Beware of trees: Pine afforestation of a naturally treeless habitat reduces flower and pollinator diversity

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ABSTRACT

Planting three billion trees to capture carbon and seeking measures to reverse pollinator decline are two key pledges of the EU Biodiversity Strategy for 2030. Although planting trees could be adequate to restore biodiversity in degraded landscapes and mitigate anthropogenic carbon emissions, it can also negatively impact biodiversity of naturally treeless habitats. To explore whether these two pledges might conflict, we focused on the European dry heathland, a treeless habitat frequent in the southwestern Iberian Peninsula, where it is locally known as herriza. The herriza stands out by its high plant biodiversity and profuse flowering that supports a wide range of insect pollinators. Yet, the herriza has been heavily afforested with pine trees until the onset of the 21st century. This past activity provides a unique natural experiment to assess the effect of afforestation on flower abundance and associated pollinator diversity. We conducted a two-year field study of the diversity and abundance of flowers and pollinators in five selected sites, each consisting of two adjacent plots of open and afforested herriza. Afforested herriza plots had consistently lower diversity and abundance of flowers and insect pollinators than open herriza plots. Our results highlight the negative impact of afforestation of a treeless habitat on its flowering pattern and associated insect pollinator guilds. We thus suggest seeking alternatives to afforesting naturally treeless habitats in order to avoid conflicts between carbon sequestration and pollinator conservation.

1. Introduction

Pollination plays a key role in the sustainability of natural ecosystems (Fontaine et al., 2005) allowing sexual reproduction of over 90% of all flowering plants (Ollerton et al., 2011). In addition, animal pollinators provide essential ecosystem services, as nearly 75% of the main crop species and 35% of food production worldwide depend partially or totally on them (Klein et al., 2007). Pollinators also contribute to acquire other crucial resources for humans, such as medicines (Glinos et al., 2019) or fibers (Cusser and Jha, 2021). There is, however, increasing evidence that pollinators are declining globally (Kearns et al., 1998; Biesmeijer et al., 2006), which not only means a loss of species abundance and diversity, but also a potential loss of the key ecosystem services they provide (Kremen et al., 2005).
2003; Ollerton, 2017).

Although a decline in pollinators can be caused by multiple drivers (Potts et al., 2010; González-Varo et al., 2013), changes in land use are one of the main threats worldwide (Steffan-Dewenter & Westphal, 2008; Potts et al., 2010; Ollerton et al., 2014), as they lead to the loss and fragmentation of natural habitats (González-Varo et al., 2013). Land-use changes are associated with a decrease in essential natural resources for pollinators (Lázaro and Tur, 2018), particularly affecting habitat and dietary specialist species (Williams et al., 2010; Winfree et al., 2011). Their impacts include the reduction of suitable nesting sites and resources (Potts et al., 2005; Williams et al., 2010), the isolation of insect populations (Ricketts et al., 2008; González-Varo et al., 2013) and the decrease in abundance and diversity of flowers, thus reducing the availability of floral resources and consequently eroding their interaction networks (Potts et al., 2003; Steffan-Dewenter & Westphal, 2008).

Afforestation with fast-growing tree species is nowadays a common and widespread type of land-use change around the planet (Lambin and Geist, 2006; Hansen et al., 2013). According to the Global Forest Resources Assessment 2020 (FAO, 2020), the afforested area worldwide has increased by 55.8 million ha between 1990 and 2020. Tree plantations can be made with both exotic and native species and, in most cases, they aim to provide economic benefits (e.g. timber, fuel, pulpwood, resin), implement ecosystem restoration, increase soil protection and water conservation, or mitigate the effects of climate change through carbon sequestration (Brockerhoff et al., 2008; FAO, 2020; but see Bremer and Farley, 2010). On numerous occasions though, afforestation has been carried out in naturally treeless habitats, negatively affecting their biodiversity and ecosystem functions (Andrés and Ojeda, 2002; Bremer and Farley, 2010; Veldman et al., 2015). Many treeless habitats, such as heathlands or meadows, are crucial for pollinators as they are important sources of floral resources (Dicks et al., 2015). However, despite their importance for biodiversity, they have often been ignored or undervalued, and included in extensive afforestation programs (e.g. Andrés and Ojeda, 2002; Buscardo et al., 2008).

An important example of flower-rich, treeless habitat is the European dry heathland (habitat 4030 of the European Natura 2000 network), of paramount importance for insect pollinators (Forup et al., 2008; Descamps et al., 2015; Moquet et al., 2017). This habitat is widely distributed across Atlantic Europe, from southern Scandinavia to the southwestern end of the Mediterranean Region (western Iberian Peninsula and Strait of Gibraltar area; Loidi et al., 2010). In the southwestern Iberian Peninsula, the dry heathland is found under mild Mediterranean climate, and is known as herriza (Gil-López et al., 2018). This Mediterranean heathland or herriza stands out among other European dry heathland formations by its exceptional plant diversity, endemism, and uniqueness, which are particularly pronounced in the Strait of Gibraltar area (Gil-López et al., 2018). This floristic uniqueness is determined by the peculiar environmental features and Pleistocene history of the Strait of Gibraltar (Rodríguez-Sánchez et al., 2008). Another striking feature of the herriza is its profuse flowering almost throughout the year (Arroyo, 1988), which favours the presence of a wide range of insect pollinators (Dicks et al., 2015).

In spite of its outstanding plant biodiversity, the herriza was ignored from a conservation perspective until relatively recently due to its treeless feature and it was included in afforestation programs using pine species (Andrés and Ojeda, 2002). Nature restoration and conservation in Spain has been, and still is, strongly forestry-centred (e.g. Vadell et al., 2022). It has been shown, however, that pine afforestation causes substantial losses of plant biodiversity and changes in some ecosystem functions in the herriza (Andrés and Ojeda, 2002; Ojeda, 2020). Surprisingly though, nothing is yet known about the effects of the afforestation of the herriza on its characteristic flowering pattern and associated insect pollinator fauna.

The European Commission has developed the EU Biodiversity Strategy for 2030, an ambitious, comprehensive plan aimed at fostering biodiversity, reversing pollinator decline, preserving natural habitats and securing ecosystem services, among other objectives (European Commission, 2020). One of the actions in the Strategy was planting three billion trees in its territory to help fight biodiversity loss and mitigate the effects of climate change (European Commission, 2020, 2021). Although trees should be planted in full respect of ecological principles (Lier et al., 2022), this forestry action has been severely criticized for being misleading and ill-advised by poor ecological understanding (Gómez-González et al., 2020; Selva et al., 2020). For instance, the afforestation of naturally treeless habitats might compromise key objectives of the EU Biodiversity Strategy, such as reversing the dramatic decline in insect pollinators (European Commission, 2023). Therefore, elucidating and understanding the potential conflicts between tree planting and pollinator conservation is of utmost importance to implement effective actions to confront the growing biodiversity crisis.

From past afforestation practices of the herriza with pine trees in the European side of the Strait of Gibraltar (Andrés and Ojeda, 2002), we established a natural experiment to evaluate how the afforestation of a naturally treeless habitat may affect its flowering pattern and associated insect pollinator diversity. Specifically, we recorded the richness and abundance of flowers and insect pollinators at five sites, each consisting of two adjacent plots of open and afforested herriza, across two consecutive years. By doing so, we were able to test the following two predictions: (1) flower diversity and abundance are consistently lower in afforested than in open herriza across seasons, thereby reducing the availability of food resources to insect pollinators; consequently, (2) pollinator diversity and abundance would also be lower in the afforested herriza. Importantly, this evaluation has been done throughout the year to account for marked seasonal variation in pollinator communities and their set of blooming plants. In addition, we tested for differences in the taxonomic composition of flower and pollinator communities between both open and afforested herriza across seasons. This study aims to draw attention and generate awareness about potential conflicts that may arise between tree planting and pollinator conservation under the umbrella of the EU Biodiversity Strategy for 2030.

2. Methods

2.1. Study area and sampling sites

The Strait of Gibraltar, where the most diverse examples of herriza are located (Gil-López et al., 2018), represents an area of
(caption on next page)
Fig. 1. (a) Geographic location of the five sites used in this study. Each site was composed of two adjacent plots (open herriza and afforested herriza). The grey area indicates the location of Los Alcornocales Natural Park. (b) Schematic design of the sampling methodology showing the two adjacent plots at each site with the four separate 25 m-line transects.

remarkable landscape diversity and floristic uniqueness resulting from its exceptional geological history and ecological peculiarities (Rodríguez-Sánchez et al., 2008). It is characterized by a mild Mediterranean climate, tempered by a marked oceanic influence, and a rugged topography of nutrient-poor, acid sandstone mountains surrounded by fertile, non-sandstone lowlands (Rodríguez-Sánchez et al., 2008). Climate and soil features account for the dominant presence of herriza (Mediterranean heathland) formations covering ridges and crests of sandstone mountains and hills. Despite harbouring high plant biodiversity (Gil-López et al., 2018), many herriza formations were afforested with pine species, particularly during the second half of the 20th century, negatively affecting their plant biodiversity (Andrés and Ojeda, 2002; Ojeda, 2020).

The study was carried out within the boundaries of Los Alcornocales Natural Park (Fig. 1), which encloses most of the herriza formations from the European side of the Strait of Gibraltar (Gil-López et al., 2018). We selected five sites along the Park’s north-south axis (Table 1; Fig. 1a), each consisting of two adjacent open and afforested herriza plots (Fig. S1). Both plots at each site had the same elevation, aspect and substrate (Oligo-Miocene siliceous sandstones or Aljibe sandstones). Pine trees in the afforested herriza plots were planted mostly during the 1960s and 1990s (Ojeda, 2020), so pine plantations have an age range of 25 to 60 years. The five selected sites have not suffered a wildfire at least in the last 20 years. The pine canopy cover in the afforested plots was measured using a concave spherical densiometer (model C; Robert E. Lemmon, Forest Densiometers, Bartlesville, OK), and varied from 66% to 94.1% (Table 1).

2.2. Sampling of flower and pollinator diversity and abundance

At each open- and afforested herriza plot within sites, we established four parallel 25 m line transects separated by 10 m from each other (Fig. 1b). In each sampling period (season; see below), we recorded all blooming plant species within 2 m x 1 m quadrats (on alternate sides of the transect) at 1 m-interval points along the transects, irrespective of their abundance. This allowed us to determine the number of flowering plant species (hereafter referred to as flower richness) and estimate flower abundance (ranging from 0 to 100 in each sampling, 25 m-interval points * 4 transects), both overall and for each species, per plot and season. To sample pollinator diversity, we conducted standardised transect walks, which have been proved an efficient method (Westphal et al., 2008). Each 25 m line transect was covered with slow walks of 14 min (i.e. 56 min/plot), in which all insects visiting flowers observed up to one meter at each side of the transect were recorded. We excluded insects with a body length under 2 mm. Transect walks were always performed under favourable weather conditions (i.e. sunny days, wind speed < 10 km/h), and in the same time slot (between 09:00 and 11:00 UTC). Therefore, only one site (two plots) per day could be sampled. Non-systematic observations suggested that higher pollination activity occur during this particular time slot. Indeed, this limited time period may imply an underestimation of the pollinator abundance and diversity inhabiting the herriza, particularly those with night activity. Pollinators were identified in the field to the lowest possible taxonomic level and, whenever possible, they were captured for later identification. The captured specimens were pinned and identified using specialized field guides and handbooks (Balls and Morris, 2015; Michez et al., 2019) and with the help of group specialists (see Acknowledgments). Pollinator species diversity (hereafter, pollinator richness) was then measured as the number of species recorded and, pollinator abundance as the number of individuals of each species.

Transect walks were carried out during two consecutive years (2020–2021, 2021–2022) across five sampling periods (seasons) per year: winter (January-February), early spring (March-April), late spring (May-June), summer (July-August) and autumn (September-October) and were always made by the same observer (APG). Since only one site could be sampled each day (see above), the sampling order of sites and the starting point within site were randomized in each sampling period. Although only five days were needed, each sampling period lasted up to 20 days because only days under favourable weather conditions could be used (see above). In total, 400 transect walks were performed (4 transects x 2 plots x 5 sites x 5 periods x 2 years).

Table 1
Location and description of the five sampling sites. OH: Open herriza, AH: Afforested herriza.

<table>
<thead>
<tr>
<th>ID</th>
<th>Site</th>
<th>Plot</th>
<th>Latitude</th>
<th>longitude</th>
<th>Altitude (m asl)</th>
<th>Canopy cover (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Marrufo</td>
<td>OH</td>
<td>36°34'26.12&quot;N</td>
<td>5°32'11.35&quot;O</td>
<td>604</td>
<td>00.0</td>
</tr>
<tr>
<td>2</td>
<td>Pico del Montero</td>
<td>OH</td>
<td>36°30'40.77&quot;N</td>
<td>5°35'57.34&quot;O</td>
<td>870</td>
<td>00.0</td>
</tr>
<tr>
<td>3</td>
<td>Peguera</td>
<td>OH</td>
<td>36°32'34.54&quot;N</td>
<td>5°35'56.33&quot;O</td>
<td>840</td>
<td>91.3</td>
</tr>
<tr>
<td>4</td>
<td>Sierra de Montecoche</td>
<td>OH</td>
<td>36°16'37.35&quot;N</td>
<td>5°32'51.59&quot;O</td>
<td>550</td>
<td>00.0</td>
</tr>
<tr>
<td>5</td>
<td>Sierra de Fates</td>
<td>OH</td>
<td>36°16'34.53&quot;N</td>
<td>5°32'56.98&quot;O</td>
<td>559</td>
<td>79.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>AH</td>
<td>36°30'10.04&quot;O</td>
<td>5°40'9.93&quot;O</td>
<td>587</td>
<td>66.0</td>
</tr>
</tbody>
</table>
2.3. Statistical analyses

All analyses were conducted in R, version 4.0.5 (R Core Team, 2021). To detect possible sampling biases in flower and pollinator richness comparisons between open and afforested herriza plots, we first explored whether our sampling method yielded comparable sample coverages for both sets of plots. To do so, we calculated the sample coverage of each plot (Chao and Jost, 2012) with the R package iNEXT (Hsieh et al., 2016). We then compared sample coverage values for both flower and pollinator richness with Student’s t-tests. To evaluate the effects of pine tree afforestation on flower and pollinator richness and abundance, we fitted a set of generalized linear mixed models (GLMMs). The interaction between plot (open vs. afforested herriza) and season was included as a fixed factor in all models. Additionally, flower abundance was included as a fixed factor in the pollinator richness and pollinator abundance models.

Site was included as a random factor in all models to account for between-site variability. For flower richness and abundance, we used the “glmmTMB()” function in the glmmTMB package (Brooks et al., 2017). We set the model family to “truncated_nbinom1 (link = “log”)” for flower richness and “truncated_genpois (link = “log”)” for flower abundance. On the other hand, for pollinator richness and abundance, we used the “glmer.nb” function in the lme4 package (Bates et al., 2015). The pollinator richness was additionally rarefied to achieve the same level of coverage through the iNEXT package, and a paired Student’s t-test was employed for comparisons. In addition, for both flowers and pollinators, we calculated the ‘inverse Simpson Index 1/D’ – as a measure of species evenness in the plots – with the function “diversity” in the vegan package (Oksanen et al., 2019), pooling the data from the two sampling years to ensure enough values in sampling seasons with low numbers.

Then, to test for differences in both flower and pollinator species evenness (1/D) between open and afforested herriza plots, we fitted two additional generalized linear mixed models with Gaussian distribution and log-link function, including the interaction between plot (open vs. afforested herriza) and season as a fixed effect, and site as a random factor for both cases. We previously assessed the effect of the year (2020–2021 versus 2021–2022) on the flower and pollinator richness and abundance. However, although the inclusion of year improved the flower abundance model according to the Akaike information criterion (AIC), it did not improve the flower richness model. Moreover, there were issues with model convergence for both pollinator richness and abundance (Supplementary Table S5). Therefore, for consistency in the statistical analyses and because we were not interested in documenting changes between years, but rather changes across seasons, we excluded year from the models and combined data from both years in all analyses.

In all instances, to further test for differences between open- and afforested herriza plots within each sampling season, we carried out post-hoc Tukey tests using the lsmeans package (Lenth, 2015). For all models, the DHARMa package was used to check the assumptions of independence, homoscedasticity and normality of the residuals (Hartig, 2022) and model selection was determined by

Fig. 2. Effect size of pine afforestation on a) flower richness, b) flower abundance, c) Flower evenness (Inverse Simpson index), d) pollinator richness, e) pollinator abundance, f) Pollinator evenness (Inverse Simpson index). Each variable shows its estimated mean value (blue dots) and 95% confidence intervals (whiskers). Drawings represent the plant Polygala microphylla, a species endemic to the herriza, and the fly Rhyncomyia columbina, a common pollinator in the herriza.
the Second-order Akaike Information Criterion (AICc) using the MuMIn package (Barton, 2013). Finally, we assessed whether there were differences in the taxonomic composition of the flower and pollinator communities between open and afforested herriza plots throughout sampling seasons. To account for non-uniform data variance, we conducted a permutational multivariate analysis of variance (PERMANOVA) using vegan package (Anderson and Walsh, 2013). PERMANOVA analyses allow us to test for differences between open and afforested herriza plots within each season. All data and main results were illustrated using ggplot2 package (Wickham, 2011).

3. Results

Overall, we registered 62 blooming plant species (flower richness), of which, 53 were in the open herriza and 40 species in afforested herriza. The flowering plants with the highest number of records were Stauracanthus boivinii (34.8%) followed by Calluna vulgaris (13.3%) and Erica australis (12.8%) (see Supplementary Table S1). Regarding pollinators, we registered 971 individuals belonging to 133 species, of which 831 individuals belonging to 130 species were in the open herriza plots and 140 individuals belonging to 40 species in the afforested herriza ones. The pollinators with the highest number of records were Bombus terrestris (6.65%) followed by Apis mellifera (6.03%) (see Supplementary Table S2). Sample coverage was relatively high for both flowers (open herriza: 99.8% and afforested herriza 99.6%) and pollinators (open herriza 92.8% and afforested herriza 87.3%). When analyzing sample coverage per site, we found that flowering was consistently high (open herriza ranged from 99.0% to 99.6%, and afforested herriza ranged from 99.2% to 99.5%). However, concerning pollinators, open herriza consistently exhibited high coverage (ranged from 81.7% to 92.7%) but afforested herriza had more variation (ranged from 56.3% to 87.3%). Although there were no significant differences between open and afforested herriza plots ($t = 1.097, p$-value $= 0.334$ and $t = 2.733, p$-value $= 0.052$ for flowers and pollinators, respectively; paired Student’s $t$-tests), the differences were verified with pollinator richness rarefied to the same level of coverage (see below).

Afforestation negatively affected flower richness and abundance (Fig. 2a, b), but not flower evenness, measured as the inverse Simpson Index (Fig. 2c). Across sampling seasons, flower richness was significantly higher in open than in afforested herriza plots in winter, early and late spring, and summer (Fig. 3a). Flower abundance, on the other hand, was significantly higher in the open herriza plots across all seasons (Fig. 3b). There were no differences across seasons in flower evenness (inverse Simpson index; Fig. 3c).

Regarding pollinators, the afforestation of the herriza negatively affected pollinator richness, abundance and evenness (Fig. 2d, e, f). Pollinator richness and abundance showed a positive relationship with flower abundance ($z$ value $= 5.924, p$-value $<0.001$; and $z$ value $= 5.526, p$-value $<0.001$, respectively). When analyzing pollinator richness rarefied at the lowest level of sample coverage, differences remained significant (Supplementary Fig. S2). Across seasons, pollinator richness was significantly higher in the open herriza than in the afforested herriza plots in winter, early and late spring, and in summer, but in autumn was not significantly different (Fig. 3d). Pollinator abundance was significantly higher in the open herriza plots during winter, early spring, and summer. However,
differences were not statistically significant in late spring or autumn (Fig. 3 e). Additionally, pollinator evenness only showed differences between open and afforested herriza plots during spring (Fig. 3 f).

Finally, the afforestation of the herriza also had an impact on the taxonomic composition of flowers and pollinators across sampling seasons (Fig. 4, Supplementary Table S4). There were statistically significant differences in the taxonomic composition of both flowers and pollinators in the five sampling seasons, with the lowest differences in autumn for flowers and the highest differences in early and late spring for pollinators (Supplementary Table S4).

4. Discussion

The afforestation of the herriza with pines, implemented decades ago, has caused negative effects on its plant biodiversity and ecological functions such as soil erosion and post-fire response (Ojeda, 2020). In this study, we have shown that afforestation also negatively affected the diversity and abundance of flowers and pollinators, resulting in significant variations in the taxonomic composition of their communities. Yet, there are structural properties of the herrizas that are maintained after afforestation. Namely, we observed similar values in the relative dominance of flowers between open and afforested herriza plots (Fig. 3 c). We interpret this result as afforestation establishing an environmental filter where plants endure the novel conditions by abating their flowering without modifying the relative abundances.

Flowers provide essential resources (mainly nectar and pollen) for the development of insect pollinators, either in the adult phase (e.g. flies, beetles, butterflies) or in all phases of their life cycle (e.g. bees; Vaudo et al., 2015). In order to reach and maintain a balanced diet, pollinators need high abundance of flowers of different species (Hendriksma and Shafir, 2016). The diversity and abundance of flowers actually provide a good predictor of pollinator diversity at the landscape scale (Potts et al., 2003; Steffan-Dewenter &
Tscharntke, 2008). Therefore, the decline in pollinator diversity and abundance in afforested herriza plots is a likely consequence of the parallel decrease in flower richness and abundance.

Regarding pollinators, richness and abundance patterns were similar to those found for flowers, with even more marked differences between open and afforested herriza plots. The apparent lack of significant differences in pollinator abundance in late spring and autumn, though, can be explained by the large variance in the number of pollinators recorded in the open herriza plots (Fig. 3c). On the other hand, the lack of significant differences in pollinator richness in the autumn season might be a reflection of the similar flower richness between open- and afforested herriza in autumn, with C. vulgaris and S. boivinii being dominant (Supplementary Table S1). These two flowering species may be attracting the same species of pollinators, although in lower abundance in the afforested herriza due to their lower flower abundance, thus providing fewer food resources (Potts et al., 2003). However, dominance is affected during the two spring sampling seasons, resulting in differences in the pollinator composition attracted to the flowers and even the exclusion of some larger groups. This is exemplified by the absence of hoverflies, social bees, and other Hymenoptera (except solitary bees) in the afforested plots during early spring. During late spring, beetles (Coleoptera) became the most prevalent pollinators in the afforested plots, while hoverflies finally disappeared (Fig. 4).

Tree plantation is often viewed by politicians and the general public as the panacea for two of the largest threats of our time: climate change and biodiversity loss (Brancalion and Holl, 2020; European Commission, 2021). However, although tree plantation seems a quick and cheap solution to mitigate those threats, there are instances where afforestation is unnecessary and potentially misleading, even causing deleterious impacts to the environment (Holl and Brancalion, 2020). The results of this study provide a cautionary example of the long-term negative effects of afforestation on the floral and pollinator biodiversity of a naturally treeless habitat. They thus help raise critical awareness of massive afforestation as an adequate strategy worldwide to counter biodiversity loss (Brockerhoff et al., 2008; Gómez-González et al., 2020).

Since initiating and maintaining tree plantations is usually costly, management costs must be considered in every afforestation project. Furthermore, the success or failure of tree plantation as a biodiversity strategy may only be assessed over a sufficiently long-time frame (Brancalion and Holl, 2020). In that sense, it shall be emphasized that our study was conducted more than 30 years after afforestation of the herriza patches. Therefore, although the short-term impact of a recently established tree plantation might be minimal, its long-term effects could be as strongly negative as we have found. Our results thus highlight the need to consider the temporal dimension in any analysis of the impacts of afforestation on biodiversity. Finally, we advocate focusing on the search for solutions for carbon sequestration other than massively planting trees (European Commission, 2021). The recovery and protection of naturally treeless habitats such as heathlands, mires and grasslands can help preserve biodiversity and ecosystem services, including carbon sequestration or water regulation (Friggens et al., 2020). This is not about purposelessly discouraging afforestation, but tree planting must be wisely planned and implemented to either restore forest ecosystems or protect heavily degraded landscapes (Bremer and Farley, 2010; Di Sacco et al., 2021). All this must be associated with a change of paradigm through education, where tree plantations are not straightforwardly associated with forest habitats and biodiversity protection.

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CRediT authorship contribution statement

Godoy Oscar: Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. Ojeda Fernando: Writing – review & editing, Supervision, Methodology, Conceptualization. Pérez-Gómez Alvaro: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary code and data

R code and data is located at 10.5281/zenodo.8083461 and will be included into an open repository upon acceptance.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02808.

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