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Lizard abundance in forest fragments: effects of patch size, patch shape, thermoregulation, and habitat quality

José A. Díaz*, Tomás Santos, Alejandro Llanos-Garrido

[1] Departamento de Biodiversidad, Ecología y Evolución,

Facultad de Biología, Universidad Complutense, E-28040 Madrid, Spain

* Corresponding author: jadiaz@ucm.es

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Abstract

The effects of forest fragmentation on ecosystems are pervasive, but little is known about the factors that influence lizard abundance in fragmented landscapes. We studied the roles of patch size and shape, thermal quality, and refuge availability as predictors of the relative abundance of *Psammodromus algirus* lizards at deciduous or evergreen forest fragments surrounded by cereal fields. Relative abundance, based on time-controlled counts, decreased from the northeast (dominated by deciduous habitat) to the southwest (with a higher cover of croplands, and dominated by evergreen habitat). Refuge availability was correlated with this gradient, decreasing from the northeast to the southwest and being larger in deciduous than in evergreen fragments. After controlling for the effects of this environmental variation, lizard abundance increased as perimeter-to-area ratio (P/A) decreased (and consequently as fragment size increased).

Although the effects of thermal quality as such were negligible, our results can be interpreted in the light of thermoregulatory requirements; given the low temperatures available at shaded locations, lizards should actively select sunlit patches while they try to minimize predation risk by basking as close as possible to the nearest refuge. Although use of fragment edges as basking sites is expected to increase with P/A ratio, lizards should avoid using them as basking sites, because both exposure to predators and risk of overheating are expected to be higher at edges and croplands than inside fragments. We conclude that long and narrow forest strips with high P/A ratios could act as ecological traps rather than as dispersion-promoting corridors.

Keywords: Croplands - Edge effects - Operative temperature - Predation - *Psammodromus algirus* - Thermoregulation

Introduction

Habitat loss and habitat fragmentation are among the commonest and most pervasive conservation problems worldwide (Lindenmayer and Fischer, 2006). Although they normally occur together, because habitat loss is often associated with the separation of the remaining habitat into a greater number of smaller patches, they actually represent different processes. While the effects of habitat loss on biodiversity are always detrimental, those of fragmentation per se (the breaking apart of habitat for a given amount of habitat loss; Fahrig 2003) might be negative (Pfeifer et al., 2017), weak (De Camargo, Boucher-Lalonde and Currie, 2018), or even positive (Fahrig, 2017). In the case of forest ecosytems, edge effects arising from boundaries between forest and non-forest habitat are characteristic of fragmentation (Pfeifer et al., 2017), irrespective of whether it is associated with habitat loss or not. The importance of these edge effects is expected to vary among different groups of organisms (Henle et al., 2004), depending on their energy demands, spatial requirements, and dispersal capacities. Reptiles, which are underrepresented in fragmentation research (Fardila et al., 2017), show a combination of traits which may have different effects on their ability to cope with fragmentation. Their ectothermic condition makes them sensitive to thermal differences between forest fragments and the surrounding matrix, reducing their dispersal capacity (Llanos-Garrido, Santos and Díaz, 2023). On the other hand, their aptitude to thrive under conditions of limited food supply may favour their persistence in small fragments.

Edges of forest patches may have positive consequences for the thermal biology of reptiles in cool climates, where they have higher temperatures than the forest core but lower temperatures than open habitats (Sato et al., 2014a). Therefore, forest edges are preferred by subalpine lizards (Sato et al., 2014b) or by snakes inhabiting northern forests (Blouin-Demers and Weatherhead, 2001). However, in most temperate and tropical environments forest fragmentation is usually detrimental (Nowakowski et al., 2018; Iglesias-Carrasco, Medina and Ord, 2023) because the agricultural matrix receives more solar radiation and attains higher and more variable temperatures than forest fragments (Murcia, 1995; Hofmeister et al., 2019). In addition, its low structural complexity minimizes not only the amount of shade, but also the availability of refuges, increasing exposure to predators in edge habitats (Hansen et al., 2019).

Edge effects can be estimated by different measures, such as the classical perimeter-to-area ratio (hereafter P/A). For a given area, more complex shapes (e.g., fragments with long narrow projections, or corridors) will have a longer edge and therefore a higher P/A ratio (Krummel et al., 1987). Also, P/A should decrease with patch size, because for a given shape perimeter reflects linear dimensions, whereas area grows with the square of linear dimensions. Thus, in fragments with high P/A ratios (i.e., small, elongated and/or narrow), forest habitat (including the shrub layer) tends to show a more clumped distribution. This should translate into less thermal heterogeneity, which decreases the efectiveness of behavioural thermoregulation and increases its energy expenditure (Sears et al. 2016; Llanos-Garrido, Santos and Díaz, 2023). All in all, habitat structure in fragments with high P/A ratios should force sun-seeking squamates to use forest edges as basking sites, which might negatively affect their performance by increasing risk of overheating (Hofmeister et al., 2019), exposure to predators (Hansen et al., 2019) or both. This should decrease population size, due to higher mortality combined with less suitable habitat.

The effects of forest fragmentation on lizards deserves special attention in the Mediterranean region, where they form a conspicuous part of ecosystems in which the expansion of croplands began more than 8,000 years ago. In fact, many widely distributed European species are rare (or absent) in cultivated areas where they should be abundant based on geography and climate. Recent studies have shown that agricultural expansion narrows the distribution range of forest lizards (Llanos-Garrido et al., 2021), and that temperatures available in croplands are too high to allow their dispersal (Llanos-Garrido, Santos and Díaz, 2023).

However, a question that needs to be addressed is how do fragment characteristics (e.g., size, shape, habitat structure, thermal environment, etc.) affect variations in the relative abundance of lizards. Abundance serves as the basic tool to quantify biodiversity and guide conservation efforts (Dirzo et al., 2014), and it may establish a link between the effects of fragmentation on individual fitness (Díaz et al., 2005; Pérez-Tris et al., 2019) and its demographic consequences at a landscape scale (Biaggini and Corti, 2021). The identification of fragment traits associated with variations in abundance may also shed light on the relative importance of fragment size per se vs. size-related changes in P/A ratio (and associated edge effects) as determinants of lizard abundance. This may be useful to produce predictive models that can suggest management decisions (e.g., the assignment of conservation priorities or the design of reserve networks) aimed to compensate or mitigate the negative effects of fragmentation.

Within this context, the purpose of this study is to model variations in abundance of a widespread Mediterranean lacertid lizard, the large Psammodromus *Psammodromus algirus*, among forest fragments surrounded by a matrix of unsuitable agricultural habitat. We try to fill several gaps of knowledge: we use abundance rather than occurrence to model the effects of fragmentation in a taxonomic group that has received much less attention than birds or mammals (Fardila et al., 2017), we explicitely address the contribution of habitat thermal quality as a predictor of abundance, and we take into account the influence of environmental gradients that may confound or complement the impact of fragmentation as such (e.g., edge effects) on the distribution of lizards.

Our goal was to address the following specific questions: 1) Considering that in central Spain lizards are more abundant at deciduous than at evergreen habitat (Díaz, 1997), does variation in lizard abundance between deciduous and evergreen fragments confirm the higher quality of the former? 2) What factors (e.g., size, shape, thermal quality, refuge availability) are mainly responsible for variations in lizard abundance, and how do they combine to produce useful predictive models? How much do these factors differ between deciduous and evergreen habitat?, and 3) What is the relationship of these models with previously reported effects of fragmentation on the reproductive investment (Díaz et al., 2005), genetic diversity (Pérez-Tris et al., 2019), and thermal biology of lizards (Llanos-Garrido, Santos and Díaz, 2023)?

Materials and Methods

Study species

Psammodromus algirus is a medium-sized (adult snout-vent length 60-85 mm; mass 6-15 g) heliothermic and insectivorous lacertid, that inhabits shrub and woodland habitats of the western Mediterranean region where it is usually the most abundant lizard (Díaz and Carrascal 1991).

Study area

Our study area, close to the northern edge of its distribution range, is an agricultural landscape located around Lerma, in central-northern Spain (42° 01’ N, 3° 45’ O). In this area, forest covers less than 10% of its former surface in the form of fragments of variable surface area interspersed across a matrix of cereal fields. Fragments penetrate the cultivated fields from the northeast (Fig. 1), where the nearby mountains produce more mesic conditions and the dominant trees are deciduous Pyrenean oaks (*Quercus pyrenaica*), to the southwest, where conditions are more xeric and the dominant trees are evergreen Holm oaks (*Quercus ilex*).

This system has been widely used as a model to examine the effects of fragmentation on the distribution and biology of lizards (Díaz et al., 2000; Díaz et al., 2005; Santos et al., 2008; Pérez-Tris et al., 2019; Llanos-Garrido, Santos and Díaz, 2023). Our first attempts to model such distribution showed that the frequency of lizard occurrence in the fragmented landscape was very low, and that historical fragmentation of the habitat was crucial to understand the current distribution of lizards (Díaz et al., 2000). Vegetation structure, a good predictor of abundance under conditions of no fragmentation (Díaz and Carrascal, 1991), failed to predict lizard occurrence in fragments (Díaz et al., 2000). Later, we found that patch size and specially habitat type were the main determinants of the occurrence of lizards in forest remnants, because above a fragment size threshold of 0.5 ha, lizards were more frequently found in deciduous than in evergreen woodlands (Santos et al., 2008). More recently, we examined the thermal biology of lizards in a sample of fragments (Llanos-Garrido, Santos and Díaz, 2023), and we gathered the data about fragment characteristics and relative abundance that are the focus of this study. These fragments were selected because they covered a representative range of surface areas (0.6-7 ha) and included both evergreen and deciduous habitat.

Lizard abundance

Lizards were counted by means of time-controlled search when meteorological conditions were appropriate for lizard activity. We sampled the fragments by walking within them and along their edges, and we recorded the exact time in which we entered and left the fragment in each visit. Abundance was expressed as the number of lizards detected per 10 min of search, after discounting the time invested in capturing lizards to measure their body temperatures (T_bs). This simple index of abundance (Table 1) does not provide a measure of the actual density of lizards, but it allows the among-patches comparison of relative abundance. Because our index relies on the number of active lizards detected, an obvious caveat of our data is that such index might reflect variations in the detectability of lizards rather than in their actual abundance (Mazerolle et al., 2007; Romano et al., 2022). However, some well-known sources of variation in detectability were held constant by design, because all censuses were done by the same researchers while controlling for the confounding effects of circadian variations in activity (see below). Concerning habitat effects, it can be argued that if our index reflected probability of detection rather than abundance, it should be higher at fragments where refuges were scarcer and/or more dispersed. Our data, in fact, revealed the opposite pattern, of higher abundance at fragments where refuge availability is higher and detectability is lower (see Results below). Also, the possibility of double counts should be higher in fragments with smaller densities, leading to a subestimation of differences in abundance that would make our analyses conservative.

Each fragment was sampled on one (fragments 2 and 3), two (fragments 12, 43, and 46) or three (fragments 6, 7, 12b, V1, and V2) different sampling days. We tried to cover morning, midday, and afternoon censuses in all sites (e.g., by moving between fragments 2 and 3 in the morning, midday, and afternoon of the single day they were sampled) to prevent the confounding effects of circadian variations in lizard activity. Effective searching time (mean ± SD) was 195 ± 47 minutes per fragment.

Independent variables

We considered several types of variables (Table 1). Firstly, those depicting the size, shape, and internal structure of fragments (area, perimeter, P/A, area covered by clearings, and mean distance to nearest refuge) or their geographical location (latitude and longitude in the form of xy coordinates; Fig. 1 and supplementary table S1). Secondly, those describing the thermal characteristics of fragments and the thermal biology of lizards, which were estimated using the protocol designed by Hertz, Huey and Stevenson (1993) to evaluate field thermoregulation by ectotherms.

Area, perimeter, and area covered by clearings were measured on aerial photographs using the SIGPAC (Agricultural Plots Geographic Information System) web viewer from the Spanish Ministry of Agriculture, Fisheries and Food (http://sigpac.mapama.gob.es/fega/visor/). We calculated surface area and perimeter directly, with the appropriate tools provided by SIGPAC. As a measure of patch shape, we used the P/A ratio. To estimate the area covered by clearings (supplementary figure S1), we processed SIGPAC photographs with the 'magic wand' tool of Adobe Photoshop CS6. We firstly counted with the 'Histogram' panel the total number of pixels in each fragment, after having cut it out from the surrounding matrix. Subsequently, we used the magic wand, with a tolerance value of 20, to select only clearings (which were distinguished by their lighter colour; fig. S1). We inverted selection to delete non-clearings, adjusted brightness and contrast to produce black-and-white ‘negatives’ (fig. S1), and counted the number of pixels within clearings. Finally, we used the quotient between the number of pixels within clearings and the total number of pixels, multiplied by fragment area, to estimate the area covered by clearings. We measured the three non-derived variables (surface area, perimeter, and proportion of area covered by clearings) twice to obtain repeatability estimates. Given that all repeatabilities were high (intraclass correlation coefficients of 0.996, 0.994, and 0.964, respectively), we used the average of the two estimates in our final database.

Variables describing the thermal environment and thermoregulatory behaviour of lizards (Hertz, Huey and Stevenson, 1993) included: mean operative temperatures (T_es, or the body temperatures that nonregulating lizards would achieve, given the interactions between their biophysical properties and those of their environment); thermal quality (d_e, or mean deviation of T_es from the selected thermal range [T_{sel}]); accuracy of thermoregulation (d_b, or mean deviation of T_es from T_{sel}); and effectiveness of thermoregulation (E, or extent to which T_bs are closer to T_{sel} than T_es [$E = 1 – d_b/d_e$]). The methods used to estimate these variables have been detailed elsewhere (Llanos-Garrido, Santos and Díaz, 2023). We estimated T_es using Thermochron iButtons (model DS1921G-F5) with the help of a previously published equation ($T_e = 5.4069 + 0.895\ T_{iB}$; Díaz et al., 2022) that allowed us to calculate T_es as a function of the temperature values registered by iBs (T_{iB}s).

Thermochron iButtons were also used to estimate availability of refuges, assuming that their regular spacing along linear transects traced on aerial views should provide an unbiased sample of habitat structure. For that purpose, we measured in the field the distance of each iButton to the nearest structure that could hide a lizard from a potential predator, such as wood logs, bushes, grass tussocks, or holes associated with tree roots. Sample sizes (i.e., numbers of iBs per fragment) were proportional to surface area, with a minimum of 12 and a maximum of 30 loggers per fragment (Table S1).

Body (cloacal) temperatures were measured with a Miller-Weber quick-reading mercury thermometer in a sample of 82 adult lizards from all fragments that were captured at different times of day (Llanos-Garrido, Santos and Díaz, 2023). The estimates of the abundance of lizards and the assessment of their thermal biology were carried out simultaneously (between 10 June and 1 July 2019).

Statistical methods

We used general linear models, principal component analyses, stepwise model selection methods, and partial least squares regression (PLS) to clarify associations between variables and to choose the independent variables that best predict variations in abundance.

Given our reduced sample size, our first step was to summarize and carefully select the set of predictors to consider in our models. A preliminary inspection of the matrix of correlations among independent variables showed two blocks of intercorrelated variables: those describing the size and shape of fragments (area, perimeter, P/A ratio, and area covered by clearings), and those describing the thermal biology of lizards (T_e, d_e, T_b, d_b, and E). All variables within the first block showed high levels of redundancy (all $r^2 > 0.57$ and all $P < 0.01$). However, we chose to retain three of the original variables rather than calculating principal components because we were interested in disentangling the effects of size (area), shape (P/A ratio), and availability of clearings on lizard abundance. Thus, we relied on partial correlations and cross-validation methods (see below) to estimate the strength of the association between abundance and each predictor of interest, after statistically controlling for the misleading effects of other confounding variables included in the model.

Latitude and longitude were summarized in a single principal component (EG-PC; loading = 0.916, explained variance = 83.5%) that represented the environmental gradient running from the northeast (dominated by deciduous habitat) to the southwest (dominated by evergreen habitat; fig. 1 and Table 2). This PC allowed us to include an explicit geographical component in our models.

With respect to variables describing the thermal biology of lizards, we obtained two principal components with eigenvalues > 1 (Table 2). The first one was a component of thermoregulatory effectiveness (PC1) giving higher scores to fragments where lizards attained higher body temperatures, leading to higher values of thermoregulatory accuracy and effectiveness (Hertz, Huey and Stevenson, 1993). The second one was a component of habitat thermal quality (PC2, Table 2) giving higher scores to fragments with higher operative temperatures that were closer to the preferred range. We discarded PC1 as a predictor of lizard abundance because the correlated variables could not be regarded as independent of the activity and behaviour of lizards, but we retained PC2 because it was correlated only with T_e and d_e (i.e., the variables that describe the thermal environment of the fragments).

Thus, the final independent variables to be considered for modelling lizard abundance were area of the fragment, P/A ratio, area covered by clearings, location along the southwest-northeast environmental gradient (EG-PC), availability of refuges (as measured by the mean distance of iButtons to the nearest refuge, hereafter D_{ref}), and habitat thermal quality (PC2). The effects of type of habitat (deciduous vs. perennial) were analysed using linear models (ANOVA and ANCOVA). To explore predictive models, we used two different approaches. Firstly, we used forward and backward stepwise regressions combined with simple and partial correlations that helped to clarify the relationships among lizard abundance and the independent variables. Secondly, we used Partial Least Squares regression (PLS), an extension of multiple regression explicitly designed to deal with numerous -relative to sample size- and highly collinear predictors (Carrascal, Galván and Gordo, 2009). PLS regression gathers the predictors in one (or more) multivariate factor(s) according to the underlying relationships among the original variables (fragment features), and forces such factor(s) to maximize the explained variance of the dependent variable (lizard abundance); each factor denotes an environmental gradient defined by a specific linear combination of predictors. The relative contribution of each of k predictors to a given factor can be assessed by the square of its predictor weight; since the sum of squared weights is equal to 100% of the explained variance, every predictor with a squared weight greater than 1/k can contribute significantly to the final interpretation of the factor (Carrascal, Galván and Gordo, 2009).

Finally, we also applied a leave-one-out cross validation approach (LOOCV). This method leaves out one data point at each iteration and builds the model on the rest of the data set, recording its goodness of fit and the size and significance of each of its terms. It then tests the model against the data point that is left out and records its prediction error. The advantages of LOOCV are twofold: it makes use of all data points, therefore reducing potential bias, and it helps identifying outliers and/or influential data.

Results

Within the final set of independent variables, and besides significant correlations between fragment size and shape variables (larger fragments had smaller P/A ratios and larger areas covered by clearings), the only relevant association was between D_{ref} and location along EG-PC (r = -0.789, P = 0.007), meaning that accessibility of refuges decreased (D_{ref} increased) from the northeast to the southwest. Interestingly, these were the only variables that differed significantly between forest types: deciduous forests had smaller distances to nearest refuge and more northern and eastern locations than evergreen ones (D_{ref} : $F_{1,8}$ = 26.41, P = 0.0009; mean ± SD = 46 ± 26 cm and 147 ± 37 cm for deciduous and evergreen fragments, respectively; EG-PC scores: $F_{1,8}$ = 5.69, P = 0.044). Consequently, the association between D_{ref} and geography weakened after controlling for the effect of type of habitat in an ANCOVA with D_{ref} as the dependent variable, EG-PC as the covariate, and habitat type as the categorical factor (EG-PC: $F_{1,7}$ = 4.69, P = 0.082; type of habitat: $F_{1,7}$ = 11.05, P = 0.013).

Location on the environmental gradient was the only independent variable whose simple correlation with lizard abundance was significant (r = 0.800, P = 0.0054; abundance increased eastwards and northwards). Correlations with D_{ref} and with variables describing fragment size and shape were marginally non-significant (D_{ref} : r = -0.617, P = 0.058; area: r = 0.605, P = 0.064; P/A ratio: r = -0.556, P = 0.095). A different picture emerged from stepwise regressions models, both forward and backward (model #1, Table 3). After controlling for the effects of EG-PC (partial correlation: r = 0.880, P = 0.002), abundance decreased as P/A ratio increased (partial correlation: r = -0.752, P = 0.019). Thus, P/A ratio was selected as a better predictor of lizard abundance than fragment area or area covered by clearings. However, residuals from model #1 deviated significantly from normality (Table 3), indicating nonlinearity and/or the presence of outliers or influential data points. For that reason, we tested a second model (model #2) with D_{ref} and P/A ratio as predictors of lizard abundance, also because availability of refuges has a clearer ecological meaning than geographical location. This second model (partial correlations: r = -0.862 and P = 0.003 for D_{ref}, and

r = -0.845 and P = 0.004 for P/A) had roughly the same predictive power as model #1 (r^2 = 0.844 and 0.823 for models #1 and #2, respectively), but with residuals that did not depart significantly from normality (Table 3). Thus, lizards were more abundant at fragments with a smaller P/A ratio (i.e., of larger size and/or lacking long, narrow projections) and with a higher availability of refuges (fig. 2). The same models, but with fragment area in the place of P/A ratio (Table 3: models #1b and #2b), were poorer predictors of lizard abundance, with lower partial correlations especially for fragment area (Table 3). Again, the adjustment of residuals to normality was better for model #2b than for model #1b.

Results of leave-one-out cross validation, which are summarized in Table S2, further clarified patterns of covariation between lizard abundance and fragment characteristics. In most cases (7 of 10), model #1 was selected in both forward and backward stepwise regressions, although model #2 performed nearly as well. However, a different picture emerged when fragments 7, 46 or V1 were excluded (Table S2). The exclusion of fragment 7, which had the lowest D_{ref} (i.e., the highest availability of refuges) and the highest P/A ratio (Table 1), led to a loss of predictive power in forward stepwise regression, with only EG-PC entering the model (r^2 = 0.766). Backward stepwise regression selected model #2, with the combined effects of D_{ref} and P/A ratio explaining a larger proportion of the variance in lizard abundance (r^2 = 0.849) across the remaining fragments. Excluding fragment 46, which had the lowest P/A ratio, changed the result of stepwise backward regression, selecting a model in which lizard abundance increased with refuge availability (partial correlation with D_{ref}: r = -0.964 and P < 0.001) and decreased with P/A ratio (partial correlation: r = -0.948 and P = 0.001) and area covered by clearings (partial correlation: r = -0.855 and P = 0.014). Finally, the exclusion of fragment V1, one of the two fragments separated from the rest at the southwestern margin of the study area (fig. 1), selected model #2 in both forward and backward stepwise regressions ($r^2 = 0.947$; partial correlations: $r = -0.940$ for D_{ref}, and $r = -0.959$ for P/A; both $P < 0.001$). Thus, fragment V1 seems to act as an influential data point (see prediction errors in Table S2) that is mostly responsible of the larger effect of geographical location on lizard abundance relative to the (correlated) effect of D_{ref}.

Given the relevance of model #2 to predict lizard abundance (fig. 2) and the relationship between habitat type and D_{ref}, we investigated whether lizard abundance differed between deciduous and evergreen fragments after controlling for the effects of P/A ratio as a covariate. The answer provided by the appropriate ANCOVA was unequivocal: for a given P/A ratio, lizards were more abundant at deciduous than at evergreen fragments (habitat: $F_{1,7} = 12.97$, $P = 0.009$; P/A ratio: $F_{1,7} = 16.68$, $P = 0.005$; homogeneity of slopes: $F_{1,6} = 0.0175$, $P = 0.899$; adjusted means [± SE] of 1.23 ± 0.10 and 0.66 ± 0.12 lizards/10 min at deciduous and evergreen fragments, respectively). Residuals of the ANCOVA model did not depart significantly from normality (Shapiro-Wilk test: $W = 0.992$, $P = 0.998$). The effects of both habitat and P/A ratio were significant in all (10 of 10) LOOCV's.

A PLS analysis with lizard abundance as the dependent variable produced two significant components (Table 4) that retained 75.23% of the variance contained in the matrix of predictors (R^2X = 0.3981 and 0.3542 for components 1 and 2, respectively). The predictors that contributed significantly to component 1 (see Methods) were D_{ref} and P/A ratio with negative weights, and A and EG-PC with positive weights. Thus, component 1 gave higher scores to larger fragments with smaller P/A ratios and larger availability refuges, located closer to the northeastern end of the environmental gradient. Component 2, which was orthogonal (by design) to component 1, gave higher scores to (smaller) fragments with smaller areas covered by clearings (Table 4). These two components explained 83.69% of the total variance in lizard abundance (R^2Y = 0.7857 and 0.0512 for components 1 and 2, respectively); regression coefficients for X-scores were positive in both cases (estimate ± 1 SE = 0.2406 ± 0.4143 for component 1, and 0.0705 ± 0.0475 for component 2).

Although the effects of habitat thermal quality on lizard abundance were negligible, because PC2 was never selected as predictor in any of the models, lizard abundance was positively correlated with mean body temperature ($r = 0.715$, N = 10, $P = 0.020$). Again, residuals did not depart significantly from normality (Shapiro-Wilk test: $W = 0.983$, $P = 0.978$), and correlations with T_b were significant for all (10 of 10) LOOCV's.

Discussion

Our results represent a significant step forward for understanding the distribution of lizards in the fragmented landscape. In fact, this is the first time that we succeed to model lizard abundance in this system ($r^2 > 80\%$ of variance explained), which is important because abundance sets a bridge between the negative effects of fragmentation on traits that are measured at the individual level (such as reproductive success, genetic diversity, or thermal biology; Díaz et al., 2005; Pérez-Tris et al., 2019; Llanos-Garrido, Santos and Díaz, 2023), and the population level which is the focus of conservation biologists.

Among the factors controlling variation in lizard numbers, the most prominent role was that of geographical location along the environmental gradient running from the NE, dominated by deciduous forest habitat, to the cropland-dominated SW area (i.e., EG-PC): it was included in nearly all regression models, and it had a high modeling power in PLS. The higher abundance of lizards at more eastern and northern fragments was partly attributable to the fact that at the study area deciduous forests offer a better habitat than evergreen ones (Santos et al., 2008). In central Spain, the former have provide more prey than the later (Iraeta et al., 2006); this allows populations from deciduous habitat to form larger clutches, grow faster and reach higher densities (Díaz, 1997; Iraeta et al., 2006). Our results confirm that the higher quality of deciduous fragments is also due, at least in part, to their higher availability of refuges. In fact, EG-PC and D_{ref} were correlated, and they played similar roles in modeling lizard abundance after controlling for the effects of P/A ratio, as it can be seen by comparing models #1 and #2. However, EG-PC has also an explicit geographic significance that may reflect dispersion dynamics from more continuous forest in the NE (potential source of dispersing individuals) to more fragmented habitat in the SW (fig. 1), where the intensity of gene flow is expected to be lower. Previous research has shown that individual relatedness is greater within fragments than among them, which is symptomatic of reduced gene flow (Pérez-Tris et al., 2019). However, more markers and much larger samples are needed to understand the traces of adaptation, dispersal and demographic history on lizard genomes (Barley et al., 2015; Winchell et al., 2023).

Patch size, and specially P/A ratio, became important predictors of lizard abundance after controlling for the effects of refuge availability. Thermoregulatory requirements may be relevant to understand the effects of these variables on lizard abundance, even if the effects of thermal quality per se are negligible (Díaz, 1997). Given the high proportion of T_es below T_{sel} at shaded locations, lizards actively selected sunlit patches (such as those available at clearings or forest edges), and they tried to do so while remaining within short reach of the habitat features that provide shade and refuge (Llanos-Garrido, Santos and Díaz, 2023).

The requirement of basking in the vicinity of a refuge (Díaz, 1992) may shed light on why P/A ratio was correlated with lizard abundance after controlling for the effects of D_{ref}. According to our results, both availability of edges and area covered by clearings covaried with fragment size, but in the opposite direction (availability of clearings increased, whereas P/A decreased, with fragment size). On the other hand, the quality of clearings as potential basking sites is expected to be higher than that of fragment edges (Hansen et al., 2019), because lizards obliged to flee in the direction of cereal fields face a high risk of predation which could hamper their survival, and they expose to overheating if they cannot readily return to the shaded forest edge (Llanos-Garrido, Santos and Díaz, 2023). These negative edge effects could explain why lizards were less abundant in fragments with a lower availability of refuges and a higher P/A ratio (i.e., of small size or with long, narrow projections). Thus, abundance was lowest in fragment V2, one the two southernmost evergreen fragments, which combined the highest value of D_{ref} with one of the highest P/A ratios. This means that in this fragment, sun-seeking lizards probably face an increased risk of predation, by being obliged to use either fragment edges or sunlit patches far from the security of a refuge. Similarly, fragment 7 was the deciduous fragment where lizard abundance was lowest, despite its very high refuge availability. This was likely a consequence of its small size and elongated shape, which was responsible of its high P/A ratio, that may have forced sun-seeking lizards to use sunlit patches along fragment edges. Moreover, fragment 7 was the one with the lowest average operative temperature (28.9ºC) and the highest percentage of T_e readings below T_{sel} (71%), which means that thermoregulating lizards were obliged to select sunlit patches more often than in other deciduous fragments.

The effect of clearings on lizard abundance, after controlling for the effects of refuge availability and P/A ratio, was negative, as shown by the significant partial correlation in LOOCV excluding fragment 46 (which had the highest surface covered by clearings; $r = -0.855$ and $P = 0.014$), and specially by the results of PLS: area covered by clearings had a negative weight on component 2 (Table 4), which was positively correlated with lizard abundance after controlling for the effects of component 1. In summary, lizard abundance, although not correlated with T_es available, increased in fragments in which lizards could thermoregulate effectively while avoiding fragment edges or sunlit sites too far from the security of a refuge, such as those available in large clearings (Llanos-Garrido, Santos and Díaz, 2023).

We can therefore conclude that lizard abundance in the fragmented landscape depends on the ability of these heliothermic lizards to select sunlit sites while minimizing exposure to potential predators (Díaz, 1992; Rusch et al., 2022). Thus, lizard abundance was positively correlated with mean T_b (even after controlling for the effects of D_{ref} and P/A ratio). This confirms the idea that the fragments where lizards reach higher densities are those that facilitate attaining higher T_bs in a thermal environment where most T_es are below T_{sel} (Llanos-Garrido, Santos and Díaz, 2023). On the other hand, these results exemplify the problems associated with purely correlational studies: the direction of causality is difficult to establish because higher T_bs promote more efficient feeding (Díaz, 1994), which translates into faster growth and increased fecundity (Iraeta et al., 2006). Also, both higher density and higher T_b may be due to other variables that interact to modify habitat quality, such as reduced risk of predation or high levels of prey abundance; thus, predator avoidance tactics may lead to less efficient basking and feeding, resulting in long-term fitness costs (Downes, 2001).

Our results showed that, for the same P/A ratio, abundance was larger at deciduous than at evergreen forests, confirming the higher quality of the former not only under conditions of unfragmented habitat at the core of the species' distribution range (Díaz, 1997; Iraeta et al., 2006), but also at a fragmented landscape close to the northern (i.e., cool and moist) limit of that range (Santos et al., 2008; Llanos-Garrido et al., 2021). Moreover, in our system both types of habitat are interspersed within the same (meta)population, thus controlling the confounding effect of location on previous comparisons in which populations occupying evergreen and deciduous forests were separated by a 600-m elevational gradient (Díaz, 1997; Iraeta et al., 2006).

At the fragmented landscape, the higher quality of deciduous habitat is mainly due to a higher availability of refuges, because D_{ref} was much smaller at deciduous than at evergreen fragments (R^2 = 76.8% variance explained in the one-way ANOVA). Moreover, average distance between sunlit and shaded patches was shorter in deciduous than in evergreen habitat (Llanos-Garrido, Santos and Díaz, 2023), producing a less clumped distribution of thermal resources that should make thermoregulation more efficient and less energy-consuming (Sears and Angilletta, 2015; Sears et al., 2016). Consistently with the fact that a patchier distribution of sun and shade improves thermoregulation under simulated predation risk (Rusch et al., 2022), lizards were more selective in their choice of sunlit sites in evergreen than in deciduous habitat (i.e., in both cases they used sunlit patches closer to shade than expected at random, but the extent of such selection was larger at evergreen habitat). Thus, the cost of thermoregulation appeared to be lower at deciduous fragments (Llanos-Garrido, Santos and Díaz, 2023).

Finally, our results offer some interesting information to select the fragments which should receive conservation priority. Such fragments should be of deciduous forest (or show a high availability of refuges), as large as possible, and with a shape that minimizes P/A ratio. We also suggest that long and narrow forest strips could hamper the conservation of small heliothermic reptiles, because they could act as ecological traps rather than as dispersion-promoting corridors. We encourage empirical studies to test the predictions of these hypotheses.

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Table 1. Variables used to model lizard abundance as a function of type of habitat (D = deciduous, E = evergreen) and fragment characteristics. See Methods for details about thermal variables.

Fragment	Habitat	Abundance (lizards / 10 min)	Mean distance (± SD) to nearest refuge (D_{ref}, in cm)	Surface area (A, in ha)	Perimeter (P, in hm)	Perimeter-to-area ratio (P/A)	Area covered by clearings (A cl, in ha)	T_e (ºC)	d_e (ºC)	T_b (ºC)	d_b (ºC)	E
2	D	0.99	65 ± 64	3.3	14.6	4.46	0.89	33.5	8.4	32.8	0.3	0.965
3	D	0.75	88 ± 76	0.6	4.0	6.56	0.17	34.29	10.1	30.9	1.7	0.824
6	D	1.55	31 ± 27	3.5	13.2	3.73	0.61	33.23	8.5	33.4	0.7	0.904
7	D	0.67	18 ± 19	0.8	6.5	7.70	0.17	28.94	7.1	31.2	1.6	0.816
12	D	1.54	36 ± 34	7.0	17.1	2.45	0.96	32.52	8.2	34.2	0.3	0.947
12b	D	1.34	37 ± 30	3.0	11.4	3.79	0.51	33.96	9.2	34.1	0.8	0.885
43	E	1.08	114 ± 80	1.4	5.3	3.92	0.20	30.29	7.2	35.0	0.7	0.913
46	E	1.19	137 ± 75	6.5	12.5	1.91	2.16	34.14	8.5	35.1	0.9	0.916
V1	E	0.60	138 ± 137	4.2	11.4	2.70	1.26	33.91	7.9	30.5	2.0	0.730
V2	E	0.35	201 ± 146	1.0	5.4	5.47	0.14	33.74	8.5	32.2	0.6	0.916

Table 2. Results of Principal Component Analyses with variables describing the geographical location of fragments (EG-PC), their thermal characteristics (PC2), and the thermal biology of their lizard populations (PC1): factor loadings, eigenvalues, and explained variances for the variables (predictors) included in each component; and factor scores for fragments.

Factor loadings (predictors)	EG-PC	PC1	PC2
Latitude (y)	0.916	---	---
Longitude (x)	0.916	---	---
T_b	---	0.874	-0.091
d_b	---	-0.964	-0.030
T_e	---	0.029	0.940
d_e	---	-0.035	0.944
E	---	0.968	0.059
Eigenvalue	1.679	2.63	1.79
% var. explained	0.840	0.526	0.357

Fragment scores (fragment #)	EG-PC	PC1	PC2
2	-0.083	0.815	0.260
3	-0.142	-1.169	1.477
6	0.207	0.377	0.172
7	0.321	-1.071	-1.870
12	1.275	1.010	-0.176
12b	1.417	0.336	0.822
43	0.050	0.699	-1.480
46	0.167	0.645	0.392
V1	-1.572	-1.892	-0.014
V2	-1.640	0.250	0.418

Table 3. Models relating lizard abundance (number of lizards/10 min of search) and independent variables EG-PC (position along a northeast-southwest biogeographical gradient), perimeter-to-area ratio ratio (P/A), surface area (A), and/or mean distance to nearest refuge (D_{ref}): model statistics (explained variance, F, and P), normality of residuals (Shapiro-Wilk W and P), model equations (estimate, partial correlation, and P-value for each term in the corresponding model), and number of leave-one-out crossvalidations (LOOCVs) in which partial correlation is significant.

Model	Formula	R^2	$F_{2,7}$	P	S-W W	S-W P	Terms in model	Estimate	Partial correlation	P	LOOCVs
1	IA = EG-PC + P/A	0.844	18.88	0.0015	0.71	0.0012	Intercept	1.4396	---	---	---
							EG-PC	0.3022	0.880	0.0018	10 of 10
							P/A	-0.1013	-0.752	0.0194	9 of 10
2	IA = D_{ref} + P/A	0.823	16.27	0.0023	0.89	0.1523	Intercept	2.0775	---	---	---
							D ref	-0.005	-0.862	0.0028	10 of 10
							P/A	-0.1501	-0.845	0.0041	10 of 10
1b	IA = EG-PC + A	0.773	11.90	0.0056	0.82	0.024	Intercept	0.7908	---	---	---
							EG-PC	0.2762	0.801	0.0095	9 of 10
							A	0.0691	0.607	0.0830	1 of 10
2b	IA = D_{ref} + A	0.677	7.35	0.0191	0.96	0.7441	Intercept	1.0310	---	---	---
							D ref	-0.0038	-0.701	0.0355	3 of 10
							A	0.0983	0.693	0.0387	4 of 10

Table 4. Predictor weights and fragment scores for the two significant components obtained using Non-Iterative Partial Least Squares, which evaluates the significance of each component by considering not only the proportion of variance explained by it, but also its predictive power through a sevenfold cross-validation process.

Predictor weights (predictors)	Component 1	Component 2
Distance to nearest refuge (D_{ref})	-0.4610	-0.3639
Surface area (A)	0.4524	-0.4294
P/A ratio (P/A)	-0.4157	0.0849
Area clearings (A cl)	0.2240	-0.7308
EG-PC	0.5983	0.3767
PC2	0.0445	0.0014

Fragment scores (fragment #)	Component 1	Component 2
2	0.172	-0.086
3	-1.231	0.856
6	0.726	0.590
7	-0.782	1.556
12	2.398	0.226
12b	1.285	1.347
43	-0.695	0.589
46	1.440	-2.325
V1	-0.572	-1.940
V2	-2.742	-0.814

Figure legends

Figure 1. Map of the study area showing the location of fragments. Evergreen forests (black on pale green) are dominated by Holm oaks (*Quercus ilex*) whereas deciduous forests (white on dark green) are dominated by Pyrenean oaks (*Quercus pyrenaica*). Silhouettes at both sides of the map show enlarged versions of the fragments, with sizes proportional to their surface areas.

Figure 2. Lizard abundance (with lizard pictures showing expected number of sightings in a 50 min search) as a function of mean distance to nearest refuge and perimeter-to-area ratio (i.e., Model 2 in Table3); deciduous and evergreen fragments are shown in dark and pale green, respectively. On the right side of the panel, silhouettes depict fragments ordered from highest (top) to lowest (bottom) abundance; mean distance to nearest refuge is also represented.

Figure 1

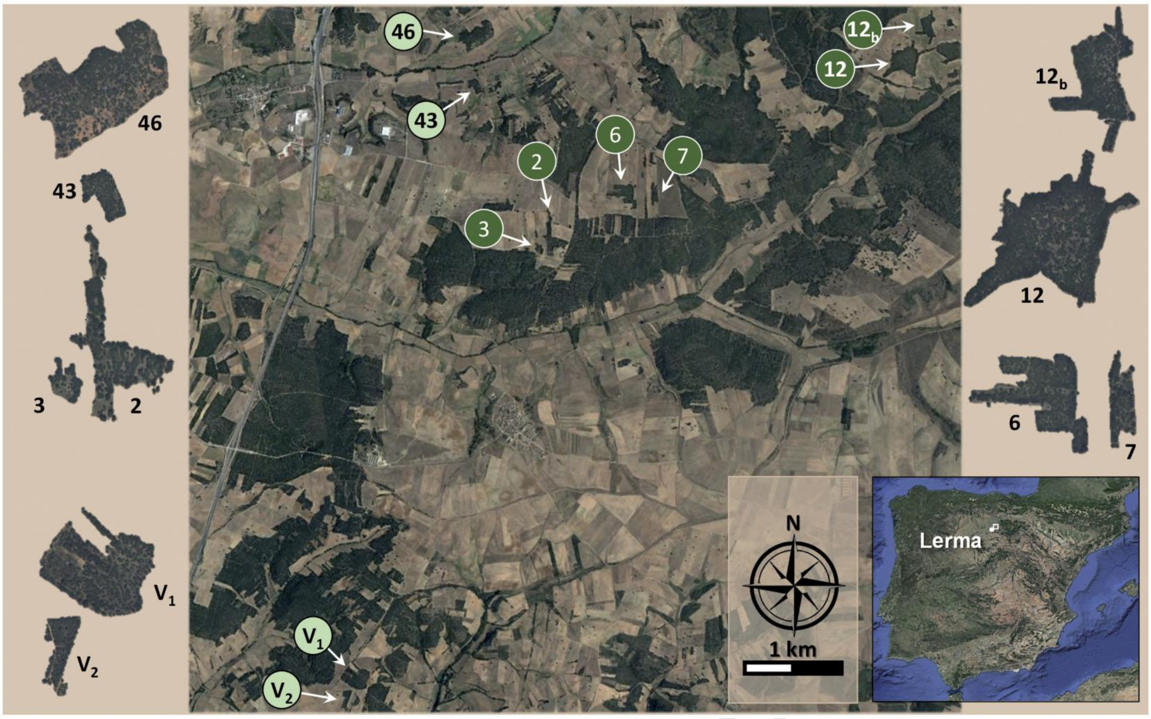
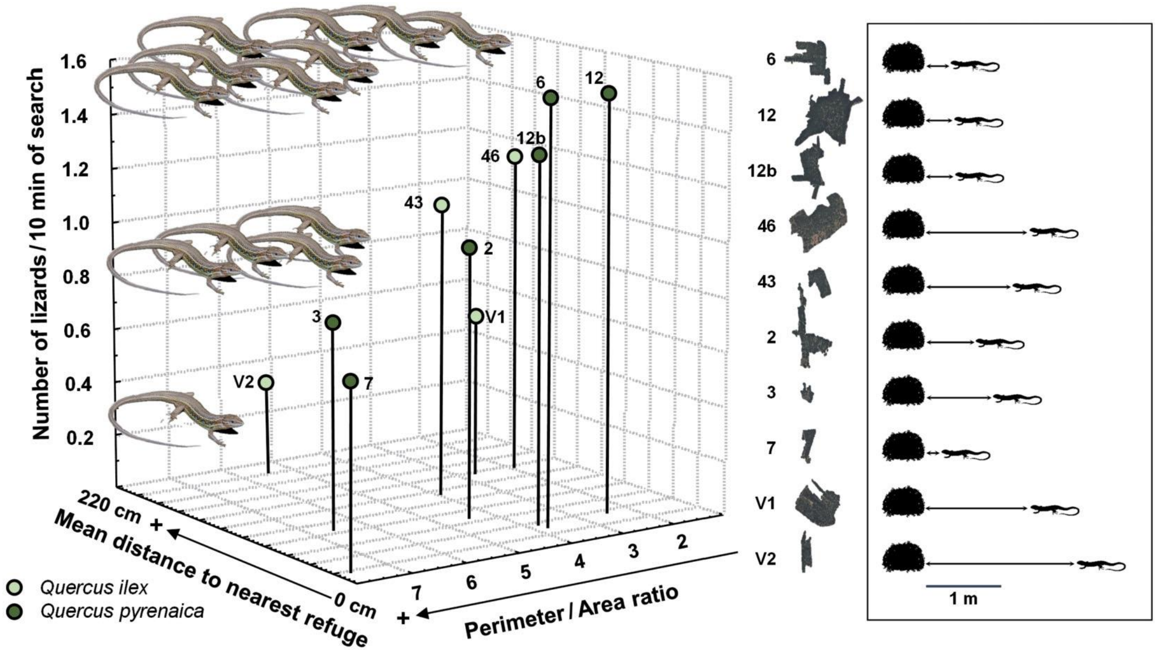


Figure 2


Number of lizards / 10 min of search
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
220 cm +
Mean distance to nearest refuge
0 cm
+
7
6
5
4
3
2
Perimeter / Area ratio
6
12
12b
46
43
2
V1
3
7
V2
Quercus ilex
Quercus pyrenaica
6
12
12b
46
43
2
3
7
V1
V2
1 m

Amphibia-Reptilia

Lizard abundance in forest fragments: effects of patch size, patch shape, thermoregulation, and habitat quality

José A. Díaz, Tomás Santos, and Alejandro Llanos-Garrido

Depto. de Biodiversidad, Ecología y Evolución, Facultad de Biología, Universidad Complutense, E-28040 Madrid, Spain

Supplementary Material

Table S1. Latitude and longitude of censused fragments, in xy and DMS coordinates, and number of iButtons used to estimate T_es and distances to nearest refuge.

Fragment	LAT (y)	LONG (x)	LAT (º N)	LONG (º W)	N
2	4,662,575.990	443,194.595	42º6’48’’	3º41’14’’	18
3	4,662,459.603	443,074.771	42º6’37’’	3º41’24’’	12
6	4,663,010.357	443,909.106	42º6’55’’	3º40’47’’	19
7	4,663,278.394	444,111.422	42º6’55’’	3º40’34’’	12
12	4,664,341.793	446,758.204	42º7’40’’	3º38’43’’	30
12b	4,664,691.581	446,996.699	42º7’51’’	3º38’34’’	19
43	4,664,125.599	442,409.965	42º7’31’’	3º41’53’’	14
46	4,664,643.003	442,417.790	42º7’48’’	3º41’52’’	25
V1	4,658,249.807	441,253.498	42º4’20’’	3º42’40’’	24
V2	4,658,064.076	441,155.005	42º4’14’’	3º42’45’’	12

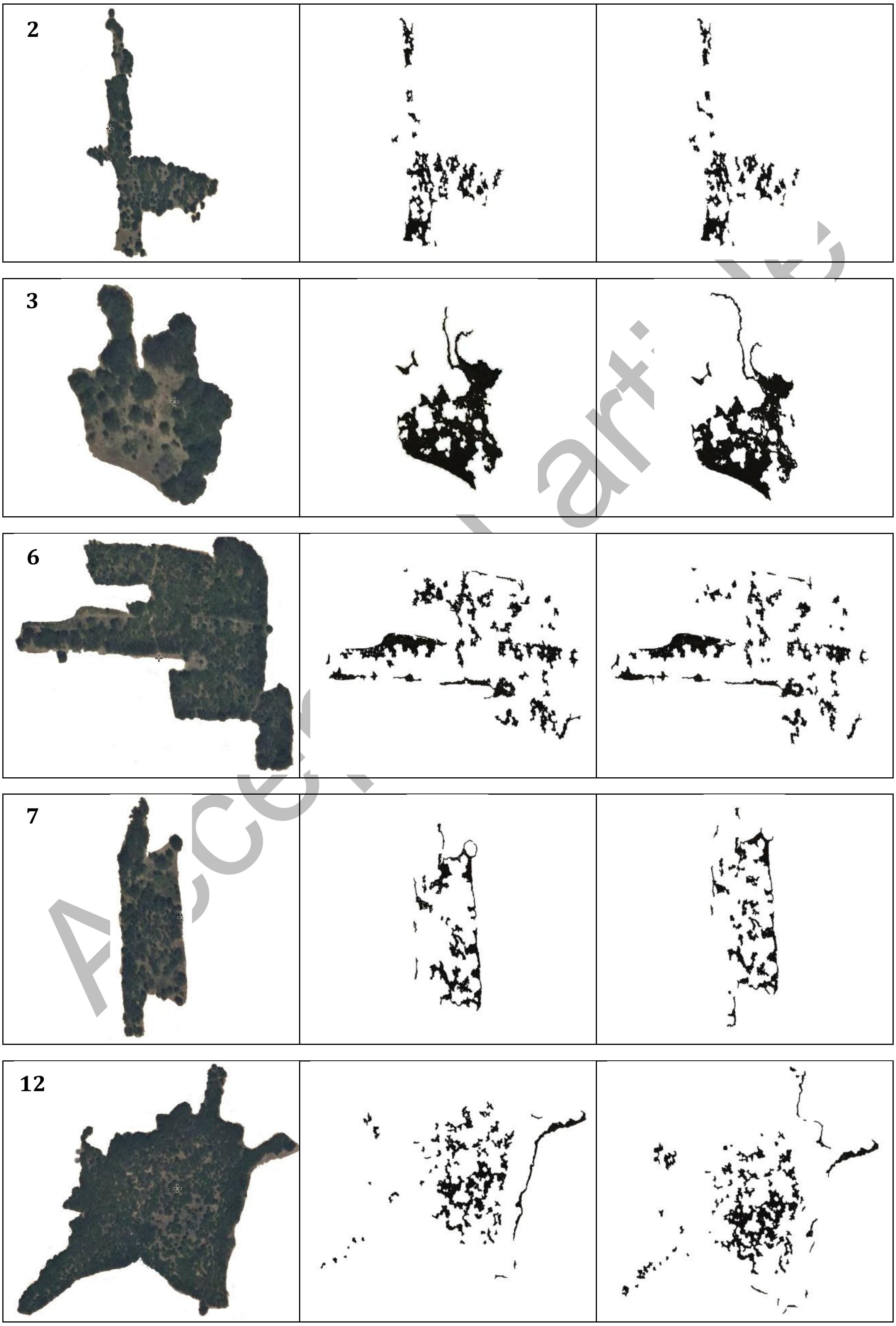
Table S2. Results of LOOCV (leave one out crossvalidation). Variables included in Models #1, 2, 1b, 2b, and 3 are shown in Table 3 of the main document. r^2 is the percentage of variance explained by each model, and o – p is the difference between the prediction of the model and the actual value of abundance in the excluded fragment. Last row gives mean values ± one standard deviation.

Fragment excluded	Forward stepwise	Backward stepwise	Model #1		Model #2		Model #1b		Model #2b		Model #3	
			r^2	o – p	r^2	o – p	r^2	o – p	r^2	o – p	r^2	o – p
2	Model #1	Model #1	0.844	0.033	0.829	-0.103	0.773	-0.002	0.686	-0.124	0.883	-0.034
3	Model #1	Model #1	0.836	0.028	0.823	0.132	0.763	-0.054	0.661	-0.002	0.880	0.080
6	Model #1	Model #1	0.976	0.484	0.812	0.242	0.911	0.516	0.677	0.365	0.976	0.487
7	Model # 3 [a]	Model #2	0.840	-0.179	0.849	-0.366	0.822	-0.362	0.811	-0.604	0.904	-0.321
12	Model #1	Model #1	0.804	-0.059	0.777	0.013	0.725	-0.162	0.595	-0.068	0.854	-0.072
12b	Model #1	Model #1	0.851	-0.209	0.807	0.020	0.755	-0.074	0.670	0.191	0.883	-0.157
43	Model #1	Model #1	0.843	0.025	0.841	0.178	0.799	0.221	0.777	0.431	0.888	0.106
46	Model #1	Model # 4 [b]	0.850	-0.148	0.825	0.121	0.777	-0.154	0.672	0.079	0.880	-0.024
V1	Model #2	Model #2	0.834	-0.179	0.947	-0.508	0.745	-0.089	0.728	-0.401	0.949	-0.579
V2	Model #1	Model #1	0.773	-0.073	0.760	0.234	0.671	-0.101	0.525	-0.021	0.838	0.174

[a] Model # 3: IA = 1.057 + 0.345 Bg-PC (r^2 = 0.766)

[b] Model # 4: IA = 2.874 – 0.006 D_{ref} – 0.245 P/A – 0.576 A_{cl} (r^2 = 0.953)

Fig. S1. Repeatibility of estimates of total surface covered by clearings. First column depicts fragment identity and aerial view obtained from the SIGPAC GIS (http://sigpac. mapama.gob.es/fega/visor/); 2nd and 3rd columns show two replicated estimates of the total surface covered by clearings (in black) as selected by Adobe Photoshop® CS4 (see main document for details about the method employed).

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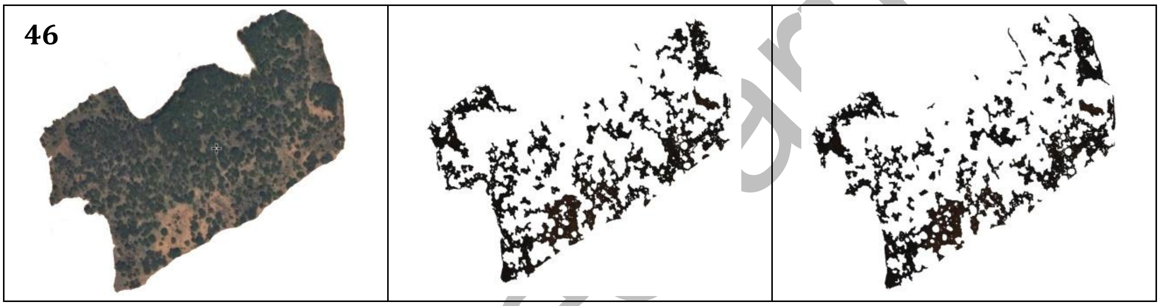
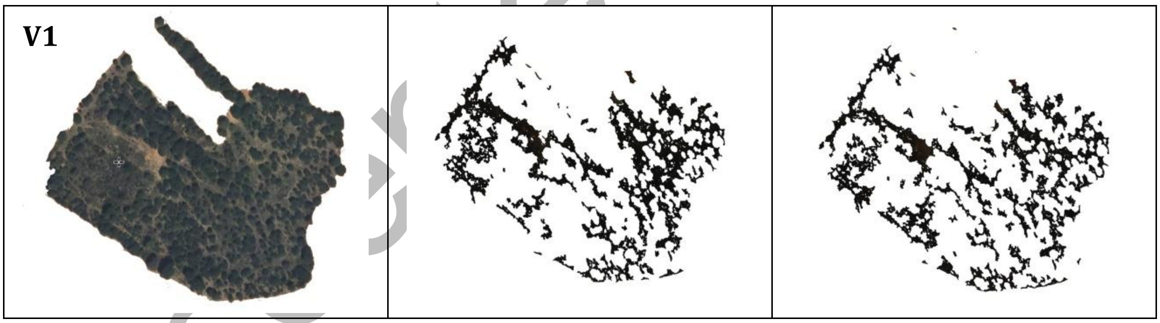
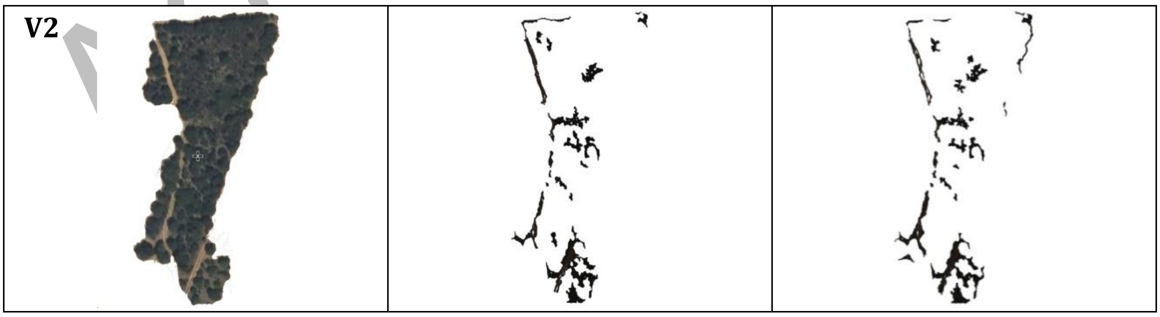

46


V1


V2