. (1995) Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. *Ecology*, **76**, 486–492.

Conell, J.H. (1978) Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a non-equilibrium state. *Science*, **199**, 1302–1310.

Dahlin, K.M., Asner, G.P. & Field, C.B. (2014) Linking vegetation patterns to environmental gradients and human impacts in a mediterranean-type island ecosystem. *Landscape Ecology*, **29**, 1571–1585.

Díaz Lifante, Z. (1996) Reproductive biology of *Asphodelus aestivus* (Asphodelaceae). *Plant Systematics and Evolution*, **200**, 177–191.

Fox, J.W. (2013) The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology and Evolution*, **28**, 86–92.

Franzén, M. & Nilsson, S.G. (2008) How can we preserve and restore species richness of pollinating insects on agricultural land? *Ecography*, **31**, 698–708.

Gess, F.W. & Gess, S.K. (1993) Effects of increasing land utilization on species representation and diversity of aculeate wasps and bees in the semi-arid areas of Southern Africa. *Hymenoptera and Biodiversity* (ed. by J. Laselle and I. D. Gauld), pp. 83–113. CAB International, Wallingford, Connecticut.

Gómez, J.M. (2003) Herbivory reduces the strength of pollinator-mediated selection in the Mediterranean herb *Erysimum mediohispanicum*: consequences for plant specialization. *American Naturalist*, **162**, 242–256.

Goncalves, P., Alcobia, S., Simoes, L. & Santos-Reis, M. (2012) Effects of management options on mammal richness in a Mediterranean agro-silvo-pastoral system. *Agroforestry Systems*, **85**, 383–395.

Goulson, D. (2003) *Bumblebees Their behaviour and Ecology*. Oxford University Press, Oxford, U.K, New York, New York.

Grime, J.P. (1973) Competitive exclusion herbaceous vegetation. *Nature*, **242**, 344–347.

Hajar, A.S.M. (1993) A comparative ecological study on the vegetation of the protected and grazed parts of Hema Sabihah, in Al-Baha region, south western Saudi Arabia. *The Arab Gulf Journal of Scientific Research*, **11**, 259–280.

Hatfield, R.G. & LeBuhn, G. (2007) Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera, Apidae), in montane meadows. *Biological Conservation*, **139**, 150–158.

Hegland, S.J., Rydgren, K. & Seldal, T. (2005) The response of *Vaccinium myrtillus* to variations in grazing intensity in a Scandinavian pine forest on the island of Svanøy. *Canadian Journal of Botany*, **83**, 1638–1644.

Hegland, S.J., Lilleeng, M.S. & Moe, S.R. (2013) Old-growth forest floor richness increases with red deer herbivory intensity. *Forest Ecology and Management*, **310**, 267–274.

Herrera, C.M. (2000) Measuring the effects of pollinators and herbivores: evidence for non-additivity in a perennial herb. *Ecology*, **81**, 2170–2176.

Hoiss, B., Gaviria, J., Leingärtner, A., Krauss, J. & Steffan-Dewenter, I. (2013) Combined effects of climate and management on plant diversity and pollination type in alpine grasslands. *Diversity and Distributions*, **19**, 386–395.

Hurvich, C.M. & Tsai, C.L. (1989) Regression and time series model selection in small samples. *Biometrika*, **76**, 297–307.

Huston, M.A. (2014) Disturbance, productivity, and species diversity: empiricism vs. logic in ecological theory. *Ecology*, **95**, 2382–2396.

Jerrentrup, J.S., Wrage-Moennig, N., Roever, K.-U. & Isselstein, J. (2014) Grazing intensity affects insect diversity via sward structure and heterogeneity in a long-term experiment. *Journal of Applied Ecology*, **51**, 968–977.

Kaltsas, D., Trichas, A., Kougioumoutzis, K. & Chatzaki, M. (2013) Ground beetles respond to grazing at assemblage level, rather than species-specifically: the case of Cretan shrublands. *Journal of Insect Conservation*, **17**, 681–697.

Kati, V., Zografou, K., Tzirkalli, E., Chitos, T. & Willemse, L. (2012) Butterfly and grasshopper diversity patterns in humid Mediterranean grasslands: the roles of disturbance and environmental factors. *Journal of Insect Conservation*, **16**, 807–818.

Kearns, C.A. & Olivera, D.M. (2009) Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. *Journal of Insect Conservation*, **13**, 655–665.

Kershaw, H.M. & Mallik, A.U. (2013) Predicting plant diversity response to disturbance: applicability of the Intermediate Disturbance Hypothesis. *Critical Reviews in Plant Sciences*, **32**, 383–395.

Kimoto, C., DeBano, S.J., Thorp, R.W., Taylor, R.V., Schmalz, H., DelCurto, T. *et al.* (2012) Short-term responses of native bees to livestock and implications for managing ecosystem services in grasslands. *Ecosphere*, **3**, 1–15.

Kizos, T., Dalaka, A. & Petanidou, T. (2010) Farmers' attitudes and landscape change: evidence from the abandonment of terraced cultivations on Lesvos, Greece. *Agriculture and Human Values*, **27**, 199–212.

Klein, A.M., Vaissière, B., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. *et al.* (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London B*, **274**, 303–313.

Koniak, G. & Noy-Meir, I. (2009) A hierarchical, multi-scale, management-responsive model of Mediterranean vegetation dynamics. *Ecological Modelling*, **220**, 1148–1158.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R. *et al.* (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, **10**, 299–314.

Kruess, A. & Tscharntke, T. (2002a) Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation*, **106**, 293–302.

Kruess, A. & Tscharntke, T. (2002b) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology*, **16**, 1570–1580.

Larson, B.M.H. & Barrett, S.C.H. (2000) A comparative analysis of pollen limitation in flowering plants. *Biological Journal of the Linnean Society*, **69**, 503–520.

Le Houerou, H.N. (1981) Impact of man and his animals on Mediterranean vegetation. *Ecosystems of the World 11. Mediterranean-Type Shrublands* (ed. by F. di Castri, D. W. Goodall and R. L. Specht), pp. 479–521. Elsevier, Amsterdam, Netherlands.

Mackey, R.L. & Currie, D.J. (2000) A re-examination of the expected effects of disturbance on diversity. *Oikos*, **88**, 483–493.

Mackey, R.L. & Currie, D.J. (2001) The diversity-disturbance relationship: is it generally strong and peaked?. *Ecology*, **82**, 3479–3492. DOI:10.1890/0012-9658.

Malavasi, R., Battisti, C. & Carpaneto, G.M. (2009) Seasonal bird assemblages in a Mediterranean Patchy wetland: corroborating the Intermediate Disturbance Hypothesis. *Polish Journal of Ecology*, **57**, 171–179.

Marathianou, M., Kosmas, C., Gerontidis, S. & Detsis, V. (2000) Land-use evolution and degradation in Lesvos (Greece): a historical approach. *Land Degradation and Development*, **11**, 63–73.

Mayer, C. (2004) Pollination services under different grazing intensities. *International Journal of Tropical Insect Science*, **24**, 95–103.

Mayer, C., Soka, G. & Picker, M. (2006) The importance of monkey beetle (Scarabaeidae: Hopliini) pollination for Aizoaceae and Asteraceae in grazed and ungrazed areas at Paulshoek, Succulent Karoo, South Africa. *Journal of Insect Conservation*, **10**, 323–333.

Michener, C.D. (1979) Biogeography of the bees. *Annals of the Missouri Botanical Garden*, **66**, 277–347.

Minckley, R.L. (2014) Maintenance of richness despite reduced abundance of desert bees (Hymenoptera: Apiformes) to persistent grazing. *Insect Conservation and Diversity*, **7**, 263–273.

Morandin, L.A., Winston, M.L., Abbott, V.A. & Franklin, M.T. (2007) Can pastureland increase wild bee abundance in agriculturally intense areas? *Basic and Applied Ecology*, **8**, 117–124.

Murray, T.E., Fitzpatrick, U., Byrne, A., Fealy, R., Brown, M.J.F. & Paxton, R.J. (2012) Local-scale factors structure wild bee communities in protected areas. *Journal of Applied Ecology*, **49**, 998–1008.

Navarro, T., Alados, C.L. & Cabezudo, B. (2006) Changes in plant functional types in response to goat and sheep grazing in two semi-arid shrublands of SE Spain. *Journal of Arid Environments*, **64**, 298–322.

Naveh, Z. & Whittaker, R.H. (1979) Structural and floristic diversity of shrublands and woodlands on northern Israel and other Mediterranean areas. *Vegetation*, **41**, 171–190.

Ne'eman, G., Dafni, A. & Potts, S.G. (2000) The effect of fire on flower visitation rate and fruit set in four core-species in east Mediterranean scrubland. *Plant Ecology*, **146**, 97–104.

Nielsen, A., Steffan-Dewenter, I., Westphal, C., Messinger, O., Potts, S., Roberts, S. *et al.* (2011) Assessing bee species richness in two Mediterranean communities: importance of habitat type and sampling techniques. *Ecological Research*, **26**, 969–983.

Noy-Meir, I. (1990) Responses of two semiarid rangeland communities to protection from grazing. *Israel Journal of Botany*, **39**, 431–442.

Pantis, J. & Margaris, N.S. (1988) Can systems dominated by asphodels be considered as semi-deserts? *International Journal of Biometeorology*, **32**, 87–91.

Petanidou, T. (1991) *Pollination ecology in a phryganic ecosystem*. PhD thesis (in Greek, with English summary), Aristotelian University, Thessaloniki. [WWW document]. URL http://www.didaktorika.gr/eadd/handle/10442/10184 [accessed on 10 March 2016].

Petanidou, T. & Ellis, W.N. (1993) Pollinating fauna of a phryganic ecosystem: composition and diversity. *Biodiversity Letters*, **1**, 9–22.

Petanidou, T. & Ellis, W.N. (1996) Interdependence of native bee faunas and floras in changing Mediterranean communities. *The Conservation of Bees* (ed. by A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich and I. H. Williams), pp. 201–226. Academic press, London, U.K.

Petanidou, T. & Lamborn, E. (2005) A land for flowers and bees: studying pollination ecology in Mediterranean communities. *Plant Biosystems*, **139**, 279–294.

Petanidou, T., Ellis, W.N., Margaris, N.S. & Vokou, D. (1995) Constraints on flowering phenology in a phryganic (East Mediterranean) ecosystem. *American Journal of Botany*, **82**, 607–620.

Petanidou, T., Kizos, T. & Soulakellis, N. (2008) Socioeconomic dimensions of the agricultural landscape change in the Mediterranean: the case of the abandonment of cultivation terraces on Nisyros island, Greece. *Environmental Management*, **41**, 250–266.

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G. & Willmer, P. (2003) Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology*, **84**, 2628–2642.

Potts, S.G., Petanidou, T., Roberts, S., O'Toole, C., Hulbert, A. & Willmer, P.G. (2006) Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. *Biological Conservation*, **129**, 519–529.

Potts, S.G., Woodcock, B.A., Roberts, S.P.M., Tscheulin, T., Pilgrim, E.S., Brown, V.K. *et al.* (2009) Enhancing pollinator diversity in intensive grasslands. *Journal of Applied Ecology*, **46**, 369–379.

Preston, K.L., Redak, R.A., Allen, M.F. & Rotenberry, J.T. (2012) Changing distribution patterns of an endangered butterfly: linking local extinction patterns and variable habitat relationships. *Biological Conservation*, **152**, 280–290.

Pykälä, J. (2004) Cattle grazing increases plant species richness of most species trait groups in mesic semi-natural grasslands. *Plant Ecology*, **175**, 217–226.

Quinn, G.P. & Keough, M.J. (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, U.K.

R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN: 3-900051-07-0 [WWW document]. URL http://www.Rproject. Org.

Roulston, T.H. & Goodell, K. (2011) The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology*, **56**, 293–312.

Scohier, A. & Dumont, B. (2012) How do sheep affect plant communities and arthropod populations in temperate grasslands. *Animal*, **6**, 1129–1138.

Sheil, D. & Burslem, D.F.R.P. (2013) Defining and defending Connell´s intermediate disturbance hypothesis: a response to Fox. *Trends in Ecology and Evolution*, **28**, 571–572.

Sjödin, N.E. (2007) Pollinator behavioural responses to grazing intensity. *Biodiversity and Conservation*, **16**, 2103–2121.

Sjödin, N.E., Bengtsson, J. & Ekbom, B. (2008) The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *Journal of Applied Ecology*, **45**, 763–772.

Stohlgren, T.J., Schell, L.D. & Vanden Heuvel, B. (1999) How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain Grasslands. *Ecological Applications*, **9**, 45–64.

Svensson, J.R., Lindegarth, M., Jonsson, P.R. & Pavia, H. (2012) Disturbance-diversity models: what do they really predict and how are they tested? *Proceedings of the Royal Society of London B*, **279**, 2163–2170.

Terzo, M. & Rasmont, P. (2003) *Xylocopa cantabrita* Lepeletier en France (Hymenoptera, Apoidea). *Bulletin de la Société Entomologique de France*, **108**, 441–445.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecology Letters*, **8**, 857–874.

Vanbergen, A.J., Woodcock, B.A., Gray, A., Grant, F., Telford, A., Lambdon, P. *et al.* (2014) Grazing alters insect visitation networks and plant mating systems. *Functional Ecology*, **28**, 178–189.

Vazquez, D.P. & Simberloff, D. (2004) Indirect effects of an introduced ungulate on pollination and plant reproduction. *Ecological Monographs*, **74**, 281–308.

Vulliamy, B., Potts, S.G. & Wilmer, P.G. (2006) The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. *Oikos*, **114**, 529–543.

Wallis De Vries, M.F., Parkinson, A.E., Dulphy, J.P., Sayer, M. & Diana, E. (2007) Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 4. Effects on animal diversity. *Grass and Forage Science*, **62**, 185–197.

Westphal, C., Bommarco, R., Carre, G., Lamborn, E., Morison, N., Petanidou, T. *et al.* (2008) Measuring bee biodiversity in different European habitats and biogeographical regions. *Ecological Monogaphs*, **78**, 653–671.

Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G. & Aizen, M.A. (2009) A Meta-analysis of bees' response to anthropogenic disturbance. *Ecology*, **90**, 2068–2076.

Xie, Z., Williams, P.H. & Tang, Y. (2008) The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. *Journal of Insect Conservation*, **12**, 695–703.

Yoshihara, Y., Chimeddorj, B., Buuveibaatar, B., Lhagvasuren, B. & Takatsuki, S. (2008) Effects of livestock grazing on pollination on a steppe in eastern Mongolia. *Biological Conservation*, **141**, 2376–2386.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, New York.

Accepted 27 January 2016
First published online 24 March 2016
Associate Editor: Chris Hassall