

Article

Habitat Suitability for Small Mammals in Mediterranean Landscapes: How and Why Shrubs Matter

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Abstract: Fires are usually seen as a threat for biodiversity conservation in the Mediterranean, but natural afforestation after abandonment of traditional land uses is leading to the disappearance of open spaces that benefit many species of conservation interest. Fires create open habitats in which small mammals can live under more favourable conditions, such as lower predation, interspecific competition, and higher food availability. We analysed the role of changes in shrub cover and shrub preference by small mammals along the Mediterranean post-fire succession. We used data (period 2008–2018) from 17 plots woodlands and post-fire shrublands present in the study area (Barcelona's Natural Parks, Catalonia, NE Spain), and vegetation structure was assessed by LiDAR technology for modelling ground-dwelling small mammal preferences. The diversity, abundance, and stability of Mediterranean small mammal communities negatively responded to vegetation structural complexity, which resulted from the combined effects of land abandonment and recovery after wildfires. We suggest that biotic factors such as vegetation profiles (providing food and shelter) and their interaction with predators and competitors could be responsible for the observed patterns. Considering the keystone role of small mammals in the sustainability of Mediterranean forest, our results could be useful for management under the current global change conditions.

Keywords: vegetation structure; structural complexity; small mammal abundance; diversity; LiDAR



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1. Introduction

Out of all the global change drivers causing the current biodiversity crisis [1], land-use change can be considered as the most relevant in Mediterranean ecosystems, where traditional land-use practices have been positively linked to biodiversity [2]. In the Mediterranean basin, an ongoing process of land abandonment due to socio-economical changes over the last decades is leading to the cessation of traditional practices and is causing the conversion of open land use (crops, grasslands, scrub) to forest habitats [3,4]. The negative impacts of land abandonment on ecosystems include loss of biodiversity and ecosystem services linked to open areas, which are essential components of Mediterranean habitats because of the key role in disturbance regimes (drought, fire) for their long-term functioning [3,5].

Fires, either natural or man-made, simplify forest structure by eliminating slow-growing tree species, allowing the regrowth of fast-growing shrubby plants and creating new habitats with short and sparse vegetation ([6] and references therein). Although wildfires can have positive effects as natural disturbances [7], they threaten human interests and so are extinguished as fast as possible, a fact that paradoxically creates conditions for even larger wildfires in the future [8]. Fires can counteract the natural afforestation process, which is leading to the disappearance of open spaces for many species of conservation concern [6]. Low-intensity prescribed fires mimicking natural fire regimes have been

proposed as the best option to fight against habitat loss of open-habitat species due to land abandonment [5] and to avoid the effects of encroachment due to abandonment and fire extinction policies on the size and intensity of wildfires [8]. In the case of small mammals (i.e., mice and shrews), natural (and prescribed) fires may allow the maintenance of patches of open habitat where these species can benefit from lower predation pressure and predation risk, lower competition, higher food availability, and lower thermal restrictions [9,10].

Vegetation structure is commonly described by canopy and shrub height, closeness/openness of vegetation layers, or vertical complexity. Until recently, measuring those variables was traditionally performed through observational ground surveys by trained observers, which are often time-consuming and subjective [11,12]. The advent of LiDAR (light detection and ranging), an active remote sensing technology whose accuracy in capturing habitat features is important for tree- and ground-dwelling small mammals, has been proved effective in several studies (e.g., [13–16] include detailed, replicable, and precise estimates of vegetation structure).

We present a conceptual framework (see graphical abstract) to analyse changes in small mammal communities along Mediterranean vegetation gradients measured by means of objective LiDAR methods. We assumed that vegetation gradients in the study area came from the opposing processes of land abandonment and wildfires, so that the framework could be generalised to similar environments and climates [3,17]. We analysed relationships between the structural complexities of the vegetation, which increase along the forest succession from open to closed habitats and are related to time since the last fire and changes in the abundance, composition, and structure of small mammal communities. Indeed, a gradient of structural complexity represents different levels of suitability as perceived by the small mammals. We hypothesised that habitats with more complexity regarding their vegetation structure (i.e., forests) would be more unsuitable for small mammals due to a combination of factors, such as a higher predation [9] and competition [18], lower food resources at the ground level [7], and more extreme temperatures than under shrub cover [19]. Hence, effects of afforestation-driven change in vegetation structure will decrease small mammal diversity unless compensated by the opposite effects of fire. Mediterranean landscapes are surely much more open than current forests resulting from land abandonment (either locally or at landscape scales) due to the effects of several processes that have now been suppressed, including the natural fire regime [3,17]. Here, we provided vegetation–small mammal relationships that can be used to help decide landscape-scale land use policies including abandonment, productive agricultural uses, and even prescribed fires than may include the goal of the conservation of maximal, or not, levels of small mammal diversity (see, e.g., [20] for a similar example using forest birds).

2. Materials and Methods

2.1. Study Area

Field work was carried out within six natural parks of the Barcelona province (Catalonia, NE Spain: Garraf, Collserola, Serralada Marina, Serralada Litoral, Montnegre i el Corredor, and Sant Llorenç de Muntill’Obac, Figure 1). Woodlands represented the main habitats (65%), followed by open habitats (grassland, scrubland; 22%), urban areas (8%), and croplands (4%) [21]. The area was affected by large wildfires at the end of the last century (i.e., 10,000 ha burned in Garraf, which represented > 90% of the surface of the protected area [22] and is currently experiencing a rapid process of scrub encroachment and afforestation [5,23]).

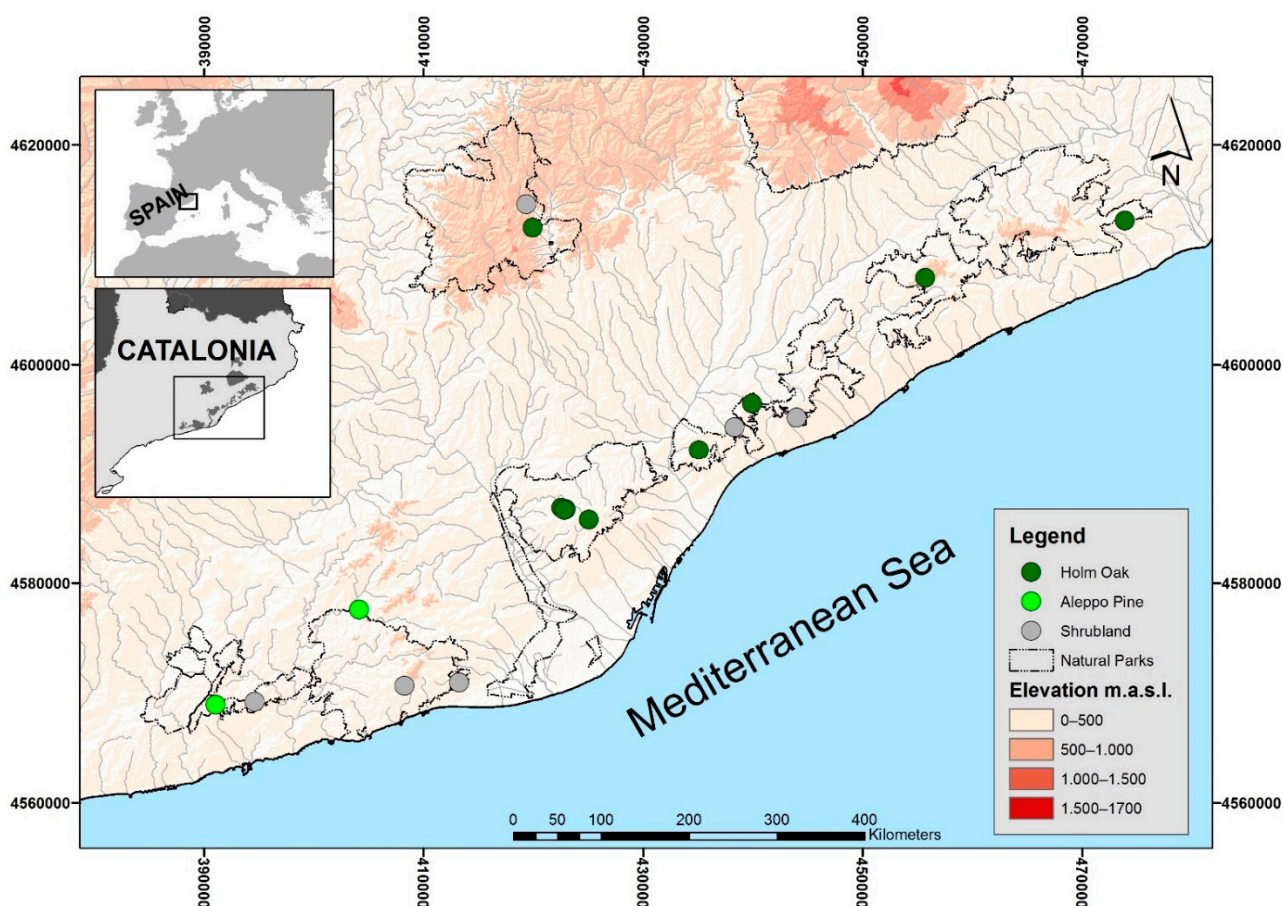


Figure 1. Study area (Barcelona province, Catalonia, NE Spain) and situation of 17 SEMICE plots according to overall vegetation structure: holm oak and mixed woodland (holm oak–stone pine), Aleppo pinewood, and shrubland (post-fire vegetation).

2.2. Small Mammal Sampling

We used data obtained from the Spanish small mammals' monitoring program (SEMICE), which has been operative from 2008 to the present (www.semice.org; accessed on 1 January 2019 [24,25]). SEMICE is a volunteer-based scheme showing some turnover but with a significant fraction of stations remaining stable throughout the study period. The program ensures enough detectability and no sampling bias for population estimates of common species [24], although slight qualitative biases related to volunteer experience were observed (i.e., aptitude to sex shrews [26]).

Study plots were selected according to available SEMICE stations, which was a non-random sample of natural Mediterranean habitats but representative of the main habitats present in the study area. Sampling was performed from spring 2008 to autumn 2018 by selecting plots situated in the Mediterranean lowlands (92–533 m a.s.l.) to avoid the effects of northern climatic influences on species' diversity/abundance in the study area [27]. We surveyed 17 plots (0.56 ha, minimum area) twice a year (spring and autumn to cover the life cycle of small mammals [28]), resulting in 209 sampling sessions during 11 consecutive years. Average number of sessions per plot was 12.0 ± 7.69 (range 2–22), since only six sampling stations were operative during the whole study period. Most (11 plots, 64%) were in forests (mostly mixed woodlands dominated by holm oaks, *Quercus ilex*, with scattered stone pines, *Pinus pinea*, and pinewoods of Aleppo pine, *Pinus halepensis*, with scattered holm oaks). The other six plots were in shrublands at different post-fire stages. All shrublands resulted from fires occurring between 1982 and 2003. Since the last fire affecting a plot was recorded in the first years of the new century, we considered the recovery of the small mammal communities to be completed [29,30]. So, we did not expect direct/indirect

effects of fire on small mammal communities, only effects derived from the secondary vegetation succession.

At each site, we set 36 live traps arranged in a 6×6 trapping grid (two plots used a 9×4 grid), consisting of 18 Longworth traps (Longworth Scientific Instrument Co., Oxford, UK) and 18 Sherman trap boxes (Sherman folding small animal trap; $23 \times 7.5 \times 9$ cm; Sherman Co., Tallahassee, FL, USA) alternating in position [31,32]. The use of two trap models avoided size-specific biases in small mammal community assessments [33]. Traps were placed on the ground spaced 15 m apart and were baited with a piece of apple and a mixture of tuna, flour, and oil, including hydrophobic cotton for bedding. Traps were operated during three consecutive nights and checked during the early mornings. Small mammals caught were identified according species, sexed, and marked with permanent ear tags in the case of rodents (Style 1005–1, National Band Co., Newport, KY, USA) and with fur clips in shrews [34]; After handling, all animals were released at the point of capture [35]. Research on live animals followed ethical guidelines [34], and we had the required permissions from the Catalan Government and other relevant institutions.

2.3. Vegetation Structure

Three-dimensional vegetation structure of sampling plots was assessed by ALS LiDAR [36,37] since those variables were better predictors than field-based variables for modelling ground-dwelling small mammal preferences [16]. LiDAR point clouds were obtained by the Institut Cartogràfic i Geològic de Catalunya with a discrete return LiDAR sensor and a point density between 1 and 4.28 points/m² (flights 2016–2017). Despite an evident temporal lag between the period of collecting the information on vegetation profiles and the start of the small mammals' series (2008), we considered it negligible since all plots were submitted to a similar change [38]. A total of 12 variables were derived from LiDAR data at the plot level to describe vertical vegetation structure and heights (see Table S1 in Supplementary Material for a detailed explanation on LiDAR variables calculation) [38].

To obtain statistical values from the laser returns we processed LiDAR point clouds with the software FUSION [39], cleaning LiDAR files with LASTools software [40]. LiDAR points classified as ground height and those less than 0.15 m height were removed from the analysis in all plots to ensure only vegetation data would be obtained and to avoid points with doubtful classification [41]. Removing this stratum represented a loss of on average 17.5% of the LiDAR information per plot.

2.4. Data Analysis

A Principal component analysis (PCA) was performed on the 12 LiDAR variables to reduce dimensions and to reveal covariance relationships. This is a statistical procedure that uses an orthogonal transformation to convert a set of possibly correlated variables into a set of values of linearly uncorrelated variables called principal components. Varimax-rotated components with eigenvalues > 1 (Kaiser criterion) were retained to interpret gradients with ecological meaning, which were then used as predictors in further analyses [42]. The use of the 12 LiDAR variables as independent predictors was disregarded taking into account the "one in ten" rule for selecting predictors in statistical modelling owing to the limitations of the sample size [43].

We analysed whether small mammal abundance (the mean number of individuals trapped in a sampling station) and species density (the mean number of species per sampling station [44]) were affected by main habitat features of plots summarised by the PCs extracted on LiDAR variables. In order to control for sampling heterogeneity in space and time, we used generalised linear mixed models (GLMMs) [45].

Response variables were mean small mammal abundance and species density (and their coefficient of variation, CV) per sampling station, with a fixed effect (season), incorporating the two first PCs as continuous covariates. Plot was included as a random effect. We also added the sampling effort (number of sampling sessions per plot) as a covariate in the models with CV as the response variable. Response variables (mean values) were modelled

by using the Gaussian error distribution and the identity function. We constructed models resulting from all combinations of explanatory variables using the dredge function of the MuMIn package for R [46], and we determined models with $\Delta\text{AICc} < 2$ to be meaningful. These models were used to interpret which explanatory variables were most likely to influence small mammal abundance. For the selected models, we calculated pseudo- R^2 values [47] by means of the R function `r.squaredGLMM` and the delta method for variance estimation, eventually showing the one with the highest conditional pseudo- R^2 .

Species accumulation curves [44] were also used to estimate species richness for the two main habitats (forest vs. shrubland). The expected richness functions were calculated with EstimateS v.9.1.0. [48] after 100 randomisations (default option) of the observed number of species as samples accumulated. Estimated species richness was calculated with non-parametrical Chao1 estimator for abundance data [48].

3. Results

3.1. Vegetation Structure

The PCA resulted in four significant factors (with eigenvalues equal or greater than one, Table S2). The first two PCs accounted for 76.13% of variance (54.35% for PC1 and 21.78% for PC2) and were considered for further analyses. PC1 showed correlations with 9 out of 12 variables measured vertical vegetation profiles and heights (Table S2) and segregated the shrublands (values < 1) from the woodlands (values > 1), which can be interpreted as a gradient of vegetation structure complexity. PC2 was mostly associated with the contribution and height of short and tall shrubs (right end of the axis). According to the situation of sampled plots within the plane generated by both factors, woodlands showed more homogeneity in their vegetation structure, and shrublands showed more heterogeneity. Interestingly, the situation of plots in the plane allowed pinewoods to be segregated from the holm oak woodlands, which represented a transition between shrublands and woodlands regarding vegetation structure (Figure 2).

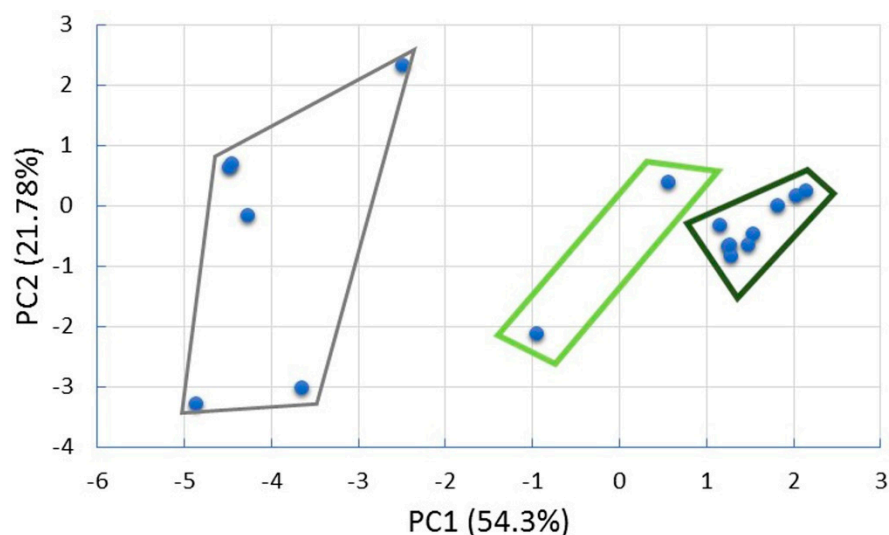


Figure 2. Situation of the 17 sampling plots within the bidimensional space defined by the two first principal components (PCs) summarizing vegetation structure of 12 LiDAR variables. The first PC segregates shrublands (grey line) from woodlands and holm oak–stone pine mixed woodlands (dark green line) from Aleppo pinewoods (light green line).

Shrublands were characterised by their high vegetation cover of short shrubs (83.4% of the mean contribution of shrubs in the 0.15–1.50 m tall class), but low vegetation cover of the tall vegetation (>2.50 m), which is consistent with the lack of trees in almost all the plots (Figure 3). Holm oak woodlands showed low vegetation cover of short shrubs (8.0% of the mean contribution of shrubs in the 0.15–1.50 m tall class) but high vegetation cover of the

tall vegetation (87.8% of the mean contribution of the >2.5 m class). This is consistent with the high volume of trees in these woodlands and the low vegetation volume of short shrubs within the forests. Pinewoods represented an intermediate phase of vegetation structure, showing more vegetation cover of short shrubs (28.2% of the mean contribution of shrubs in the 0.15–1.50 m tall class) but less vegetation cover of the tall vegetation (61.3% of the mean contribution of the >2.50 m class) than holm oak woodlands, since the top of the trees were not very dense, and they allowed light pass through; thus, shrubs and other plants could grow.

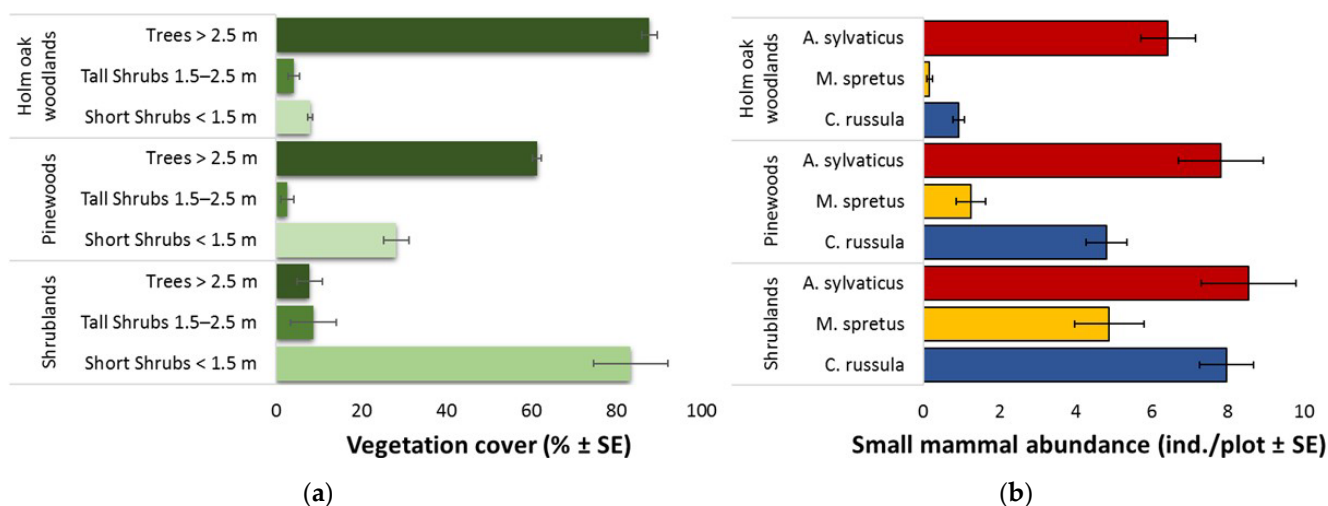


Figure 3. (a) Mean values of contribution ($\% \pm SE$) in the three main vegetation strata calculated from LiDAR variables of the three structurally different habitats (shrublands, Aleppo pinewoods, holm oak–stone pine woodlands) and (b) their corresponding mean values ($\text{ind./plot} \pm SE$) for the three common small mammal species captured during the study period (2008–2018). Trees > 2.5 m \geq CON > 2.5 m; tall shrubs 1.5–2.5 m \geq CON 1.5–2.5; short shrubs < 1.5 m \geq CON 0.15–1.5 m. Sum of the three contributions is 100.

3.2. Small Mammals and Vegetation Structure Relationships

We captured 2662 small mammals of five species in 22,572 trap nights (11.79% capture success), including the wood mouse, *Apodemus sylvaticus*, the most abundant small mammal (1522 individuals, 57.2%), followed by the greater white-toothed shrew, *Crocidura russula* (763 ind., 28.7%), and the Algerian mouse, *Mus spretus* (361 ind., 13.5%). Less abundant small mammals included the bank vole, *Clethrionomys glareolus* (nine ind., 0.3%), and garden dormouse, *Eliomys quercinus* (three ind., 0.1%). Observed and estimated species richness reached the same values, since non-parametric estimators converged with the species accumulation curves (Figure 4). Estimated richness was higher in shrublands (Chao1 = 5 ± 0.23) than in forests (Chao1 = 4 ± 0.22 ; Figure 4).

The best model selection of the GLMMs explained more than half the variance of the response variables (conditional R^2 : 0.48–0.86; marginal R^2 : 0.26–0.67, Table 1 and Table S3), suggesting that the predictors used were ecologically relevant. *A. sylvaticus* abundance was mostly related to seasonality (higher abundance in spring) but also by mean profiles of vegetation structure at the plot level (PC1, which represents a gradient from open shrubland, with no tree contribution and high vegetation contribution at the ground level, to dense woodland, with large tree contribution and low vegetation at the ground level). *M. spretus* and *C. russula* abundances were mostly related to the PC1 gradient, but the latter also showed significant seasonal variability (higher abundances in autumn). Overall mean small mammal abundance per plot was negatively associated with the PC1 gradient, and the same pattern was observed for the average species density (Figure 5). Variation (CV) of mean abundance was positively associated with PC1, with lower among-years variation towards the shrubby extreme of the gradient. Mean small

mammal abundance was three times higher in shrublands than in holm oak woodlands ($21.70 \pm 1.72SE$, $n = 61$; vs. $7.49 \pm 0.74SE$, $n = 112$), and pinewoods showed intermediate values ($13.86 \pm 1.27SE$, $n = 36$). *M. spretus* was 30 times more abundant in shrubland than in oak woodlands, and *C. russula* was nine times more abundant in shrublands. *A. sylvaticus* showed moderate differences in mean abundance between the two habitats (1.33 times more abundant in shrublands).

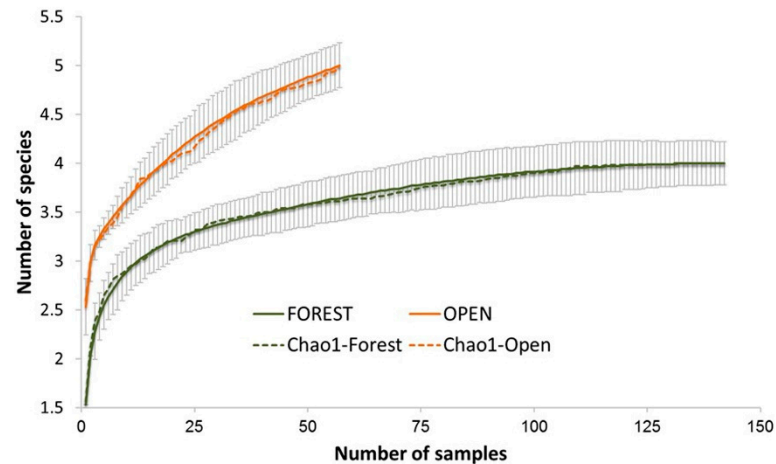


Figure 4. Species accumulation curves (sample-based, solid line) and Chao1 estimator ($\pm SD$) of species richness according to overall vegetation structure of sampling plots. Samples were collected from the trapping sessions lasting three days, each of which was conducted during the study period in the 17 sampling plots (11 forests and 6 shrublands).

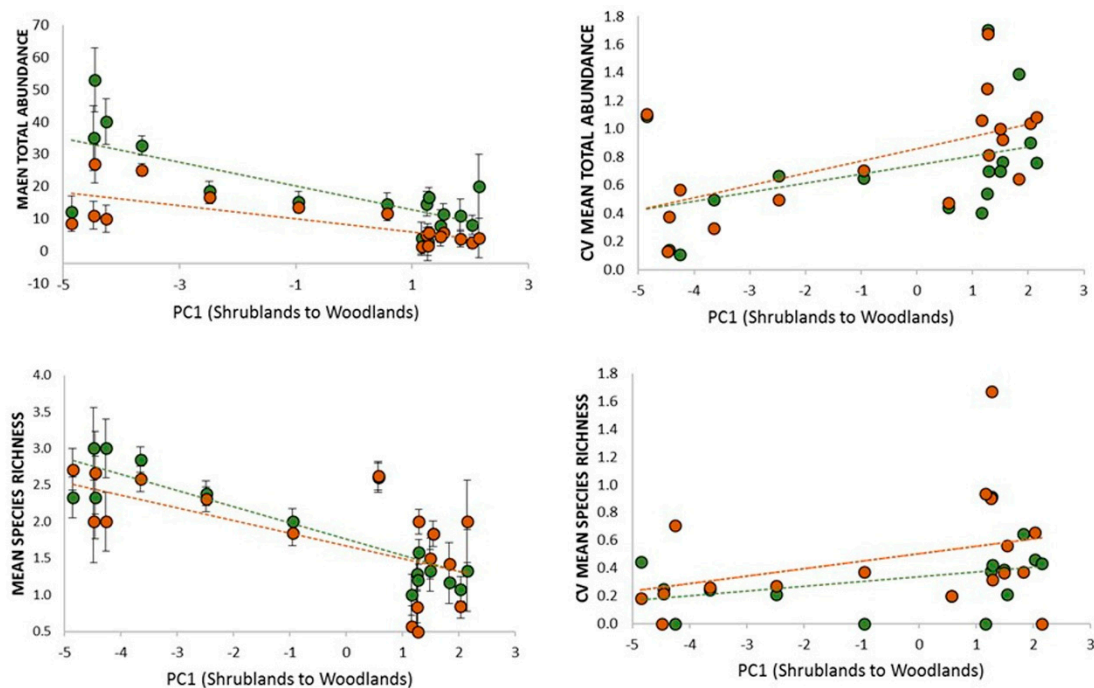


Figure 5. Mean values of abundance ($\pm SE$) and species richness/density ($\pm SE$) and their CV on 17 SEMICE plots during the study period (2008–2018) according to vegetation structure profiles summarised by the first principal component extracted from a PCA analysis on 12 LiDAR variables (green dots: spring; brown dots: autumn).

Table 1. Generalised linear mixed models (GLMM) showing the effects of season (fixed effect) and vegetation structure (covariates, PC1, and PC2) on mean small mammal species abundance, total abundance, and species richness/density (and their coefficients of variation CV), and on mean abundance of common species. Since CV can be affected by sample size, we also included the number of sampling sessions conducted in every plot as a covariate. Sampling stations were incorporated as a random effect in all models. Only the selected model for every response and their significant effects are shown.

VARIABLES	<i>C. Russula</i>	<i>A. Sylvaticus</i>	<i>M. Spretus</i>	TOTAL	Richness	CV-TOTAL
(Intercept)	1.84 ** (0.65)	14.13 *** (1.28)	1.33 * (0.55)	17.91 *** (1.67)	1.79 *** (0.17)	0.75 *** (0.06)
LiDAR-PC1	−0.91 *** (0.21)	−2.21 *** (0.46)	−0.68 ** (0.20)	−3.64 *** (0.60)	−0.18 *** (0.04)	0.07 ** (0.03)
LiDAR-PC2		1.81 (0.91)		1.88 (1.19)		
Season (Autumn)	1.35 * (0.64)	−10.79 *** (1.81)		−9.79 *** (1.99)		
PC1 X Season		2.07 ** (0.65)		1.82* (0.71)		
PC2 X Season		−2.26 (1.29)		−1.86 (1.41)		
Log Likelihood	−76.93	−95.36	−68.31	−102.10	−24.70	−8.95
AICc	165.99	212.48	146.01	225.95	58.78	27.56
Delta	0.00	0.00	0.00	0.00	0.00	1.40
Weight	0.70	0.48	1.00	0.40	1.00	1.00
R ² marginal	0.49	0.67	0.38	0.67	0.41	0.26
R ² conditional	0.73	0.67	0.86	0.77	0.76	0.48
Num. obs.	34	34	34	34	34	29

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

4. Discussion

The diversity, abundance, structure, and stability of Mediterranean small mammal communities showed clear-cut responses to LiDAR-estimated gradients of vegetation structure. Shrublands, resulting from both abandonment and recent fires, held the most diverse and stable communities and showed the highest mean abundance, whereas forests showed the lowest diversity, stability, and abundance during the study period (Figure 3b) [17]. Studies in shrubland habitats outside the Mediterranean showed, however, that recent fires decreased species diversity and abundance [49,50]. There, small mammals' foraging activity increases with vegetation recovery and vertical complexity [51], although the abundance of small mammals and small mammal predators has only been weakly affected by past fires, if at all [50,51]. Fires' effects on small mammals has been mostly studied in desert shrubland habitats, where fires remove vegetation and its associated food resources and increase predation risk. Fires in Mediterranean forests enhanced rather than suppressed the spread of shrubland habitats by eliminating slow-growing tree species and by allowing the regrowth of fast-growing shrubby plants [6]. This new open habitat, consisting of sparse shrubs surrounded by grasslands, can be successfully colonised by pioneering (*M. spretus*) and generalist small mammal species (*A. sylvaticus* and *C. russula*), but is barely colonised, if at all, by small mammal predators (tawny owls, *Strix aluco*, and genets, *Genetta genetta*) and competitors (red squirrels, *Sciurus vulgaris*, black rats, *Rattus rattus*, or wild boars, *Sus scrofa*), even after a long duration since the last fire. Furthermore, the use of common silvicultural practices after forest fires such as salvage logging [30] will additionally reduce habitat suitability for fast recolonization by forest predators and competitors.

Responses of small mammals to vegetation structure can be due to the effects of several biotic and abiotic factors and their interactions. Abiotic factors (climate) are known to influence small mammal abundance/diversity change on either a seasonal and/or yearly basis, both locally [10,52,53] and at a larger scale [54,55]. In addition, biotic factors linked to vegetation profiles as providers of food, shelter, and antipredatory cover could be partly

responsible for the observed responses at the local scale such as those analysed in our study [56].

A. sylvaticus abundance was strongly affected by seasonality, as was previously found by other authors [52,53,57], suggesting that population dynamics were mostly influenced by yearly regimes caused by climate [58]. Opposite patterns as compared to other temperate areas (lower abundances in spring than in autumn [55,59]) are associated with high food availability in winter after crops of acorns and other large seeds fall to the ground in autumn [53], as well as to suppressed summer reproduction due to drought [60]. Exceptional variations of these dynamics were also associated with climatic events typical of the Mediterranean climate that may sometimes reverse the normal seasonality [52,53]. *C. russula* was also affected by seasonality, although their abundance increased from spring to autumn, suggesting that winter was the lean season for this small temperature-dependent insectivore [10]. Finally, *M. spretus* abundance was not seasonal, suggesting a long reproductive season encompassing both summer and winter seasons [60].

Forests are usually expected to harbour more diverse and stable communities than open or treeless habitats because heterogeneous environmental conditions provide more niches and resources, thus increasing species diversity [61,62]. Increased environmental heterogeneity (from floor to canopy) has in fact been shown to influence small mammal diversity, but this is mainly found in tropical forests [63,64], which are typically heterogeneous, and complex environments with trees up to 40 m tall [64]. However, Mediterranean forests harbour less diverse and more fluctuating small mammal communities than treeless areas nearby. The low diversity and different microhabitat preferences of Mediterranean mammals as compared to other temperate and tropical small mammals could account for this unexpected result. Only three species represent the bulk of Mediterranean communities [24,28], and most are ground-dwellers (*C. russula* and *M. spretus*) or show only moderate arborealism (*A. sylvaticus* and *C. glareolus*), are they restricted to low, <1 m, vegetation levels [65]. Arborealism increases exposure to predators in these species, a fact that seems to overcompensate for the increased food availability linked to access to the tree layer [65].

Vertical vegetation in Mediterranean forests seems to provide roosting places for generalist predators such as tawny owls and genets [66,67], likely increasing the predation pressure on small mammals in woodland as compared to shrubland habitats [9,68]. Both tawny owls and genets base their diets on common small mammals [24,69], so we expected higher small mammal predation in forests due to a combination of a higher predation risk (low biomass of vegetation at the ground level) and higher predation pressure (more abundance and diversity of predators). In fact, 95% of small mammal individuals consumed by genets were the same species as those trapped in this study [24], suggesting their role as keystone species in trophic webs. In a former study with spatial but not temporal replication, we hypothesised a role of predators that would explain small mammal community variation and responses to vegetation structure along a post-fire structural gradient. Responses to antipredatory near-ground shrub cover were weak or negative in recently burnt areas and positive and stronger in unburnt areas, suggesting weaker predation pressure in open, shrubby areas burnt recently [9]. Here, we provide additional support to the hypothesised role of small mammal predators in shaping responses to vegetation structure gradients, even though no data on actual predation pressure was available at our plot-level scale. Parallel studies at larger scales in our study region showed, however, that mesocarnivore abundance increases along gradients from open to forest patches [70], suggesting that forests are under higher predation pressure than open habitats. Indeed, the role of predators on small mammal populations may decrease along gradients of ecological disturbance [71], as burnt habitats (shrublands) are more disturbed than unburnt forests.

Both predation risk (exposure of small mammals to predators when foraging due to low vegetation cover at ground level; [9,72]) and predation pressure (local abundance of small mammals' predators) were likely to increase along the studied vegetation structure gradients. Changes in the abundance/diversity of small mammals along these gradients would thus vary from low levels in the more favourable profiles (high cover at low vegeta-

tion heights (<1.50 m) and low cover at tall heights) to high levels at more unfavourable profiles (low cover at short heights (<1.50 m) and high cover at tall heights). The maintenance of understorey cover (i.e., short shrub cover) could be a management strategy used to improve microhabitat favourability for small mammals within unfavourable habitats (forests), but it would negatively impact fire risk management strategies in fire-prone Mediterranean regions [28,55]. The use of LiDAR technology allowed us to establish these vegetation thresholds precisely, as it is known that vegetation structure is more important than vegetation composition for small mammals at the local level [73], and LiDAR allows for more accurate estimates than visual estimates (e.g., [16]).

Land use change in the Mediterranean region and forest fires are driving vegetation structure changes, producing rapid small mammal community change. Forest fires have created new favourable habitats (shrublands) with different abiotic and biotic components/properties, whereas fire recurrency will contribute to their maintenance by hampering vegetation recovery [7]. However, the conceptual framework presented here needs to be properly addressed and validated by specific studies focusing on the role of predators and competitors on the observed small mammal patterns along structural gradients. Nonetheless, the combination of long-term monitoring of small mammal communities with LiDAR-based high-resolution measurements of vegetation structure allowed us to parametrise clear-cut responses of small mammals to human-driven vegetation changes. Bearing in mind the keystone role of small mammals in the long-term sustainability of managed Mediterranean forest [72], this investigation can provide useful criteria for the management of Mediterranean forests under the current global change conditions [17,74].

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/su14031562/s1>. Table S1: Calculation of the 12 LiDAR variables used in this study; Table S2: Pearson correlations of 12 LiDAR variables (measured on 17 sampling plots) with the four first principal components (PCs) extracted from the PCA. The first PC (PC1) had significant correlations with 9 out of 12 LiDAR variables, and the second (PC2) had four significant correlations; Table S3: Best GLM models selected by the dredge function ($AICc < 2$) for all the response variables.

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