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RESEARCH ARTICLE

Overabundant populations of large wild herbivores disrupt plant–pollinator networks in a Mediterranean ecosystem

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Keywords

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ABSTRACT

- Large herbivores are keystone species, so changes in their population abundance can have cascading effects on ecosystems. Over the last decades, many species of deer (Cervidae) have experienced unprecedented densities across many areas of the Northern Hemisphere, potentially leading to simplification of plant–pollinator communities, disruption of their interactions, and destabilization of ecological networks. Our study explores the impacts of increasing red deer (*Cervus elaphus*) densities on plant–pollinator networks.
- We describe, to our knowledge, the first large wild herbivore manipulative experiment with increasing densities, consisting of comparable hectare-scale enclosures in a Mediterranean ecosystem. We simulated two current scenarios of deer overabundance: high densities (>30 individuals km^{-2}) and hyper densities (>90 individuals km^{-2}). We compared these scenarios to an adjacent control exclosure (no deer).
- Deer herbivory reduced flower abundance of shrubs, as well as flowering plant and pollinator richness. Remaining plants and pollinators lost interactions, and some plants lost pollinator visitors. Network specialization and modularity decreased because modules (groups of strongly connected species) formed by herbs and specialist pollinators were gradually extirpated as deer density increased. This simplification increased network connectance and nestedness. Network robustness (a measure of stability) remained unaltered because the dominant plant, which attracted most pollinators, was unpalatable to deer.
- We conclude that, in overabundant deer scenarios: (1) impacts on plant–pollinator networks will increase with increasing deer density; (2) plant–pollinator networks will be eroded, especially if composed of palatable, rare plants, visited by specialist pollinators; but (3) plant–pollinator network stability will not be affected if dominant plants are generalists and unpalatable.

INTRODUCTION

Large herbivores are key components of most terrestrial ecosystems, influencing several functions and associated services. In particular, large wild herbivores modulate important ecosystem properties and processes, such as habitat structure, plant diversity, nutrient cycling, or wildfire regimes (Huntly 1991; Velamazán *et al*. 2020). However, the magnitude and direction of the effects of large herbivores on ecosystems strongly depend on their density (e.g. Gill 1992). This aspect is of utmost importance, as populations of large wild herbivores, particularly deer (Cervidae), have increased across Europe and North America over recent decades (Côté *et al*. 2004; Carpio *et al*. 2021). In this context, environmental benefits from moderate grazing (Jerrentrup *et al*. 2014) can be truncated in scenarios of high abundance, leading to multiple negative effects on ecosystems (Mysterud 2006).

Red deer (*Cervus elaphus* Linnaeus, 1758) and elk (*Cervus canadensis* Erxleben, 1777) are paradigmatic examples of unprecedented increases in density, mostly as a consequence of rural and traditional livestock abandonment, increase in commercial and intensive hunting management, and parallel expansion of protected land where hunting is either limited to deer culling or is prohibited (Côté *et al*. 2004; Bradford & Hobbs 2008; Carpio *et al*. 2021). Thus, at a regional scale, overabundant deer populations can be found in natural and protected areas (Bradford & Hobbs 2008; Apollonio *et al*. 2010; Borkowski *et al*. 2019) as well as in hunting reserves (Azorit *et al*. 2012a). Increasing deer densities may negatively affect plant communities (Borkowski *et al*. 2019). Importantly, these direct negative effects can result in indirect, cascading effects on other components of the food web (Bressette *et al.* 2012). Ultimately, whole networks of interacting species, including plant–pollinator networks, may be affected.

Large herbivores forage selectively to meet dietary requirements (Azorit *et al.* 2012b). In plant communities dominated by flowering species, foraging preferences can lead to non-random changes in the flowering landscape and will be more pronounced as deer density increases (Sjödin *et al.* 2008); therefore, pollinator communities might also be affected (Kruess & Tscharntke 2002; Lázaro *et al.* 2016a). Specific responses of pollinators strongly depend on effects on specific floral resources (Mayer *et al.* 2006). Plants affected by intense herbivory might become less attractive to pollinators and ultimately receive fewer visits from fewer pollinator species (Strauss 1997; Gómez *et al.* 2009). In that situation, secondary extinctions of pollinators are expected unless they can redistribute their interactions (Biella *et al.* 2019). In impoverished communities, plant–pollinator interactions are expected to weaken (Vázquez & Simberloff 2003), which could subsequently alter pollen transfer and ultimately affect the reproductive success of flowering plants (Vázquez & Simberloff 2004).

The set of co-occurring plant and pollinator species, together with the interactions they establish, form an ecological network. Plant–pollinator networks are mutualistic systems that are clearly generalized, that is, species tend to interact with several other species (Waser *et al.* 1996). The organization of the interactions, or network topology, has several invariant structural properties. On the one hand, plant–pollinator networks are nested, because specialist species interact with a subset of the species interacting with generalists. On the other hand, plant–pollinator networks are modular, as there are groups (modules) of strongly interacting species (Vázquez *et al.* 2009a). Nestedness can emerge from neutral processes, whereas modularity may reflect ecological and evolutionary constraints (Vázquez *et al.* 2009b; Dormann *et al.* 2017). Together, diversity of species and interactions, generalization, and topology are related to the stability of these systems (Okuyama & Holland 2008; Thébault & Fontaine 2010; Tylianakis *et al.* 2010; Grilli *et al.* 2016). In plant–pollinator networks, system stability is normally measured as robustness against local extinction of species, which can lead to secondary extinctions of interacting partners (Memmott *et al.* 2004; Kaiser-Bunbury *et al.* 2010).

The few studies exploring the influence of large herbivores on plant–pollinator networks have produced contrasting results. On the one hand, large herbivores can reduce floral resources and therefore pollinator abundance and diversity, reducing visitation to plants and interaction diversity, as well as network generalization, modularity, and stability (Guy *et al.* 2021; Rakosy *et al.* 2022). On the other hand, if large herbivores preferentially feed on grasses or in closed habitats such as forests, they can increase floral resources, reversing the former patterns, but with contrasting effects on network nestedness and therefore on stability (Vanbergen *et al.* 2014; Welti & Joern 2018). In contrast, when large herbivores avoid dominant flowering plants, plant–pollinator networks are generally unaffected (Oleques *et al.* 2019). These diverse results arise from variations in the study systems, such as different habitats with different herbivores and plant communities leading to unique cascading effects on networks (Robinson *et al.* 2018; Goulnik *et al.* 2021). Generally, positive effects on plant–pollinator networks are expected at intermediate large herbivore densities (Lázaro *et al.* 2016b). Most of the above studies examined effects of domestic livestock, but no research has examined the impact of large wild herbivores on plant–pollinator networks in comparable ecological settings with similar ecological conditions and known ungulate densities.

In this study, we explore the effects of increasing red deer densities on plant–pollinator communities, interactions, and networks (Fig. A1). We conducted an unprecedented field experiment in a Mediterranean ecosystem in which we experimentally manipulated red deer densities in adjacent comparable hectare-scale enclosures to simulate two current scenarios of increasing deer abundance. We hypothesize that (1) browsing intensity will be proportional to red deer density and will differ across plant species depending on deer preferences; consequently, (2) flowering plants and, in turn, (3) pollinator communities will be simplified. As a result, at increasing red deer densities, (4) pollinators will 'rewire' their interactions, and plants will receive fewer visits and fewer visitors; and (5) networks will be less complex, less structured, and less robust (Fig. A1).

MATERIAL AND METHODS

Study area

The study was performed in the Valdeyernos valley, at ca. 950 m a.s.l., within the public estate of Los Quintos de Mora, in Montes de Toledo rangeland, south-central Iberia (Toledo province, Spain, 4°5′57.38″W, 39°26′48.57″N) (Fig. A2). The climate is Continental Mediterranean, with mean annual rainfall of ~600 mm and mean annual temperature of ~14°C. Vegetation consists of a mosaic of small woodlands dominated by oak trees (*Quercus ilex* subsp. *ballota* (Desf.) Samp., 1919 and *Q. pyrenaica* Willd., 1805) and large scrubland patches dominated by *Cistus ladanifer* L., 1753, *Rosmarinus officinalis* L., 1753 and *Erica* spp. L., 1753 (San Miguel *et al.* 2011).

Red deer have been recorded in the Iberian Peninsula since the Upper Pleistocene and never disappeared from Los Quintos de Mora (San Miguel *et al.* 2011). Valdeyernos valley (~200 ha) was fenced in 2011 and had a density of ~10 deer km^{-2}, considered the sustainable natural deer density for these areas (*e.g.* Morales-Molino *et al.* 2019). The presence of other large herbivores in the study area is anecdotal.

Experimental setup and red deer introduction

We installed an enclosure encompassing ~17 ha, which was divided into three sub-enclosures (7.4, 7.1, and 2.6 ha) separated by 2-m high wire fences (Fig. A2). All enclosures had similar environmental features and contained a similar proportion of the vegetation types (oak forests and scrublands). Analyses of vegetation surveys from May 2020 (before the experiment) showed that both floristic composition and cover of plant communities were similar among enclosures (Cuerdo et al., 2025). Fences were established in October–November 2020. We experimentally manipulated red deer densities in the 7.4 and 7.1 ha enclosures by introducing young female individuals (yearlings) on 16 March 2021. Herbivory and pollinator-associated processes can be studied at the hectare scale, provided herbivore density is realistic (Pringle *et al.* 2023), and according to pollinator foraging distances (e.g. Gathmann & Tscharntke 2002), making the size of all the enclosures suitable for these processes to manifest without any potential limitations or biases.

We recreated three scenarios of contrasting herbivory, one per enclosure (hereafter treatments), namely: high density (7 young female deer, 95 deer km^{-2}, equivalent to 63 deer km^{-2} of a standard population with 1/1 sex ratio of all ages; Peláez *et al.* 2017), and hyper density (12 young female deer, 169 deer km^{-2}, equivalent to 113 deer km^{-2} of a standard population) (Fig. A2), and control (no deer). The control treatment recreates a management scenario commonly used to preserve vegetation in protected areas. The high-density treatment mimics the situation in many natural areas in Iberia (>30 deer km^{-2}; Vicente *et al.* 2007; Perea *et al.* 2014), Central Europe (Borkowski *et al.* 2019) and areas of North America where red deer have been introduced (Charro *et al.* 2018). The hyper density treatment simulates a typical commercial and intensively managed game estate in Central and Southern Iberia (>90 deer m^{-2}; Acevedo *et al.* 2008; Azorit *et al.* 2012a).

Experimental design, herbivory, and pollinator surveys

The magnitude of the experiment prevented us from generating spatial replicates. We therefore included spatio-temporal variability as follows: (1) we set several transects per treatment and sampled patchily distributed plant species; and (2) we surveyed each treatment on different days. We generated three independent observations (replicates) per each of the three treatments, each replicate being pooled data from transects and patchily distributed plants on a sampling day (9 sampling days in total).

In each treatment we established three main transects 50-m long and 2-m wide, located within the scrubland (N–S direction; Fig. A2). The set of transects encompass all the floral variability present in each treatment (including both abundant and rare species) and maximizes independence between treatments and the surrounding area by being situated in the center of each enclosure. Independence is enhanced by the presence of unfavourable habitats for pollinators (e.g., forests) between treatments, which, combined with their limited foraging range (a few hundred meters; see Gathmann & Tscharntke 2002), reduces the likelihood of pollinator movement between treatments. Main floral resources in the study period included *Cistus ladanifer* (dominant species according to woody plant species coverage and flower surveys, Table A1), *Cistus populifolius* L., 1753 (Cistaceae), and *Thymus mastichina* L., 1763 (Lamiaceae) (subdominant species, Table A1). *C. ladanifer* presented a dense, continuous distribution in the scrubland, and dominated vegetation of the transects. In contrast, *C. populifolius* and *T. mastichina* exhibited patchy distribution with scattered individuals, therefore we selected both patches and scattered individuals in comparable sampled areas for each treatment. These three species (including all individuals) will hereafter be referred to as focal plants. Because of the process studied, deer, plants, and pollinators of the transects of each treatment make up a single community: deer move throughout each enclosure, potentially affecting all the plants; and pollinators potentially visit all the plants within the enclosure. Because of the heterogeneous distribution of flowers, we were unable to establish independent and comparable blocks. Therefore, for each survey, we pooled data from the three transects together with species that were patchily distributed.

We surveyed at the flowering peak of *C. ladanifer*, which lasts for about 14 days, from 17 to 26 May 2021: 1 survey day^{-1} over 9 days. The number of surveys and therefore the number of replicates per treatment was limited by the number of researchers with expertise in pollinator surveys and the number of potential sampling days during the flowering peak. We sampled each treatment on three non-consecutive days (3-day span from one survey to another), nine surveys in total. Sampling was carried out between 09:00 and 15:00 h and under optimal and consistent weather conditions for pollinator activity. This period coincides with the life cycle of *Cistus* spp. flowers, the dominant plants in the community, and therefore with activity pattern of most pollinators. One-day surveys are useful to survey several plots under similar phenological conditions (Reverté *et al.* 2019). Because *Cistus* spp. flower lifespan is 1 day (e.g. Talavera *et al.* 1993), flower resampling among surveys from the same treatment was minimal. In addition, flower communities from the same treatment differed similarly from one day to another, with ~75% variation in the abundance of the dominant flowering plant. As such, pollinator communities (which are characterized through plant–pollinator interactions) varied with time (sampling day, $F = 6.04$, $P = 0.01$), with consistent variation among treatments (sampling day × treatment, $F = 1.96$, $P = 0.1$; Fig. A3).

Hence, despite sampling limitations due to the experimental setting, studied organisms, and flower phenology, our experimental design maximizes the number and independence of the three replicates from the same treatment, as they are physically and temporarily disconnected, and are truly and consistently different in time.

In the first survey of each treatment, deer herbivory on all focal plant species was evaluated. At least 10 individuals of each focal plant, evenly distributed along each transect, were selected, and degree of browsing of each individual (30 in total, range 11–71 depending on number of individuals present) was measured following Perea *et al.* (2015), with a semiquantitative measure of herbivory that ranges from 0 (no browsing evidence) to 5 (maximum browsing intensity).

In each survey we quantified number of flowers of all plant species along the transects and populations of *C. populifolius* and *T. mastichina*. In *T. mastichina*, for individuals with hundreds of flowers, we extrapolated total number of flowers, counting the flowers in 10 inflorescences and the total number of inflorescences. Pollinator surveys consisted of plant–pollinator censuses conducted by an expert. In each survey we conducted several rounds (4–6 rounds) of varying time (0.5–1.5 h), depending on flower abundance and pollinator activity. Sampling effort was similar in all surveys (~6 h), and sampling coverage was >95% (see Data analysis below). In each round we walked along a transect and visited populations of subdominant plants, recording abundance and identity of all pollinators visiting the flowers of each plant. We define pollinators as floral visitors contacting the reproductive organs of the flowers. Each transect was visited once or twice, and each population of subdominant plants visited two to three times. To record an adequate number of interactions in each plant (i.e., record all their pollinators), rare plant species (those with relatively few flowers) or those receiving few interactions were surveyed more frequently, that is, their individuals or patches of individuals were sampled more than once in each round. Pollinators were identified *a visum* to the lowest taxonomic rank possible, generally to genus + morphospecies (e.g., bees) or to species (e.g., ants). Difficult groups, such as most flies and wasps, were generally identified to family + morphospecies. Some specimens were captured for later identification in the laboratory. The names of pollinators can be found in the pollinator community database (see Data availability statement).

We standardized the information from pollinator surveys and calculated pollinator abundance based on visitation rates and interaction frequencies. The visitation rate was calculated as the number of pollinators recorded on a plant species divided by the number of flowers surveyed for that plant. Interaction frequency was calculated as the visitation rate of each pollinator to a plant species multiplied by the number of flowers of that plant. The abundance of a pollinator is the sum of all the interaction frequencies in which it is involved.

Data analysis

Unless otherwise indicated, for comparisons we used ANOVA followed by post hoc Tukey's tests or Kruskal-Wallis followed by post hoc Dunn's tests, depending on normality distribution. In all analyses, treatment was used as a fixed factor.

Herbivory

We compared browsing degree of focal plants between treatments using cumulative link models (CLMs), suitable for ordinal regression. These models are usually performed with categorical response variables, including herbivory (i.e., 0 to 5 rank; Perea *et al.* 2015). We used a model for each focal plant, with browsing damage as response variable, fitted using the Laplace approximation with a Probit link function.

Plant community

To compare plant communities among treatments we analysed overall flower abundance of the community as well as flower abundance of each focal plant. Because for *C. populifolius* and *T. mastichina* the number of individuals differed between treatments, we standardized the number of flowers by the number of individuals. We also calculated flower richness, diversity (Shannon index), and evenness (Hurlbert's PIE index), as well as plant composition. Composition was analysed with PERMANOVA, using the Bray–Curtis dissimilarity index on square-root transformed data, followed by pairwise comparisons and SIMPER analyses (to detect which species differed between treatments).

Pollinator community

To compare pollinator communities among treatments, we calculated the same variables and followed the same procedure as for plant communities. Richness was calculated as the asymptotic estimator through individual-based rarefaction-extrapolation curves following Chao & Chiu (2016). Sample coverage was >95% for all communities. We used this approach to standardize sampling effort and achieve comparable species estimates, as our communities are extremely diverse with a large proportion of rare species that are difficult to detect.

Plant–pollinator interactions

We built a plant–pollinator network with interaction frequency data from each plant–pollinator survey. These networks were built based on >7000 interactions between 13 plant and 158 pollinator species, comprising 327 distinct interactions.

To evaluate how plants and pollinators redistribute their interactions among treatments, we calculated interaction dissimilarity following Noreika *et al.* (2019). We used quantitative data from interaction frequencies and the Ruzicka index of dissimilarity. We calculated β_{OS} (the interaction dissimilarity considering the subset of shared species of two networks) between pairs of local networks within the same treatment and across treatments, as well as the proportion explained by rewiring (changes in foraging decisions and interaction frequency) and richness of interactions. We compared β_{OS} using beta regression models (link = logit). Model significance was assessed with Wald tests, and we calculated least-squares means for multiple comparisons between treatments.

For focal plants, we calculated visitation rate and generality for each network. Generality is the weighted mean number of pollinator species visiting a plant species. For pollinators, we calculated the generality of the whole trophic level.

Network structure

To compare plant–pollinator network structure among treatments, we calculated the following network metrics from each local network of each treatment, that is, the network resulting from each survey (3 local networks per treatment). For network complexity, we calculated metrics of diversity: network size (sum of interacting species of plants and pollinators), interaction richness (number of distinct plant–pollinator interactions), interaction diversity (Shannon diversity index of interactions), and interaction evenness (Shannon evenness index of interactions); generalization: network connectance (weighted quantitative proportion of realized interactions) and network specialization (H_2', which ranges from 0 in completely generalized networks to 1 for extremely specialized ones); and topology: network nestedness (*WNODF*, which ranges from 0 to 100 for perfectly nested quantitative interactions), network modularity (Q, which is proportional to the number and isolation of modules, and ranges from 0 to 1 for networks composed of perfect compartments) and number of network modules (nQ, groups of strongly connected species). For modularity, we used the algorithm of Becket (2016) re-run 100 times to stabilize modularity computation. As for network stability, we calculated network robustness against the local extinction of plants (with least abundant plants going extinct first, a reasonable pattern under a red deer overabundance scenario), measured as the area below the secondary extinction of pollinators curve produced after the extinction of plants. Robustness ranges from 0 to 1 for very stable networks where the extinction of plants has little consequence for pollinators. Further information on these variables and original references can be found in Dormann *et al.* (2022).

For each network, we assessed the significance of nestedness and modularity using null models, which generate 1000 random networks using algorithms from Vázquez *et al.* (2007), which randomize interactions according to species abundances, and Patefield (1981), which maintain species total interactions, and are therefore adequate to evaluate the nested and modular structure, respectively. The observed values were compared with the 95% confidence interval of the null distribution, and *z-scores* were used to evaluate whether the observed structure differed from a random organization, calculated as $z = \text{obs.} - \text{mean(null)}/\text{sd(null)}$. These values are usually referred to as relative nestedness and relative modularity, and indicate the degree of network order (structure *sensu stricto*) in relation to a random network.

Because all network metrics can be influenced to some extent by network size (Dormann *et al.* 2009), analyses were repeated including network size as a covariate. To visualize patterns in network structure we generated a bipartite and a modular meta-network for each treatment, built from the three local networks per treatment.

Software

All analyses were performed in R v. 4.2.3 (R Core Team 2023). We used the *ordinal* package (clm function) (Christensen 2022) for cumulative linear models (CLMs); *iNEXT* (Hsieh *et al.* 2022) for rarefaction curves; *vegan* (Oksanen 2022) for multivariate statistics; *betalink* (Bartomeus 2019) for interaction dissimilarity; *betareg* (Zeileis *et al.* 2022) for beta regression models; *emmeans* (Lenth 2023) for multiple comparisons; and *bipartite* (Dormann *et al.* 2022) for network analyses.

RESULTS

A summary of the main variables calculated in this study can be found in Table A2.

Herbivory

Cistus ladanifer was not affected by red deer density ($X^2_2 = 2.19$, $P = 0.33$; Fig. 1a). In contrast, *C. populifolius* ($X^2_2 = 84.4$, $P < 0.01$) and *T. mastichina* ($X^2_2 = 33.9$, $P < 0.01$) suffered from higher deer browsing in the Hyper density treatment (Fig. 1b,c).

Plant community

Deer density did not affect overall flower abundance of the community ($F_{2,6} = 2.4$, $P = 0.17$), but did affect flower abundance of some focal plants (Fig. 1d–f). While *C. ladanifer* was unaffected ($F_{2,6} = 0.07$, $P = 0.93$), *C. populifolius* had fewer flowers per individual in the High and Hyper density treatments compared to the Control treatment ($F_{2,6} = 13.89$, $P = 0.006$; Tukey's $P < 0.05$). Furthermore, *T. mastichina* had fewer flowers per individual in the Hyper density treatment compared to the Control and High density treatments ($F_{2,6} = 13.42$, $P = 0.006$; Tukey's $P < 0.05$) (Fig. 1d–f).

Deer density affected flower richness ($F_{2,6} = 6.16$, $P = 0.035$). The Hyper density treatment had 1.9-fold fewer flowering species than the Control treatment (7 ± 0 vs 13 ± 2, Tukey's $P = 0.03$). Deer density did not affect flower diversity ($X^2_2 = 3.82$, $P = 0.15$) nor flower evenness ($X^2_2 = 4.62$, $P = 0.1$). Deer density affected plant composition ($F_{2,6} = 5.99$, $P = 0.019$). The Hyper density treatment had a different plant composition compared to the Control ($F_{1,4} = 11.30$, $P < 0.05$) and High density ($F_{1,4} = 10.13$, $P < 0.05$) treatments.

In the Hyper density treatment, the herbs *Tuberaria guttata* (L.) Fourr., 1860 (Cistaceae) (vs Control and High density treatments), *Crepis* spp. L., 1753, and *Tolpis* spp. Adans. 1763 (Asteraceae) (vs Control treatment) were absent, and the shrub *Rosmarinus officinalis* (Lamiaceae) (vs Control treatment) was less abundant (SIMPER, contribution to similarity >5%, $P < 0.05$).

Pollinator community

Deer density did not affect overall pollinator abundance ($X^2_2 = 5.42$, $P = 0.07$); however, pollinator richness changed across treatments ($F_{2,6} = 5.45$, $P = 0.045$). High and Hyper density treatments had 1.3-fold fewer pollinator species than the Control treatment (75 ± 3 and 77 ± 37 vs 96 ± 3 pollinator species). Deer density affected pollinator diversity ($F_{2,6} = 6.56$, $P = 0.031$). The Hyper density treatment had 1.2-fold lower pollinator diversity than the Control and High density treatments (3.55 ± 0.14 vs 4.16 ± 0.21 and 4.32 ± 0.10 bits). Deer density did not affect pollinator evenness ($X^2_2 = 5.07$, $P = 0.08$). Deer density affected pollinator composition ($F_{2,6} = 2.20$, $P = 0.015$). The Hyper density treatment had a different pollinator composition compared to the Control ($F_{1,4} = 2.28$, $P < 0.05$) and High density ($F_{1,4} = 3.01$, $P < 0.05$) treatments. However, SIMPER analyses revealed no important changes in contribution to similarity of species between treatments.

Plant–pollinator interactions

Deer density did not affect interaction dissimilarity (β_{OS}) involving Control networks ($X^2_2 = 4.76$, $P = 0.093$). In contrast, deer density affected β_{OS} involving both High ($X^2_2 = 36.27$, $P < 0.001$) and Hyper density ($X^2_2 = 6.94$, $P = 0.031$) networks. In both cases, local networks of High and Hyper density treatments presented lower β_{OS} when compared to network pairs involving both treatments (High–High vs High–Hyper, $z = -5.11$, $P < 0.001$; Hyper–Hyper vs High–Hyper, $z = -2.13$, $P = 0.028$). The importance of interaction richness to rewiring for interaction dissimilarity increased as deer density increased (Fig. A4).

Deer density did not affect visitation rate of any focal plant ($F_{2,6} < 1.46$, $P > 0.30$) (Fig. A5a–c). Deer density did not affect generality of *C. ladanifer* and *C. populifolius* ($F_{2,6} < 4$, $P > 0.08$) (Fig. A5d,e), but affected generality of *T. mastichina* ($F_{2,6} = 11.22$, $P = 0.009$). *T. mastichina* had lower generality in the Hyper density treatment than in the Control treatment (Tukey's $P = 0.008$) (Fig. A5f). Pollinator generality was unaffected by deer density ($F_{2,6} = 1.14$, $P = 0.38$).

Network structure

Deer density did not affect network size, interaction richness, or interaction diversity (Table 1). However, deer density affected interaction evenness. The Hyper density treatment had lower interaction evenness than the High density treatment (Table 1). Similarly, the High density treatment had higher network connectance than the Control and the Hyper density treatments (Table 1). Finally, the Hyper density treatment had lower network specialization than the Control and the High

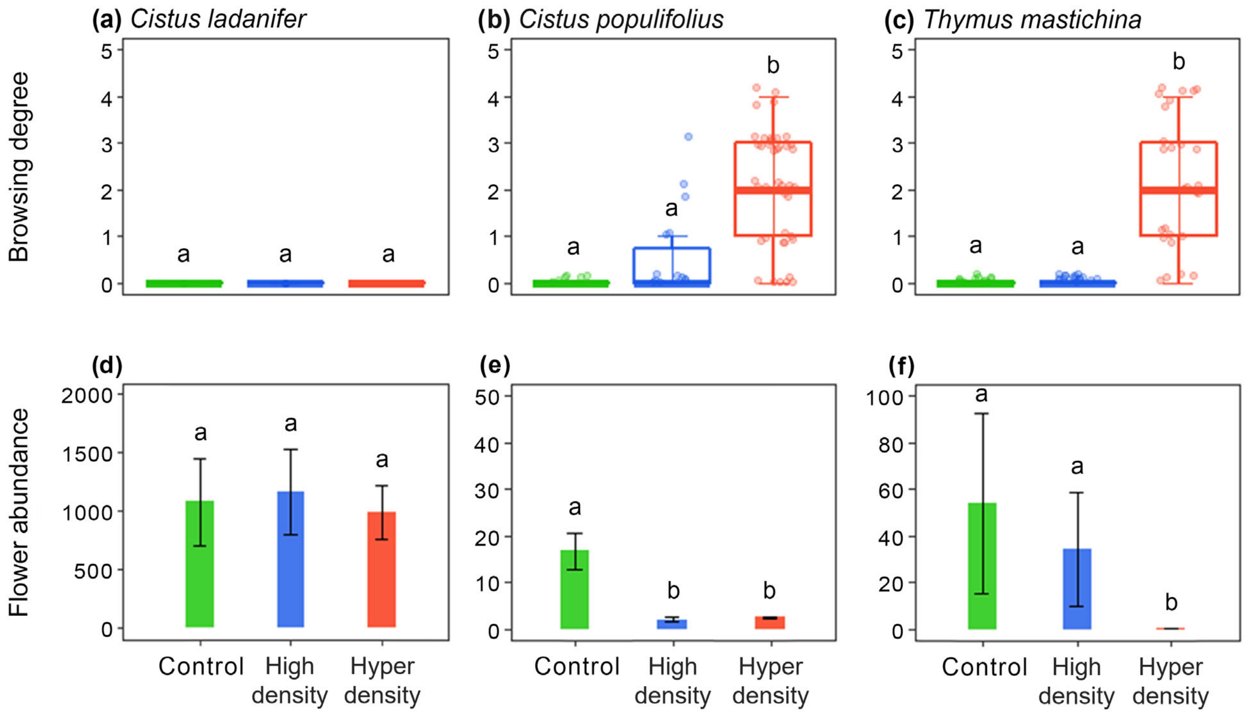

Fig. 1. Browsing degree (a–c) and flower abundance (number of flowers) (d–f) of each focal plant species in Control (green), High density (blue), and Hyper density (red) treatments. For *Cistus populifolius* and *Thymus mastichina*, number of flowers is standardized by number of individuals (see Material and Methods). Different letters above bars indicate significant ($P < 0.05$) differences between deer density treatments.

density treatments (Table 1). Most results were identical when network size was included as a covariate (Table 1). Bipartite meta-networks from each treatment are shown in Fig. 2.

All networks were significantly less nested and more modular than random (Table A3). The Hyper density treatment had the least structured networks as presented the lowest *z-scores* among networks (Table A3). The Hyper density treatment also had higher nestedness than Control and High density treatments and lower modularity than the Control treatment (Table 1). Hyper and High density treatments had lower numbers of modules than the Control treatment (Table 1). Most of these significant differences disappeared when network size was included as covariate (Table 1). Deer density did not affect network robustness (Table 1).

All treatments had a module characterized by frequent interactions between *C. ladanifer* and beetles (mainly *Heliotaurus* gr. *ruficollis* (Fabricius, 1781)), medium-sized flies (mostly Anthomyiidae), and ants (*Plagiolepis schmitzii*

Table 1. Measures of network structure in Control, High density (High), and Hyper density (Hyper) networks ($N = 3$ per treatment). Model 1, ANOVA (treatment as fixed factor); Model 2, ANCOVA (network size as covariate). Significant differences ($P < 0.05$) are in bold.

network metric	control mean ± SE	high density mean ± SE	hyper density mean ± SE	model 1 $F_{2,6}$	model 1 P	contrasts Tukey's $P < 0.05$	model 2 $F_{2,5}$	model 2 P	contrasts Tukey's $P < 0.05$
Network size	76.7 ± 5.9	63.3 ± 0.33	65 ± 4.16	2.94	0.13				
Interaction richness	115 ± 13.1	85.7 ± 8.17	91.7 ± 4.18	2.81	0.14		0.13	0.88	
Interaction diversity	3.4 ± 0.18	3.37 ± 0.14	2.97 ± 0.04	3.26	0.11		4.89	0.067	
Interaction evenness	0.72 ± 0.02	0.76 ± 0.02	0.66 ± 0.01	9.35	**0.014**	Hyper < High	13.71	**0.009**	Hyper < High
Connectance (weighted)	0.085 ± 0.001	0.12 ± 0.007	0.089 ± 0.002	6.49[a]	**0.039**	High > Control	14.21	**0.009**	High > Control, Hyper
Specialization (H_2')	0.55 ± 0.03	0.59 ± 0.03	0.29 ± 0.02	33.09	**< 0.001**	Hyper < Control, High	34	**0.001**	Hyper < Control, High
Nestedness (*WNODF*)	23.3 ± 1.6	23.7 ± 1.9	30.9 ± 0.45	8.76	**0.017**	Hyper > Control, High	9.05	**0.022**	Hyper > High
Modularity (Q)	0.34 ± 0.05	0.29 ± 0.05	0.16 ± 0.003	5.62	**0.042**	Hyper < Control	3.94	0.094	
Module number (nQ)	6 ± 0	4 ± 0	4 ± 0	8[a]	**0.018**	Hyper, High < Control	NA[b]	NA	NA
Robustness	0.73 ± 0.004	0.72 ± 0.02	0.67 ± 0.04	1.93	0.23		1.24	0.37	

[a] Kruskall Wallis–Dunn's tests.

[b] Same statistical pattern. Test not performed because variance is 0.

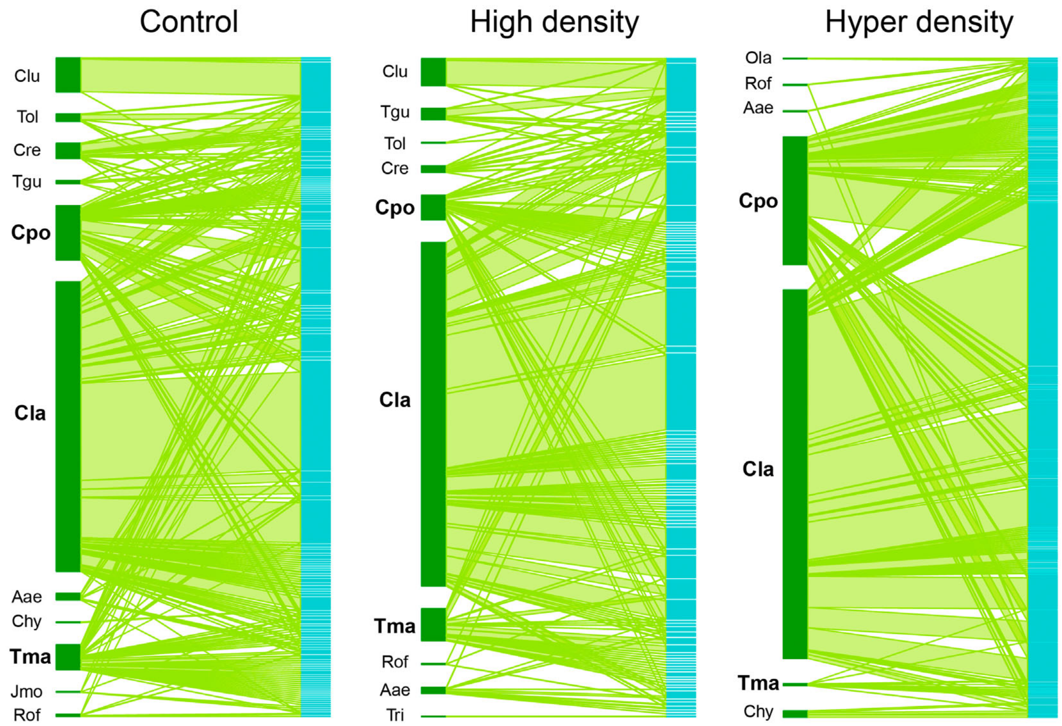

Fig. 2. Bipartite meta-network of Control, High density, and Hyper density treatments (*N* = 3 local networks per treatment). Plants are represented in dark green and pollinators in sky blue. Focal plants are indicated in bold (Clad, *Cistus ladanifer*; Cpop, *Cistus populifolius*; Tmas, *Thymus mastichina*). The remaining plant species are Clu, *Campanula lusitanica*, Tol, *Tolpis* spp., Cre, *Crepis* spp., Tgu, *Tuberaria guttata*, Aae, *Asphodelus aestivus*, Chy, *Cytinus hypocistis*, Jmo, *Jasione montana*, Rof, *Rosmarinus officinalis*, Tri, *Trifolium* spp., Ola, *Orobanche latisquama*. Link (pale green) thickness indicates the frequency of interactions between plants and pollinators.

Forel, 1895) among others (Fig. 3a). The Control treatment had two exclusive modules: one characterized by frequent interactions between *C. populifolius* and short-tongued small bees (*Lasioglossum* spp. Curtis, 1833) and ants (mainly *Iberoformica subrufa* (Roger, 1859)), and another formed of *T. mastichina* and nomad bees (*Nomada* spp. Scopoli, 1770) and tachinid flies (Tachinidae) (Fig. 3a). In the High density treatment these two modules merged (Fig. 3b). In the Hyper density treatment, the *T. mastichina* module weakened (interaction frequency decreased and the plant became trivial within the module; Fig. 3b). The Control treatment had two more exclusive modules characterized by frequent interactions between *Crepis* spp. and *Tolpis* spp. (Asteraceae) and the pollen specialist *Panurgus calcaratus* (Scopoli, 1763) (Andrenidae), and between *Campanula lusitanica* L. in Loefl, Iter. Hisp. 111 (1758) (Campanulaceae) and *Usia* spp. Latreille, 1802 (Bombyliidae) (Fig. 3a). In the High density treatment these modules weakened and merged whereas in the Hyper density treatment they disappeared (Fig. 3b).

DISCUSSION

In this study we evaluated the effect of increasing red deer densities on plant–pollinator networks. We found that grazing and browsing by red deer extirpated several herbs and reduced the number of flowers of abundant shrubs, leading to a decrease in pollinator richness. Remaining plants and pollinators lost interactions, and some plants lost pollinator visitors. Network specialization and modularity decreased because modules formed by herbs and specialist pollinators were gradually extirpated as red deer density increased. Paradoxically, this simplification may confer stability, because the disappearance of strong interactions involving specialist species increased network connectance and nestedness. Network robustness remained unaltered, because the dominant plant, which attracted most pollinators, was unpalatable to red deer.

Effects of red deer overabundance on plant–pollinator communities and interactions

Red deer overabundance affected shrubs through browsing, but only at the highest deer densities. This is in accordance with Gill (1992) and suggests a density threshold between High and Hyper density of deer (at ~60 deer km^{-2}) above which most plants are negatively affected by deer browsing. *Cistus ladanifer* remained unbrowsed, probably because it is unpalatable to deer (e.g. Perea *et al*. 2014) and is very abundant, which provides a low-quality abundant food source. However, the unpalatable and subdominant *T. mastichina* was affected by browsing. This might be especially likely in the Hyper density treatment, where the scarcity of palatable plants could result in browsing on unpalatable species (Borowski *et al*. 2021).

The abundance of flowers in shrubs was reduced proportionally to browsing. However, the plant community changed

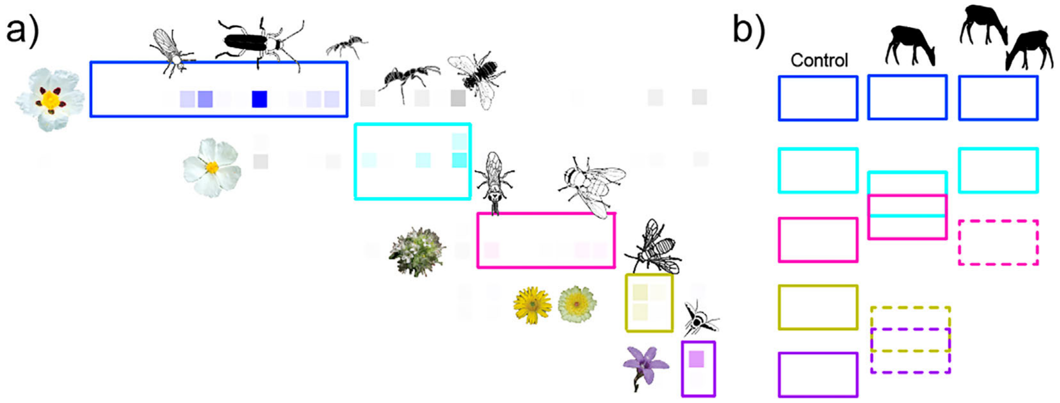

Fig. 3. (a) Modular meta-network of the Control treatment (N = 3 local networks). Each module is coloured differently, and colour intensity denotes interaction frequency. For clarity, we omitted several weak interactions and only the most connected plants (in rows) and pollinators (in columns) are represented, maintaining the relative size of modules. Icons represent frequent interactions between plants and pollinators. Blue module: *Cistus ladanifer*—Anthomyiidae, *Heliotaurus* gr. *ruficollis*, *Plagiolepis schmitzii*. Sky-blue module: *C. populifolius*—*Iberoformica subrufa*, *Lasioglossum* spp.; Pink module: *Thymus mastichina*—*Nomada* spp., Tachinidae; Yellow module: *Crepis* spp., *Tolpis* spp.—*Panurgus calcaratus*; Purple module: *Campanula lusitanica*—*Usia* spp. (b) Effects of High (one deer) and Hyper (two deer) density treatments on network modules. Overlapping modules: modules merged; dashed-lined module: module weakened; no module: module disappeared. See text for details.

mainly through the extirpation of several herbs at highest densities. This result can be explained by two complementary mechanisms. First, red deer avoided the dominant and unpalatable flowering species (*C. ladanifer*), so overall floral resources and the community structure were unaffected. Second, red deer foraged preferentially on herbaceous plants, and when herbs became rare or disappeared, they increasingly incorporated shrubs into their diet (Azorit *et al.* 2012b).

The simplification of plant communities resulted in a concomitant simplification of pollinator communities. As such, pollinator richness was reduced in the Hyper density treatment, but also in the High density treatment, where flower richness was unaffected. This situation is likely in a scenario where flower numbers are reduced due to herbivory, reducing floral display and therefore pollinator attraction (e.g. Thompson 2001). Indeed, the simplification of the pollinator community also involved a reduction in species diversity, probably because relatively abundant pollinator species found in relatively rare flowers declined.

Flower abundance is also a determinant for the realization of plant–pollinator interactions (Carstensen *et al.* 2014; CaraDonna *et al.* 2017), and therefore red deer herbivory may prevent pollinators from interacting with affected plants. At the community level, remaining plants and pollinators (shared species among treatments) interacted differently, and our results indicated that interactions were presumably lost at increasing deer densities. At the species level, the generality of *T. mastichina* was reduced. High browsing levels in the Hyper density treatment resulted in *T. mastichina* minimum presentation of floral display (few flowers per individual). In addition, the restricted pollination system of *T. mastichina* may constrain pollinator visitation to affected individuals (Stang *et al.* 2006). Because the diversity of pollinators is usually positively related to pollination function (e.g. Albrecht *et al.* 2012), this situation may negatively affect the reproductive success and therefore the long-term persistence of *T. mastichina* in the local community. However, and because *T. mastichina* flowers remained receptive for several days after the end of the censuses, we may have underestimated the interactions that this species receives.

Effects of red deer overabundance on plant–pollinator networks

The simplification of plant–pollinator communities and interactions resulted in profound changes in plant–pollinator networks. We argue that these changes are mediated by (1) the extirpation of interactions involving herbaceous plants; (2) gradual simplification of interactions involving subdominant plants (*C. populifolius* and *T. mastichina*); and (3) conservation of interactions involving the dominant plant (*C. ladanifer*).

Network modules formed by herbaceous plants and associated specialist pollinators were simplified in the High density treatment and extirpated in the Hyper density treatment, as grazing increased with increasing deer density. Similarly, the modules formed by the subdominant plants were maintained, but simplified proportional to level of deer browsing. As such, network specialization and modularity decreased in the Hyper density treatment. Consequently, the loss of unexpected interactions (those not driven by neutrality) may have caused an increase in nestedness. Nevertheless, the Hyper density treatment had the least structured networks (lower relative nestedness), probably as a result of missing expected interactions (Dormann *et al.* 2017). Because network size seems to explain some differences in network nestedness between deer density treatments, high network nestedness may be reached simply through partner constraints (Vázquez *et al.* 2007, 2009b). Therefore, the theoretical stability gained by higher network connectance and nestedness (Thébault & Fontaine 2010) might be a consequence of the simplification of the system. Modularity patterns also vanished when network size was considered, suggesting that the effect of deer density on modularity was mediated exclusively by the extirpation of plants and, most probably, the secondary extinction of related pollinators. Thus, the topology of networks may be resistant to red deer overabundance provided it is composed of unpalatable or relatively abundant flowering plants (Oleques *et al.* 2019). In contrast, networks may be vulnerable if composed of palatable, relatively rare flowering species which are visited by specialist pollinators (Rakosy *et al.* 2022).

Interactions involving *C. ladanifer*, the dominant plant, were unaffected. Thus, red deer density did not affect network robustness (system stability). Our measure of network robustness used an abundance-based extinction sequence that matches that of red deer preferences: (1) herbs, including rare species, with few interactions, (2) subdominant shrubs (*C. populifolius*, *T. mastichina*) with a substantial number of interactions, and (3) dominant shrub (*C. ladanifer*), unpalatable and with many interactions. Because the most connected plant is indeed the least prone to becoming extinct, it is not unexpected that the overall robustness of the network was not affected by red deer density. Both theoretical and experimental studies show that secondary extinctions increase with the loss of abundant and generalist species (Memmott *et al.* 2004; Bain *et al.* 2022). To date, studies analysing the effects of large herbivores on the robustness of plant–pollinator networks have found little support that large herbivores destabilize these systems (Welti & Joern 2018; Guy *et al.* 2021).

Implications for conservation

Our manipulative experiment recreated two scenarios of overabundant populations of large wild herbivores that will be more recurrent in protected and abandoned areas of the Northern Hemisphere. The impact of deer overabundance on plant–pollinator networks was evident in both examined scenarios, but the magnitude of the impact increased with increasing deer density. Nevertheless, network robustness was unaffected. In light of these results, we conclude that high and hyper deer densities (>30 deer km^{-2}) erode plant–pollinator networks. This disruption will strongly depend on local plant ecology: while the extirpation of palatable rare species that interact with specialist pollinators may drive simplification patterns, unpalatable, dominant species that are highly connected may confer stability to the system. We therefore recommend that managers apply measures such as habitat management, restoration of trophic interactions, or deer population control (see Black *et al.* 2011; DeBano *et al.* 2016) to maintain red deer at natural densities of about 10 individuals km^2, comparable to those present in structured Mediterranean ecosystems. In addition, the use of unpalatable, generalist plants in restoration practices may ensure to some extent the stability of plant–pollinator networks under possible scenarios of deer overabundance. The relationship between plant palatability and plant–pollinator network stability clearly deserves further attention through additional modelling efforts and more detailed long-term studies.

Limitations of the study

In a recent study, Pringle *et al.* (2023) reviewed the experimental approaches used by ecologists to study the impacts of large herbivores on terrestrial ecosystems. Exclosures are the most widely used approach but tend to be smaller than the scale at which ecosystem processes operate, with unknown species-specific effects and densities. To overcome these limitations, the authors propose the use of large plots combined with experimental manipulation of specific herbivores at known densities. This is exactly the approach adopted in the present study. However, the main limitation of this approach is the lack of spatial replicates (in comparisons of several small exclusion plots). In our study, we obtained a single independent community per plot (i.e. treatment). We tried to overcome this limitation by generating several temporal replicates from each plot, taking advantage of the high flower community variability during the study period. Similar experiments are needed in other regions and climates to allow generalizations on the impacts of large herbivore overabundance on ecosystems. In addition to multiple large-scale experiments, long-term studies are needed to evaluate ecosystem dynamics under these scenarios.

AUTHOR CONTRIBUTIONS

CH-C: methodology, investigation, formal analysis, writing—original draft, supervision; DNV: investigation, formal analysis, writing—original draft; JAC: methodology, investigation, writing—review and editing, supervision; ES: funding acquisition, conceptualization, writing—review and editing, supervision; RP: funding acquisition, conceptualization, formal analysis, writing – review and editing.

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.tqjq2bw67.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Supporting Information.

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