Forest Systems
31 (2), e007, 12 pages (2022)
eISSN: 2171-9845
https://doi.org/10.5424/fs/2022312-18779
INIA-CSIC

RESEARCH ARTICLE

OPEN ACCESS

Vegetation patches in semiabandoned olive groves: using generalised linear mixed models to determine the effect of area on community composition of woody plants

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Abstract

Aim of study: The existence of distinct vegetation habitats within semiabandoned olive groves provides a unique chance to study the plant community within semiabandoned Mediterranean landscapes. We investigated changes in community composition of woody plants across a gradient of patch sizes by providing an example of a novel statistical technique. We also aimed to determine if commonness, life form and dispersal mechanisms of woody plants are key factors influencing species presence at vegetation patches of different sizes.

Study area: Three traditional, partially managed mountain olive groves (La Soledad, Las Niñas and Piquín) were selected within Sierra Morena de Córdoba, in Central Southern Spain.

Materials and methods: The woody vegetation within patches at the three groves was sampled in July 2020 following a stratified random approach. All woody plants were identified and recorded. Variation in community composition across patch area was examined using generalised linear mixed models (GLMMs) with a binomial distribution.

Main results: There were significant changes in the community composition of woody plants as patch area increased. There was turnover of species with increasing area, characterised by the gain of species. This was observed both as a general and site-specific trend. Patterns in presence across area showed clear among species variation. Including dispersal strategies and life form variables improved model fit, revealing these are important factors influencing the community composition within the patches.

Research highlights: The GLMM analysis demonstrated that patches of larger areas support higher richness without incurring in any loss of species. Thus, maintaining large patches is important for woody plant conservation within semi-abandoned groves.

Additional key words: land abandonment; mosaic landscapes; species turnover; presence-absence data; natural regeneration; seed dispersal; life form

Abbreviations used: GLMM (Generalised Linear Mixed Model)

Authors' contributions: FNR and MBVB conceptualised the study and designed the sampling procedure. FNR undertook the fieldwork and plant identification, completed the statistical analysis, produced figures and tables, and wrote the draft versions of the manuscript. MBVB supervised the statistical and writing work, and revised the manuscript drafts.

Citation: Navarro-Rosales, F; Bell, MBV (2022). Vegetation patches in semiabandoned olive groves: using generalised linear mixed models to determine the effect of area on community composition of woody plants. Forest Systems, Volume 31, Issue 2, e007. https://doi.org/10.5424/fs/2022312-18779

Supplementary material: (Figs. S1, S2 & S3; Tables S1 & S2) accompanies the paper on *FS*'s website.

Received: 22 Aug 2021. **Accepted:** 18 May 2022.

Funding: The authors received no specific funding for this work.

Competing interests: The authors have declared that no competing interests exist.

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Introduction

Mediterranean ecoregions contain nearly 20% of the Earth's total plant diversity, despite covering less than 5% of the world's terrestrial surface (Cowling *et al.,* 1996). The Mediterranean Basin is one of the 36 global biodiversity hotspots supporting up to 290 taxa of native trees, 201 of which are endemic (Médail *et al.,* 2019). The huge ecological diversity of Mediterranean landscapes is generated by complex geography and topography, by the convergence of tropical and temperate zones (Simón López-Villalta, 2016), and by diverse human management and fire disturbances (Pinto Correia, 1993). However, since the mid 20th century, European society has become urbanised and seminatural landscapes have been abandoned. Social and demographic change has been particularly evident in the olive-producing regions of Southern Spain, where the rural population is aging, shifting cultivation is disappearing and abandoned fields are being covered by shrubs (Rallo, 2007).

Field abandonment has the potential to increase rates of carbon capture in biomass and soils (Palese *et*

al., 2013; Atallah *et al.,* 2015; Bateni *et al.,* 2019), to enhance soil biodiversity and protection (Solomou & Sfougaris, 2011, 2015), and to provide a suitable habitat for vulnerable species like arthropods, birds, amphibians and reptiles (Carpio *et al.,* 2016, 2018; Assandri *et al.,* 2017). However, abandonment can also negatively impact biodiversity, landscape dynamics and human activities due to the loss of mosaic structure. As olive groves are abandoned, they become indistinguishable from the surrounding shrubland (Blasi *et al.,* 2000), leading to a loss of cultural and ecological values (Allen *et al.,* 2006). The abandoned areas become less accessible, opportunity costs rise, and the chances of future exploitation become limited. Fuel build-up increases fire risks, and inadequate maintenance of terraces potentially leads to more intense soil erosion (Duarte *et al.,* 2008). Whilst the impact on biodiversity is largely unknown, a decrease in landscape heterogeneity increases the rate at which vulnerable flora is being lost (Allen *et al.,* 2006). As large shrubs and trees start to dominate the landscape, the overall number of vascular plant species decreases (Debussche *et al.,* 1996; Bonet & Pausas, 2004).

To avoid negative consequences of complete land abandonment and landscape homogenisation, some landholders in the hills around Córdoba (Southern Spain) have been actively maintaining an open vegetation structure in marginal mountain olive groves, creating partially abandoned landscapes (Allen *et al.,* 2006). Here, the trees are not maintained nor harvested, and agricultural management is minimal, but the open habitat structure is maintained by ploughing the spaces between the olive trees and by introducing grazers. Ploughing and grazing are some of the most common weed-control methods in olive agriculture. These strategies remove competing plants in a cost-efficient way, whilst even potentially providing additional economic returns (Carbonero Muñoz *et al.,* 2013). The use of ploughing and grazing in semiabandoned properties is an extension of traditional grove management. However, ploughing and grazing pressure has been moderate, meaning patches of vegetation have developed around the olive trees. These patches of vegetation are mainly composed of woody plants, and are evidently distinct from the herbaceous vegetation around them (Fig. 1).

The formation of vegetation patches around larger 'nurse' plants is a naturally occurring phenomenon driven by ecological facilitation, protection and nucleation (Padilla & Pugnaire, 2006). In semi-arid environments, plant canopies facilitate shrub growth by mitigating environmental stress, bringing shade, and reducing evaporation, temperature and desiccation (Maestre *et al.,* 2001; Andivia *et al.,* 2017). Nurse plants also increase soil water content by lifting water from deeper soil layers and increasing nutrient availability by accumulating litter and sediments (Padilla & Pugnaire, 2006). They also provide protection against grazing because seedlings are covered by non-palatable plants and because farmers cannot plough beneath orchard trees (Rühl *et al.,* 2011). Furthermore, nurse plants can also promote patch formation via nucleation, by attracting seed-dispersing animals and enhancing colonisation of endozoochorous species (Blasi *et al.,* 2000). Bonet (2004) concluded facilitation, protection and nucleation processes have promoted the formation of vegetation microsites around orchard trees in Southern Spain.

The existence of distinct vegetation habitats within semiabandoned olive groves provides a unique chance to study patterns of plant community assemblage and to examine the role of key variables such as patch area. Navarro-Rosales & Bell (2022) investigated the species-area relationship of woody plants within the vegetation patches at the three groves and found that richness increased significantly with patch area. Patches of 2.5 m^2 supported about 3.3 woody plant species and patches of 250 m^2 held 18, corresponding to a 5.5-fold increase in richness. The authors concluded that increases in richness with patch area corresponded to increases in habitat variability (Hart & Horwitz, 1991), since species with different tolerances and requirements would be able to survive within the more protected environment of larger patches. The authors suggested that increases in richness would be accompanied by evident increases in presence of forest-adapted plants and highlighted the need for determining area-related changes in community composition. Determining how the woody plant community changes with patch size has potentially useful applications in conservation, agriculture and forestry: knowing what plants are found at different patch sizes could allow managers to encourage the establishment of ecologically or economically useful species. Studying the relationship between composition and patch size would also allow researchers to determine how much area is required for an ecologically functioning patch of Mediterranean forest to develop, at least in terms of community composition of woody plants.

However, the community composition of the patches cannot be adequately studied via typical approaches – which involve descriptive approaches and the use of similarity indices – since these are constrained by the existence of a strong ecological gradient. Small patches hold inherently different communities compared to larger patches, meaning similarity indices like Jaccard's or Sorensen's will show increasing divergence across area but will not directly distinguish between species nestedness and turnover, nor highlight species-specific sensitivities across the area variable (Borcard *et al.,* 2018). However, the use of binomial generalised linear mixed models (GLMMs) provides a significant advantage towards studying changes community composition across a gradient such as patch area (Shutt *et al.,* 2020). Binomial GLMMs readily distinguish nestedness or turnover, and can allow researchers to obtain presence/absence responses for each

Figure 1. Vegetation patches surrounding olive trees at semiabandoned groves in Sierra Morena de Córdoba, Southern Spain (July 2021). A-B) La Soledad. C-D) Las Niñas. E-F) Piquín.

particular species in an easier and less repetitive way. Presence-absence GLMMs can even allow ecologists to concisely investigate and quantify the additive and interactive effects of different sets of ecological gradients and categories, as demonstrated by Shutt *et al.* (2020).

Thus, in this study, we aimed to investigate how the community composition of woody plants changed across patch area, investigating three semiabandoned olive groves in Sierra Morena de Córdoba, Southern Spain. We specifically focused on testing if there is turnover in species presence as the size of the vegetation patch increases by using a generalised linear mixed model with a binomial response. Therefore, our second aim was to provide an applied case study that makes use of this methodology, since this investigation represents one of the first examples of how applying a GLMM to presence/absence data can allow one to estimate changes in taxon turnover along ecological gradients (Shutt *et al.,* 2020). We expected to find significant turnover in species presence with increasing patch size, since larger patches should support a greater proportion of woodland plants (Hart & Horwitz, 1991; Andivia *et al.,* 2017). Our third aim was to explain some of the compositional patterns in species presence across patch area by investigating how the probability of finding woody plants with different commonness, life form and dispersal mechanism is affected by area. This allowed us to find if any of these categorical descriptors is a key determinant influencing species presence at vegetation patches of different sizes, as a way of evaluating the appropriateness of the results obtained from our GLMM.

Material and methods

Study site

Three traditional mountain olive groves (La Soledad, Las Niñas and Piquín) were selected within Sierra Morena de Córdoba, in Central Southern Spain (Fig. 2). The three groves are located about 6 km northwest of the city of Córdoba, in the southernmost edge of the Sierra Morena hills. All three groves have been historically dedicated to

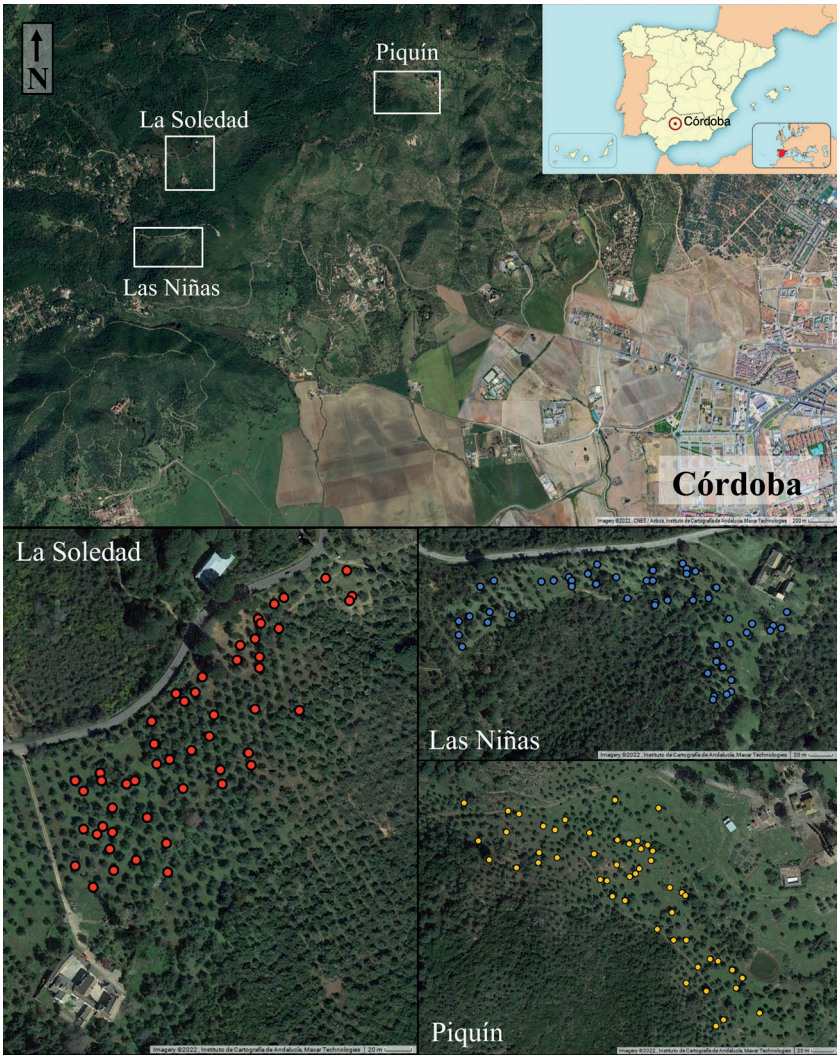

Figure 2. Location of the study sites with respect to the city of Córdoba in Southern Spain (top) and distribution of the sampled vegetation patches within each of the groves (bottom). Source: © Google Maps, Wikimedia Commons, Maps.co.

olive oil production and agriculturally managed up to the beginning of the 21st century (Cantizani Oliva & Córdoba Estepa, 2006; Moriana Elvira *et al.,* 2020). Aerial photographs reveal there were no major remnants of pre-agricultural vegetation within any of the sampled areas in the mid-20th century. In the last 20 years, the groves have become semi-abandoned, and olives are no longer harvested. The groves have been intermittently ploughed and grazed at moderate intensity, and vegetation patches have developed around the olive trees, since these provide increased protection against grazing and ploughing, as well as improved environmental conditions.

Woody plant species have spread from the surrounding habitats, which is comprised of secondary growth woodland, maquis and garrigue-type scrub. Woodland is dominated by *Pinus pinea* L., *Castanea sativa* Mill., *Quercus suber* L. and *Quercus ilex* L.; with understory species like *Viburnum tinus* L., *Smilax aspera* L., *Rubus ulmifolius* Schott and *Erica arborea* L. (López-Tirado, 2018). Maquis is dominated by *Quercus coccifera* L., *Rhamnus alaternus* L. and *Arbutus unedo* L.; and the garrigue is comprised of *Olea europaea var. sylvestris* (Mill.) Lehr., *Pistacia* sp. and *Cistus* sp. Agricultural and ornamental species like *Prunus* sp., *Ficus carica* L., *Laurus nobilis* L. and *Melia azedarach* L. have also dispersed within the groves.

All three study sites are located on areas with flat topography (500 m asl) within a broader, topographically complex area characterised by strong south-eastern slopes towards the Guadalquivir Valley (IGN, Mapa Ráster 25, http://www.ign.es/iberpix2/visor/). The area is dominated by dolomite and limestone rock from the Lower Cambrian and neutral to alkaline soils (Moriana Elvira *et al.,* 2020; IGME, 2021). A Mediterranean climate persists, with cool rainy winters and hot dry summers (http://www.aemet.es/es/serviciosclimaticos). Mean annual temperature is 18.2ºC and mean annual rainfall is 605 mm.

Sampling and data collection

The woody vegetation within different-sized patches was sampled at the three groves in July 2020. Patches were selected randomly, but following a stratified approach. There were 12 different patch size categories, based on work by Hong *et al.* (2007). The size categories were 0.25, 0.5, 1, 4, 9, 16, 25, 50, 100, 150, 200 and 250 m^2 (area was allowed to vary ±10%). We obtained the area of patches by adding up area of circular and polygon shapes, which were measured manually. Patches that were adjacent to paths or located on slopes were excluded to minimize confounding factors of slope, disturbances and altered environmental conditions.

All woody plants within each of the vegetation patches were identified, and the abundance of each species was recorded. Non-woody plants were excluded due to their variable temporal abundance and their progressive decline during the summer months (Simón López-Villalta, 2016). Including herbaceous plants would have therefore biased our results. Moreover, identification of species within dry herbaceous vegetation would have been unfeasible. All first-year seedlings – plants with evident dicotyledons or having less than 10 cm and no branches (Rühl *et al.,* 2011) – were also excluded because mortality during the first summer is disproportionately high (Simón López-Villalta, 2016). Suckers and basal shoots were omitted. Plants were identified using the guide "Flora Vascular del Término Municipal de Córdoba" (López Tirado, 2018), upon which taxonomic nomenclature was based. Commonness, life-form and seed dispersal mechanisms of all the sampled species were determined by reviewing the literature (see Table S1 [suppl]). Finally, the groves' management history was understood by interviewing the site managers and by reviewing the historical database of aerial photographs at the Spanish Geographical Institute (http://fototeca.cnig.es).

Data analysis

Community composition across area

All statistical analyses were performed using R Statistical Software version 3.6.3 (R Core Team, 2020). Variation in community composition across patch area was examined using GLMMs with binomial distribution, following the method applied by Shutt *et al.* (2020). These models predict an average presence/absence response for all species on average, but include species-specific trends as random effects. First, we ran a GLMM using data from all three sites and including the presence or absence of all sampled species as the response variable. Patch area was fitted as fixed effect to quantify the change in average species presence across the patch sizes. Therefore, the slope represents the average change in the probability of appearance of all species. Patch identity was treated as a random factor to account for non-independence within a patch. We included species identity as a random effect to account for the fact that some species are globally common and some are globally rare – so the probability of a species being present in any patch is partly driven by species identity. We then created a random slope for each species by interacting the random term for species identity with patch area – this allows the effect of area on the probability of a species being present to differ between species. This interaction term (variance in species-specific slopes) represents turnover across area. We then ran an additional model in which the area term was eliminated from the species interaction, removing individual slopes for each species. The two models were compared via likelihood ratio testing to determine the significance of the turnover term. In this case, a statistically unsignificant turnover term represents a perfectly nested set of communities where species show equal responses across. A significant turnover term would reveal there is substitutional turnover since the probability of sampling different species would vary across area. Finally, separate, site-specific GLMMs were run using data from each grove, following the same procedure as above but eliminating species that were absent from each site.

Explaining patterns in species presence across area

We ran separate GLMMs using presence/absence data from all three sites to test if the probabilities of finding groups of species with different commonness, life form and seed dispersal strategy showed significant differences in their relationship with patch area. We separately incorporated commonness, life form and seed dispersal variables (see Table S1 [suppl]) as fixed categorical effects which were allowed to interact with area. We used coefficient *p*-values to determine the significance of each category, and AIC values to see if incorporating trait improved model performance.

Results

A total of 154 vegetation patches were sampled across the three groves, with a total of 15,863 individual woody plants recorded from 50 species and 22 botanical families (Table S1 [suppl]). Whilst woody species composition varied between sites, there was no clear pattern governing the distribution of species across the groves. Each site supported tree species that belong to climax and secondary growth woodlands, as well as typical maquis and garrigue scrub species, dwarf shrubs, woody forbs, and vines. Sampled plants also included species with varying degrees of commonness, and with different strategies of seed dispersal.

Species turnover across area

The binary response GLMM that examined how the probability of species presence changes over patch area revealed the average probability of finding woody species increased significantly across area (binomial GLMM, AIC=3994.5, gradient=0.0121, z=6.76, $p<0.001$; see Fig. 3). Please note we will be referring to model coefficients (gradient/intercept) in the logit scale. The average species had a 2.96% chance of being present at hypothetical patch sizes of zero area (corresponding to the intercept), and a probability of 38.8% at patch sizes of 250 m2. There was also significant turnover of species across area, since the comparison between GLMM models revealed significant variance in species-specific slopes (variance = 7.071e-5, likelihood ratio test, χ^2 = 54.256, df=2, p=1.654e-12).

Presence probability increased with area for all species, but trends in presence across area show clear among species variation. Slope and intercept coefficients were evidently higher for the four most common and abundant species: *Asparagus acutifolius, Rhamnus alaternus, Rubus ulmifolius* and *Smilax aspera*. Slope coefficients for each species (see Table S2 [suppl]) were strongly and positively correlated with intercept coefficients. The species that most diverges from this trend is *Quercus ilex,* which had a disproportionately smaller sensitivity to area. Models that used site-specific data also showed increasing probability of average species presence across area, significant area turnover and similar trends in species presence probabilities (Figs. S1, S2 and S3 [suppl]).

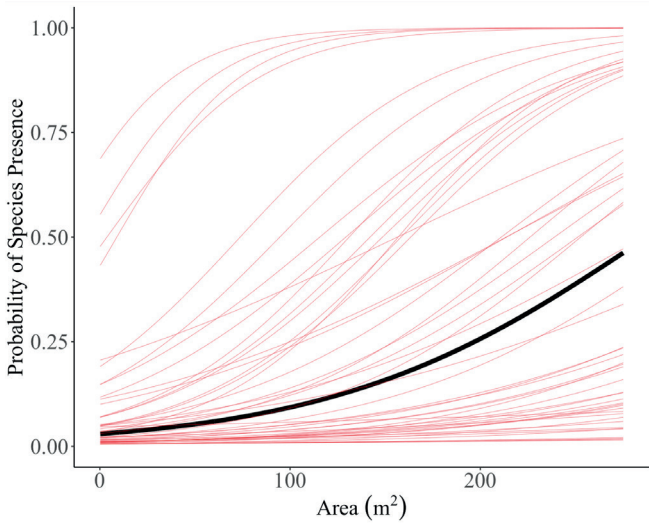

Figure 3. Changes in the probability of woody plant species being present at vegetation patches of different areas. The black line represents change in average species presence probability across area and the red lines represent individual species responses across area (see Table S2 [suppl] for species-specific coefficients).

Explaining patterns in species presence across area

Incorporating the commonness trait into the GLMM model for all three sites did not improve model fit, but revealed sporadic species have a significantly lower probability of being present at zero-areas when compared to common species (Binomial GLMM, n=7700, AIC= 3996.73, sporadic gradient =-2.097±0.745, z=-2.798, p=0.005; see Fig. 4A).

Incorporating life form into a separate GLMM model did improve model fit, and showed that compared to dwarf shrubs, vines had significantly higher presence probabilities

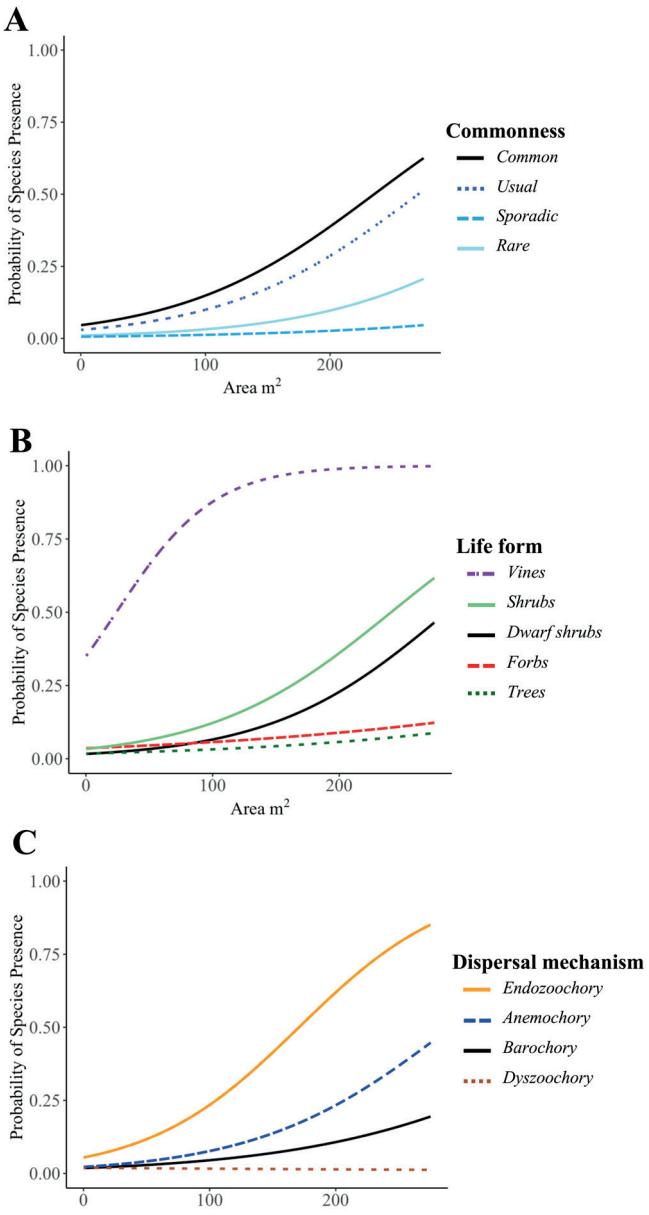

Figure 4. Changes in the presence probability of plant species of different commonness (A), life form (B), and dispersal mechanism (C) across vegetation patches of different areas. The lines represent the average trend for each commonness, life form and dispersal category group.

at zero-areas and almost significantly higher sensitivity to area (Binomial GLMM, n=7700, AIC=3979.87, vine intercept=3.4692±0.8135, z=4.265, $p<0.001$; vine gradient=0.0115±0.0059, z=1.941, $p=0.0522$; see Fig. 4B), while trees and forbs had significantly lower area slopes (Binomial GLMM, n=7700, tree gradient=-0.00825±0.00349, z=-2.365, $p=0.018$; forb gradient= 0.00956±0.0048, z=1.964, $p=0.050$).

Including dispersal mechanism into another GLMM also improved model fit, revealing that the probability of finding endozoochorous species at patches of zero area was higher than for anemochorous species (Binomial GLMM, n=7700, AIC=3987.25, endozoochory intercept=1.1254±0.5028, z=-2.083, $p=0.037$, see Fig. 4C). Probability of finding endozoochorous species also showed a significantly larger increase per unit area (Binomial GLMM, n=7700, endozoochory gradient=0.00741±0.00289, z=2.562, $p=0.010$). However, dyszoochorous species had a significantly lower sensitivity to area (Binomial GLMM, n=7700, dyszoochory gradient=-0.0109±0.0047, z=-2.306, $p=0.0211$).

Discussion

Community composition across area

The Binomial GLMM revealed there was increase in the probability of the average species being present at larger patches. There was also significant turnover of woody species as patch area increased, and this turnover was characterised by increases in the presence probability of all woody species. This means larger patches are able to support additional woody species whilst maintaining species that were already present at smaller areas, suggesting larger patches are providing increased forest-like conditions in the centre but maintaining edge-like conditions at the outside (Andivia *et al.,* 2017). Indeed, larger patches were able to support sun-loving plants like *Cistus albidus* L. and *Phagnalon saxatile* L., as well as shade-adapted species like *Viburnum tinus* L. and *Lonicera implexa* Aiton. These results provide direct evidence supporting the hypothesis that habitat variability is driving the increase in species richness across patch area within the semiabandoned olive groves (Hart & Horwitz, 1991).

Our results demonstrate how binomial GLMMs can be suitably used to study changes in communities that exhibit different trends in compositional change across an ecological gradient. A perfectly nested set of communities will show equal response across area for all species, and therefore, will have a statistically unsignificant turnover term. A set of communities exhibiting clear substitutional turnover – where the probability of sampling some species increases along the gradient and the probability of finding other ones decreases – will have a clearly significant turnover term. Our analyses show an intermediate trend, where the probability of finding all species within the patches increases across area, but at a different rate. There is compositional turnover because the probability of finding a particular species over another will change as patch area increases (Whittaker, 1972), yet the community arrangement within smaller patches will still be nested within that of larger patches.

Species with the highest intercepts (or preference for zero-area patches) were *R. alaternus, A. acutifolius, R. ulmifolius* and *S. aspera.* The intercept value represents the probability of each species if the effect of area is completely ignored. It can be interpreted as the probability of finding species outside the patches. These species also showed the highest sensitivity to increases in area. These plants are highly common and abundant, are often found around disturbed environments, and three of them have evident defence mechanisms, potentially explaining why the probability of finding them at zero-area patches – or at a random point within the groves – is already high. They are also relatively shade tolerant species (Valdés Castrillón *et al.,* 1987), meaning slight increases in patch area will facilitate their establishment by providing increased protection (McIntyre *et al.,* 1995). Larger patch areas therefore provide much better environments and even greater competitive advantages for these species. Future analyses of species cover and abundance would allow us to determine if these four species have become ecologically dominant within the patches. This could potentially have implications towards the composition of the broader plant community since strong competitive interactions could inhibit the survival and growth of the rest of species.

Alternatively, *Q. ilex* showed a relatively high affinity for zero-area patches but disproportionately low sensitivity to increases in patch area. Low sensitivity to increases in area could mean *Q. ilex* requires patches of much larger areas to establish, since it is a slow-growing woodland species that would only obtain a significant competitive advantage at true forest-like habitats (Puerta Piñero, 2008). Forest-like conditions may not be achieved even within the largest patches. Perhaps, edge effects are still too high, and plants within the patches still experience non-optimal temperature insolation or humidity (Hart & Horwitz, 1991; Andivia *et al.,* 2017). However, it is important to note that the probability of finding *Q. ilex* at patches of zero-area is already quite high (0.21), suggesting it is also able to establish in relatively open habitats (López Tirado, 2018). *Q. ilex* is a generalist, sclerophyllous and spiny species, meaning it should be unaffected by moderate changes in topography, hydrology, microclimate and grazing pressure (Valdés Castrillón *et al.,* 1987). We conclude that *Q. ilex* shows lower patch-area sensitivity because vegetation patches just do not provide it with as much facilitation and protection. The relatively high probability of finding *Q. ilex* throughout the range

of patch areas is particularly noteworthy, given that it is a keystone species in Mediterranean woodlands, and that it has been extensively used to restore degraded ecosystems (Pemán García *et al.,* 2014).

Site-specific GLMMs showed there was turnover across area at each of the sites, and that patterns of species presence across area were similar to the general trend. However, it is important to acknowledge these GLMMs are not directly comparable because the models are constructed upon different sets of species. Despite this, *R. alaternus, A. acutifolius, R. ulmifolius* and *S. aspera* continued to have highest preference for zero-area patches and highest sensitivity to area increases, while *Q. ilex* showed disproportionately low area sensitivity, suggesting species presence-absence dynamics across area are similar at different sites. It is also important to note that site-specific GLMMs showed larger increases in the probability of the average species being present due to the removal of absent species. This is an important statistical artifact to consider. Building a model with data from all sites meant we included a high number of zeros, since some species were absent at one or two groves. Increases in the average species for all three sites were smaller, because the model takes into account all of these zero-value datapoints, dragging down average presence probability at higher areas. Future research is needed to clarify this point using different approaches such as GLMMs with zero-inflated distributions (*e.g.* Hurdle regression).

Explaining compositional patterns across area

Incorporating commonness into the turnover GLMM did not improve model fit and revealed that only sporadic species had a significantly different slope coefficient. Worse model fit and a majority of non-significant group coefficients suggest commonness groups determined by López Tirado (2018) do not translate into the actual degree of commonness of woody species within the groves. These commonness groups were based on the abundance of species across the entire municipality. It is likely that species presence within the groves instead relates to the vegetation community in the immediately adjacent area, since seed dispersal is limited to distances of a few kilometres (Debussche & Lepart, 1992; Rühl, 2007). Ignoring the exact presence and abundance of plant species at the areas directly surrounding our study area was one of the main limitations of our project. Future investigations could therefore focus on sampling the adjacent vegetation, rather than relying on broader vegetation surveys. Knowing the distribution of woody species at the area around the groves would provide insight into local grove colonisation dynamics. Researchers would be able to see if the group of plants that have colonised the vegetation patches accurately represent the surrounding vegetation community, or if plant establishment within the patches is constrained by factors such as plant life form and dispersal mechanisms.

Including life form into the turnover GLMM did improve model fit, revealing that vines had significantly higher intercept and almost significantly higher slope compared to dwarf shrubs. Higher vine sensitivity to changes in area and higher probability of presence at smaller areas could be explained by the fact that vines obtain a direct competitive advantage from the presence of tree trunks and larger canopies (Simón López-Villalta, 2016). Alternatively, the low probability of finding trees at low and high patch areas could be explained by trees requiring much larger patches with more forest-like environments to develop (Pemán García *et al.,* 2014). Edge effects could mean optimal environmental conditions may not be achieved even within the largest patches (Hart & Horwitz, 1991). Many trees are also dyszoochorous species, meaning seeds will be dispersed across long distances and should have a similar probability of arriving at a vegetation patch regardless of its area (Vittoz & Engler, 2007). Woody forbs perhaps showed low area sensitivity and preference for smaller patches because they are thermophilous, sun-loving species adapted to open habitats (López Tirado, 2018), meaning shade and protection provided by smaller and larger patch areas should not provide a significant competitive advantage. Finally, shrubs and dwarf shrubs followed a similar and intermediate trend, probably because the groups include a wide range of species adapted to forest, scrub and open habitats (Valdés Castrillón *et al.,* 1987; López Tirado, 2018).

Adding dispersal mechanism into the turnover GLMM also improved model fit, and revealed endozoochorous species having higher probabilities of being present at zero areas and higher area sensitivity when compared to anemochorous species could be caused by the perch and nucleation effects (Blasi *et al.,* 2000; Bonet, 2004). Olive trees could attract seed-dispersing birds that deposit seeds around the patch periphery, and more seed dispersers could seek refuge within larger patches. Alternatively, probabilities of finding barochorous (non-significant) and dyszoochorous (significant) species showed lower increases per unit area, which could be attributed to generally lower dispersal capabilities. Dispersal of exclusively barochorous species will be limited as seeds will not be likely to roll across the flat distances that separate the patches (Vittoz & Engler, 2007). Similarly, dispersal of dyszoochorous species into patches of different areas will also be limited by the low abundance of larger seed dispersers within partially disturbed olive landscapes (Assandri *et al.,* 2017). It is also important to note that the effect of secondary dispersal strategies, such as ant-mediated dispersal (Bonet & Pausas, 2004), may have introduced further sources of uncertainty into our study.

The results suggest that both life form and dispersal strategies represent important mechanisms influencing the community composition of woody plants within the vegetation patches. However, it is important to note that the effect of each variable might be exacerbated by correlation between the factors, limiting our ability to discern between the mechanisms explaining patterns in composition. Temporal effects could have also limited our ability to unravel compositional dynamics, since patch size determined by an equilibrium between growth vs grazing and ploughing. Composition would also be affected by successional processes, and the current assemblage could have arisen as a result of different waves of establishment and interactions between different traits. We believe that after abandonment, patch size increased following an initial growth spurt as vegetation occupied the area beneath the olive canopies, but then became a relatively stable property. The spatial extent of ploughing around the trees has been generally constant, and most common species show a range of age structures with individuals of up to a couple of decades old. Still, further research into temporal changes is needed to understand the potentially confounding effects of patch size and time.

Nevertheless, the results revealed that anemochorous and endozoochorous plants, as well as vines and shrubs, are particularly benefited by increases in patch area, whereas the presence of plants with other life forms and dispersal mechanisms might not be significantly encouraged by area modifications. Presence-absence patterns observed within life form and dispersal category groups seem consistent with patterns observed by previous studies that focused on the colonisation and facilitation dynamics within abandoned landscapes, and this strengthens the validity of our binomial GLMM analysis.

Implications for management and future studies

The results reveal that patches of larger areas will support higher species richness without incurring in any loss of species. Therefore, we suggest that landholders could enhance woody plant diversity within their groves by enlarging the size of the current patches, since the presence of all woody species will be encouraged as long as there is open space between the patches. Patches could be enlarged by depositing dead wood and branches to protect growing vegetation, following the principles of common forest management strategies such as dead-wood hedge laying (Auerswald & Weigand, 1996). Enlarging patches whilst maintaining patch structure will promote plant diversity, and this has the potential to enhance seed dispersal and floral availability for pollinators (Carpio *et al.,* 2018), and to provide a wide range of vegetation microhabitats that will encourage patch occupancy by larger animals (Carpio *et al.,* 2016; Assandri *et al.,* 2017). Maintaining and enlarging patch structures could also provide increased grazing sustainability, by providing higher quantities of fodder resource, and by relieving grazing pressure thanks to the presence of a range of shrubs with different palatabilities and defence mechanisms (Papanastasis *et al.,* 2008). Woody vegetation within the patches could even act as an alternative food source during periods of scarcity such as the summer months.

We suggest that encouraging the formation of vegetation patches could indeed provide an alternative to active reforestation within grove landscapes, at least in terms of species richness and species presence. Introducing more flexibility into the European, Spanish and Andalusian reforestation schemes (BOJA, 2009; Jarský & Pulkrab, 2013; MAPA, 2014; BOCYL, 2015), could allow landholders to apply for reforestation grants by pooling the area occupied by the patches. Reforesting property owners would experience fewer costs since they would not need to plant and protect seedlings. Landowners would also be encouraged to introduce grazers into the groves, potentially providing an additional source of income (Lawson *et al.,* 2002; Carbonero Muñoz *et al.,* 2013). Furthermore, the maintenance of strong populations of *Q. ilex* in semiabandoned olive groves could eventually give rise to highly diverse and open woodland communities, meaning natural regeneration in semiabandoned olive could potentially encourage the development of seminatural systems that maintain high biodiversity, mosaic landscape structure and ecosystem services (Surová *et al.,* 2018; Torralba *et al.,* 2018).

We would therefore like to highlight the importance of using novel statistical methods such as binomial GLMMs to investigate changes in community composition within patch-like landscapes, and we encourage experts to continue investigating the underlying mechanisms determining the composition of these communities. Studying parameters such as soil properties, insolation and average air or soil moisture content would give more insight into the processes explaining differences in composition by incorporating site-related variables into the presence/absence GLMM (Shutt *et al.,* 2020). Phytophysiological factors such as plant life form, defence adaptations and average dispersal distances could also be included within the presence-absence model, to test if different adaptations are having a significant effect on the colonisation ability of species. We also acknowledge that the spatial replication within our study was limited, and we encourage fellow researchers to extend this framework into semiabandoned groves at different locations within Spain and other Mediterranean countries. This would allow researchers to determine which locations show unique compositional patch dynamics, and would encourage governments to design especial management and conservation strategies for particularly vulnerable Mediterranean plant communities.

Acknowledgments

The authors would like to thank the Ecological and Environmental Sciences staff (School of GeoSciences) at the University of Edinburgh for their support and guidance. Special thanks to Dr Kyle Dexter for his comments and recommendations during the analysis of results and the construction of the paper. Thanks to Dr Pilar Fernández Rebollo and her team at Universidad de Córdoba (Dept. Ingeniería Forestal) for their inestimable advice. We are grateful to Antonio Vargas Jiménez, Manuel Guijo García, Encarnación Cabrera Díaz, Rubén Guijo Cabrera and Rafael Nieto Galván for granting access into the estates.

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