Isolation limits spring pollination in a UK fragmented landscape

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Abstract

Context

Animal-mediated pollination is a key factor that determines the reproductive success of the most flowering plants; this process however can be disrupted by environmental degradation, with habitat fragmentation highlighted as a key driver of pollinator declines. Despite habitat fragmentation being one of the most pervasive anthropogenic stressors worldwide, we still have rather limited empirical evidence on its effects on pollination, especially for early spring pollination syndromes.

Objectives

We experimentally study the effect of patch area and isolation on the pollination of English Bluebell (*Hyacinthoides non-scripta*), a species largely pollinated in spring by queen bumblebees.

Methods

In a fragmented landscape in Bristol, United Kingdom, we selected 51 woodland patches which vary in both size and distance from each other, and placed 153 bluebell plants in those selected patches for *c.*4 weeks to measure pollination.

Results

Measuring pollination through the number of seeds produced and seed capsules formed, we show that while patch area had no effect, the main determinate of overall reproductive success of plants was patch isolation which negatively correlated with both seed number and capsules.

Conclusion

Our results highlight the importance of connectivity in maintaining pollination services in fragmented landscapes.

Introduction

Animal-mediated pollination is an important ecosystem service providing substantial benefits to both humans and wild populations. Thus 75% of crops and 87.5% flowering plants rely on pollination from animals (Klein et al. 2007; Ollerton et al. 2011), primarily insects, representing an economic value of US$195–387 billion (Porto et al. 2020). In addition, pollination is a key driver to the diversification of

plants and their associated pollinators, with considerable evolutionary and ecological implication for biodiversity (Ollerton 2017).

The loss and fragmentation of natural habitats, primarily due to increased human activities, is widespread in terrestrial ecosystems. There is clear evidence of a decline in pollinators and their interactions with plants (Biesmeijer et al. 2006; Powney et al. 2019), and habitat fragmentation is considered as one of the top factors driving this pattern (Potts et al. 2010; Winfree et al. 2009). Previous studies have shown that fragmentation resulted in a reduction in pollinator visitation (Goverde et al. 2002; Hermansen et al. 2017), and changes in pollinator assemblages (Delnevo et al. 2020; Taki et al. 2007), with further consequences on pollen dispersal (Delnevo et al. 2020; Gonzalez-Varo et al. 2009), and seed and fruit production (Aguilar and Galetto 2004; Aizen and Feinsinger 1994; Farwig et al. 2009; Hadley et al. 2014), and plant population viability (Naaf et al. 2021; Newman et al. 2013). However, some studies demonstrated a species-specific or no effect of fragmentation on pollination (Donaldson et al. 2002; Hauber et al. 2022; Ward and Johnson 2005). Due to the multiple interdependent processes involved in fragmentation (i.e., reduced patch size, isolation, changed configuration, etc) and contrasting responses of species to habitat change (Lazaro et al. 2020), the impact of fragmentation on pollination is not fully understood and its impacts on ecosystem services and functions is difficult to predict.

The theory of island biogeography provides a theoretical backdrop for understanding the effect of habitat fragmentation (MacArthur and Wilson 1967). It assumes that habitats are “islands” surrounded by the unsuitable matrix of “ocean”, and the number of species found on an island increases with the area of the island, but decreases with distance to the “mainland”. Numerous studies have been undertaken to investigate the effect of fragmentation, where patch area and isolation are used as predictors for the occurrence of species such as birds (e.g. Ferraz et al. 2007). For insect pollinators, patch area and isolation are important variables associated with their activities and occurrences, as studies showed that pollinator richness and visitation decreased with isolation (Garibaldi et al. 2011), and a high density of pollinators was found in large habitat patches with rich resources (Blaauw and Isaacs 2014). Hence, patch area and isolation may jointly shape the reproductive outcomes of plants, by influencing the activity of pollinators.

Spring flowering plants provide pollen and nectar for overwintered pollinators such as queen bumblebees, and the availability of those resources has been shown important for subsequent colony development (Goulson 2010). The timing of overwintered pollinators visiting spring flowers can affect the reproductive success of those plants, as spring bloomers are not only more susceptible to pollinator limitation (Gezon et al. 2016; Kudo and Cooper 2019), but strongly responsible to climate change (Fitter and Fitter 2002). However, to our knowledge, there is relatively few fragmentation studies focusing on early spring pollination.

Here we empirically investigate the effect of patch area and isolation on pollination in a fragmented landscape, using the English bluebell (*Hyacinthoides non-scripta*)—a pollinator limited plant species largely pollinated by early spring bumblebee queens in the UK (Corbet 1999) as a model system.

Bumblebees are known as efficient pollinators of many crops and wild plants (Garratt et al. 2014; Kovacs-Hostyanszki et al. 2013), with about 20 bumblebee species recorded in the UK (Dicks et al. 2015). To assess how patch area and isolation affect pollination services in the fragmented landscape, we placed bluebell plants in habitat patches that vary in size and distance from each other, and use seed and fruit set as a measure of pollination success.

Methods And Materials

Study site

Our experiment was conducted between April to May 2022 at Durdham Downs, Bristol, United Kingdom (51.4661 N, -2.6237W). The 1.7km^2 study site mainly consists of urban meadows, with numerous patches of woodland and scrub scattered within this area (Fig. 1). The meadows are either mown regularly or managed as hay meadows, whilst the woodland and scrub patches are left largely unmanaged. The most common plant species in woodlands are ash (*Fraxinus excelsior*), oak (*Quercus robur*), hawthorn (*Crataegus monogyna*) and elder (*Sambucus nigra*). Spring-flowering plants are wild cherries (*Prunus avium*), cow parsley (*Anthriscus sylvestris*), hogweed (*Heracleum sphondylium*), alexanders (*Smyrnium olusatrum*). Bumblebees such as *Bombus terrestris* are common pollinators in early spring (Timberlake et al. 2021).

Fragmentation metrics

A total of 51 woodland patches that varied in size and shape were selected as experimental fragmented landscape (Fig. 1). The edges of patches were marked according to the location of the tree canopy in QGIS (v 3.22, QGISDevelopmentTeam 2022), using the most recent version of Google satellite map with a limited accuracy of 2m (Google 2021). We measured the areas and the edge-to-edge distance between all the patches, and used a proximity index (Gustafson and Parker 1992) to examine the degree of isolation from a focal patch to the rest of all neighbour patches. The proximity index is the area-based index weighted by distance (Munguia-Rosas and Montiel 2014), so that

$$Px = \sum_{i=1}^{n} A_j * D_{ij}^{-1}$$

For focal patch *i*, A*j* is the area of a neighbour patch *j*, D*ij* is the nearest edge-to-edge distance between a focal patch *i* and a neighbour patch *j*, and n is the total number of patches. The value of the index is larger when a patch is surrounded by a cluster of larger and/or closer neighbour patchers, indicating a lower degree of isolation. We included all the patches in the calculation of Px because bees (especially bumblebees) are expected to forage within a whole landscape (Osborne et al. 2008).

Placement of plants

Bluebell (*Hyacinthoides non-scripta*) is a native species and mostly found in the UK woodland understorey. Bluebells flower in spring and are largely pollinated by bees (Guitián and Guitián 2022). Its flowers are self-incompatible and pollinator limited, producing more seeds and seed capsules after cross

pollination (Corbet 1998). Three bluebell bulbs were grown in a plant pot as an experimental unit and kept isolated from pollinators before being placed in the field.

Plants were placed in each woodland patch when they were about to flower. Three pots of plants were put in a tray so they could be easily watered, and trays (each containing 3 pots and a total of 9 plants) were placed in the understory of woods but avoiding patch edges. Plants were placed outside when they were about to flower, and remained outside until each plant had finished flowering, which took *c.* four weeks. All the plants stayed outside for a same length of time and were then returned to an unheated greenhouse to keep them free of pollinators. A muslin bag was placed over each flowering racemes when flowering finished, this enabling the collection of the seeds.

Seed set was counted after seeds were fully matured. We counted the number of seeds, the number of fruit capsules, and the number of undeveloped flowers (i.e., flowers that fail to set any seeds) as measures of pollination. We measured these variables because the number of capsules indicates how many flowers have been visited by pollinators, the number of seeds indicates how many pollen grains were brought to stigma, and the number of undeveloped flowers indicates how many flowers were unvisited. Together these data provide a picture of the quantity and quality of pollination. To evaluate the effect of open pollination, 6 pots of bulbs (i.e., 3 plants in each) were kept separate from pollinators in greenhouse as the control. Finally, we surveyed the plant species in the selected woodland patches to investigate the island biogeography of plant species in our landscape (see *supplemental material*).

Data analysis

A one-way analysis of variance (ANOVA) was used to determine the effect of open pollination, by comparing differences on the number of seeds per capsule between the pollinator exclusion plants and plants placed in the patches. To investigate the joint effects of patch area and isolation on pollination rates, we used generalized linear mixed effect models (GLMMs) to fit data on (1) the number of seeds, (2) the number of seed capsules, and (3) the number of undeveloped flowers that were collected from each experimental unit. Each GLMM was fitted with a quasi-Poisson distribution on the seed, capsules, and undeveloped flowers count data; patch area, patch proximity, and their interaction were included as a fixed effect; the identity of experimental units (i.e., plant pots) and the occurrence of wild bluebells (either 0 or 1) based on plant survey were included as a random effect. All the models were fitted using 'glmmTMB' package (Magnusson et al. 2017) in R (v 4.0.2, RCoreTeam 2022).

Results

Compared with the pollination exclusion plants, open pollination increased the number of bluebell seeds per capsule by 155% (one-way ANOVA, $F_{1,127}$ =9.541 p = 0.002). Whilst we found both the number of seeds and seed capsules were positively and significantly related to patch proximity (Table 1, Fig. 2b, 2d), patch area had no significant effect (Table 1, Fig. 2a, 2c). There was also no significant effect of the interaction between patch area and proximity on the number of seeds and capsules (Table 1). Finally, the number of undeveloped flowers was unaffected by any of our predictor variables (Table 1, Fig. 2e, 2f).

Table 1
The effect of patch area, proximity, and their interaction on the number of seeds, number of seed capsules, and number of undeveloped flowers.

Response variables	Predictors	Estimate	Stand error	Z value	*p*	
Number of seeds	(Intercept)	4.4708	0.2002	22.328	< 0.001	***
	area	0.1657	0.2694	0.615	0.5385	
	proximity	0.4375	0.1796	2.437	0.0148	*
	area: proximity	-0.3452	0.3218	-1.073	0.2834	
Number of seed capsules	(Intercept)	2.3383	0.1864	12.545	< 0.001	***
	area	0.1545	0.2274	0.679	0.4970	
	proximity	0.4297	0.1555	2.763	0.0057	**
	area: proximity	-0.3374	0.2686	-1.256	0.2090	
Number of undeveloped flowers	(Intercept)	2.3393	0.1535	15.241	< 0.001	***
	area	0.1227	0.1865	0.658	0.510	
	proximity	0.1296	0.1557	0.832	0.405	
	area: proximity	-0.1423	0.2303	-0.618	0.537	
Significant levels: 0 '***', 0.001 '**', 0.01 '*', 0.05 ' '						

Discussion

We show that whilst patch area had little effect on bluebell pollination, isolation significantly reduced its reproductive success, as both seeds and seed capsules increased with proximity to other patches. In what follows we discuss the limitations of our study, then consider the effect of fragmentation on pollination, along with the conclusions based on our results.

There are two main limitations in our study. First, our experimental scale is relatively small (study site < 1.7 km^2), compared with previous studies examining the effect of fragmentation in much larger landscapes (e.g., Hadley et al. 2014). In our study, we found that patch isolation limited the seed and capsule production of bluebells, but this effect may be stronger in a larger scale, because the movements of pollinators would be more affected if patch distance is longer than their foraging distances. Second, bluebells are known predominantly visited by bumblebee queens, but which other taxa visited our

experimental plants were unobserved. If bluebells were also visited by other insects, fragmentation may impact pollination by differentially affecting the movements of different pollinators. For instance, isolation may be more detrimental to the pollination of less mobile pollinators rather than bumblebees (Krewenka et al. 2011). Ideally, testing this requires a community level approach (e.g. Fontaine et al. 2006) where plant communities that attract different groups of pollinators are needed.

Our results showed that both seed set and capsule development of bluebells increased with proximity index, a phenomenon which largely agrees with previous findings that isolation is the key factor limiting pollination (e.g. Farwig et al. 2009; Steffan-Dewenter and Tscharntke 1999; Townsend and Levey 2005). We interpret these results by the fact that patch isolation reduced pollinator visitation and thus pollen exchange, causing lower reproductive outcomes of this species. A previous study found that bluebells were largely self-incompatible and produced more seeds and capsules with cross pollination (Corbet 1998), and we also showed here that open pollination produced more seeds per capsule than pollinator exclusion. Thus, it is possible that more isolated patches had less pollinator activity and had a lower probability of cross pollination, as a decrease in pollinator occurrence and visitation with isolation was also shown in other studies (Ricketts et al. 2008; Steffan-Dewenter and Tscharntke 1999). Meanwhile, a high proximity index means more large and close patches nearby, hence pollen transfer between neighbour patches might be encouraged. Overall, our results suggest that habitat fragmentation negatively impact the pollination of bluebells, by increasing isolation between habitat patches.

We found that patch area did not affect the reproductive success of bluebells, which contracts with predictions that increased occurrence of bee pollinators with patch area (e.g. Bommarco et al. 2010; Steffan-Dewenter 2003). However, some studies found that patch area had less or even no effect on the occurrence of bee pollinators (Storck-Tonon and Peres 2017; Taki et al. 2018), suggesting that pollination may not always be affected by patch area. Indeed, the presence of pollinators are often positively correlated with the availability of floral resources (Blaauw and Isaacs 2014), which may possibly increase pollination. In our study site, the number of spring flowering species was found less correlated with area than total number of species (Fig. S1a-b), which may suggest that large patches had a lower proportion of flowering species and thus were less attractive to pollinators. Furthermore, larger patches may not necessarily contribute to higher pollination, as visiting a small proportion of flowers in a patch has been shown as an optimal foraging strategy for some bee pollinators, regardless of increased patch area (Diekotter et al. 2007; Goulson 2000). This result may support the idea that small habitat patches have a similar conservation value as large patches for pollinators.

In summary, our study provides empirical evidence on how patch area and isolation affect pollination in a UK fragmented landscape, highlighting the importance of small habitat patches and connectivity in maintaining pollination services. As spring pollination is particularly susceptible to climatic disturbances (Kudo and Cooper 2019), finding an effective strategy to conserve populations of spring flowering plants is important. Reducing isolation, for example by using pollinator corridors, may improve the fitness of spring flowering plants and increase their population resilience. From a practical perspective, these results shed some light on the mechanisms underlying the effect of habitat fragmentation on pollination,

and provide some pointers for landscape managers as to the best approaches for conserving the pollination of early spring flowers.

Declarations

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Author contribution

DL and JM conceived the ideas, DL conducted the experiment and wrote the manuscript, with suggestions from JM and CFC. All the authors gave final approval for publication.

Conflict of interest

There is no conflict of interests in authors.

Data Availability statement

Data and codes are available in GitHub repository(https://github.com/Dongboli/experimental-data.git).

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Figures

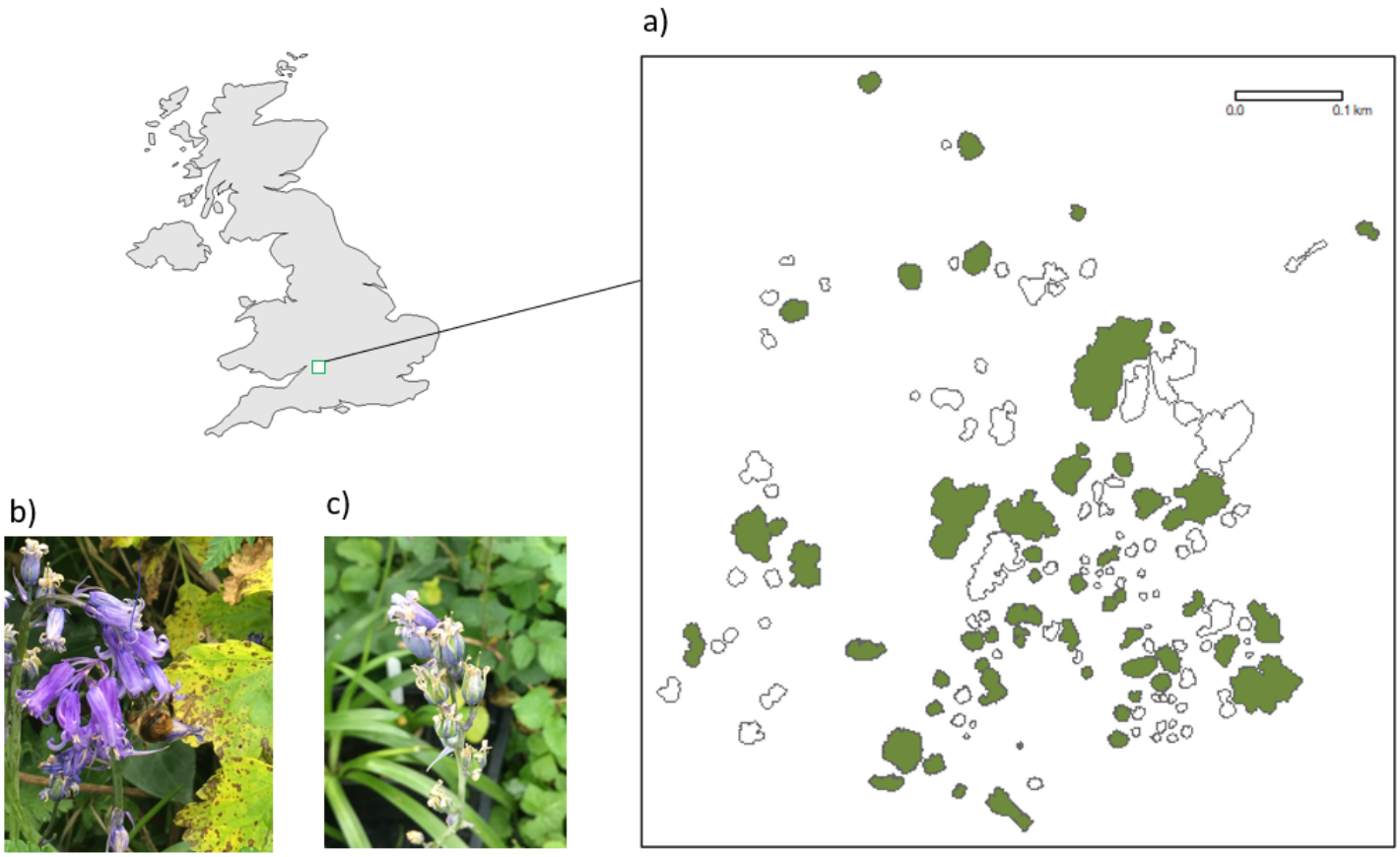

Figure 1

(a). Map of study site shows the layout of the woodland patches used for the field experiment (n=51, green) and other surrounding patches (n=81, unfilled). (b) Bluebells were pollinated by bumble bees (*Bombus spp.*). (c) Seed capsules of bluebell, *H. non-scripta*.

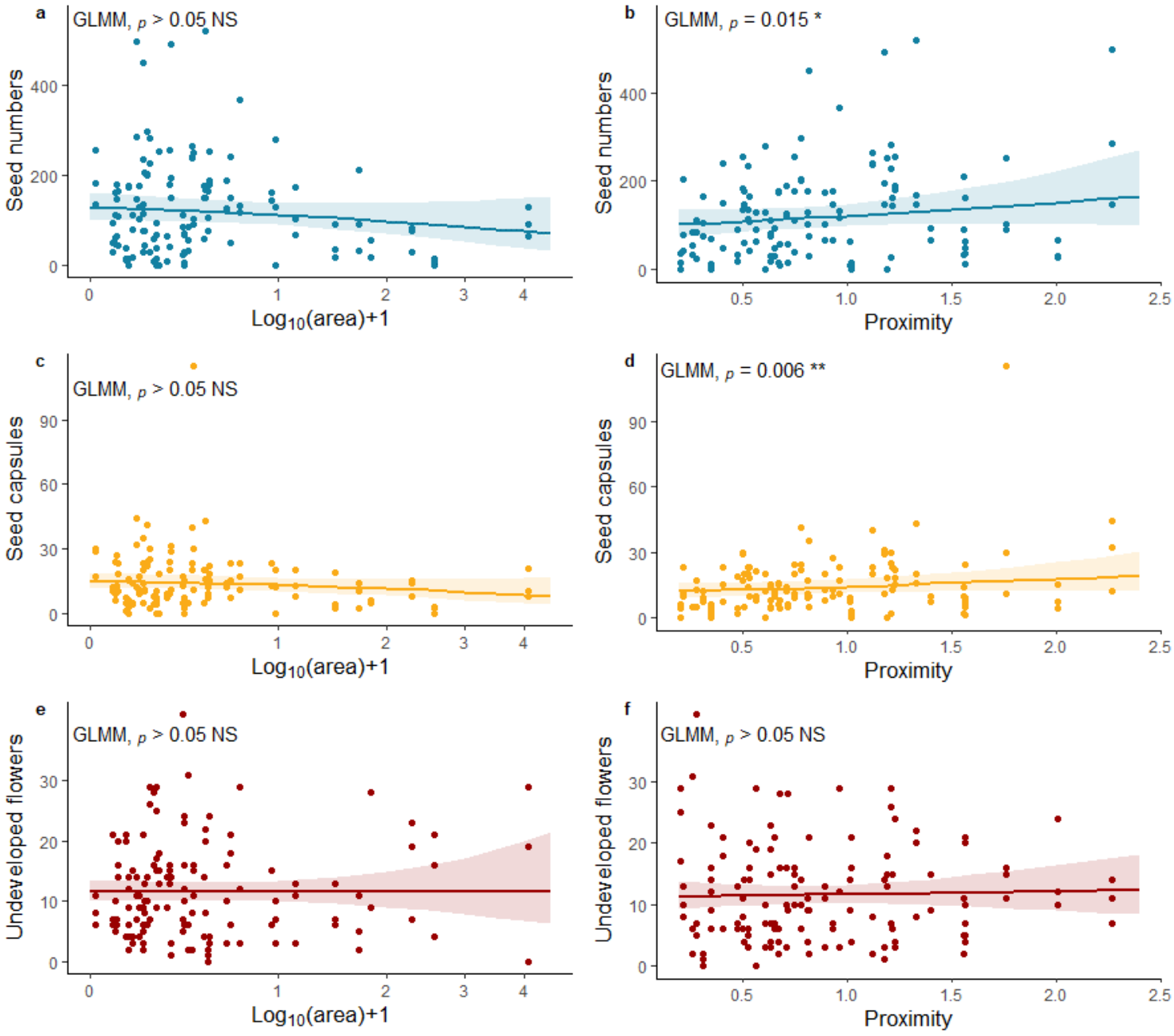

Figure 2

The effect of area and proximity (i.e., the opposite of isolation) on the number of seeds (a, b), seed capsules (c, d), and undeveloped flowers (e, f) of bluebells. Dots represent data points and lines are model outputs, with 95% confidence intervals. Significant levels: 0 '***', 0.001 '**', 0.01 '*', 0.05 'Not significant (NS)'

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