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Long-interval effects of wildfires on the functional diversity of land snails

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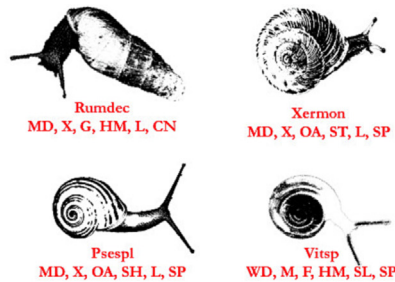


HIGHLIGHTS

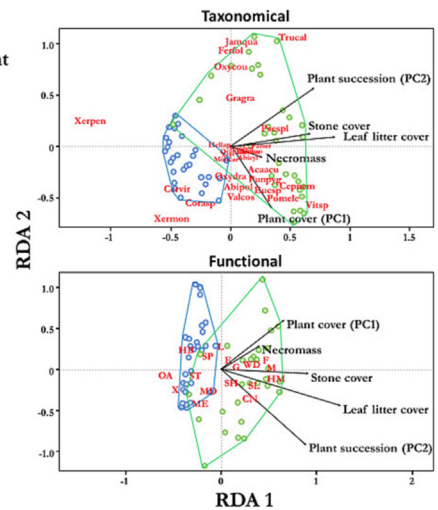
- Land snail assemblage responds to fire both taxonomically and functionally.
- Community variation is attributed to species traits, habitat changes, and environmental drivers.
- Xerophilic and mesophilic preferences play an important role after fire and are determined by the microhabitat complexity.
- Knowing the functional traits of species is important to determine the impacts of disturbances on community resilience.

GRAPHICAL ABSTRACT

Long-interval taxonomic and functional changes occurring in a snail community after 2003 fire in Sant Llorenç del Munt i l'Obac Natural Park



2007 short-term snail community sampling
 2021 large-term snail community sampling



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ABSTRACT

In fire-prone regions, fire is a major natural disturbance which shapes ecosystem function and community composition. Fire has a direct and dramatic effect on soil fauna and, especially, on non-mobile species such as land snails. The factors that make the Mediterranean Basin a fire-prone region may also lead to the appearance after fires of certain functional traits related to ecological and physiological characteristics. Knowledge of how community structure and function change along the post-fire succession will be useful for understanding the processes that drive biodiversity patterns in burnt areas and for implementing appropriate biodiversity management strategies. Here, we examine long-interval taxonomic and functional changes occurred in a snail community four and 18 years after a fire in the Sant Llorenç del Munt i l'Obac Natural Park (NE Spain). Our field-based study demonstrates that the land snail assemblage responds both taxonomically and functionally to fire and that there was a clear replacement of dominant species from the first to the second sampling period. Variation in community composition between different post-fire ages can be attributed to snail species traits and successional changes in post-fire habitat conditions. At taxonomic level, there was great variation in snail species turnover between both periods, being the development of the understorey vegetation structure the main driver of this variation. The replacement of functional traits between times since fire suggests

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that xerophilic and mesophilic preferences play an important role after fire and are largely determined by the complexity of post-fire microhabitats. Our analysis indicates that immediately after a fire there is a time-window of opportunity that attracts species specializing in early successional habitats, which thereafter are replaced due to the changing conditions resulting from succession. Consequently, knowing the functional traits of species is important for determining the impacts of disturbances on the taxonomic and functional communities.

1. Introduction

Wildfires drive the evolution of a variety of traits that enable species to persist in fire-prone landscapes (Pausas and Parr, 2018). Consequently, the identification of the functional groups that share the ability to adapt to fires will potentially help improve fire knowledge and how to manage for biodiversity (Rainsford et al., 2022). Most studies attempting to explain post-fire spatiotemporal changes in community composition use a taxonomic approach, although this strategy has never been able to unravel the causal mechanisms behind responses to environmental variation over temporal scales. Trait-based approaches are regarded as much more useful in this respect (Messier et al., 2010), since the functional traits of species directly link their performance to environmental conditions (Astor et al., 2017; Chergui et al., 2020). Functional traits are measurable properties of organisms that have a critical influence on performance (McGill et al., 2006). In fire-prone ecosystems, the functional traits that affect post-fire occurrence are related to ecological (i.e. habitat use) and physiological (i.e. water stress, thermal tolerance) characteristics (Kiss and Magnin, 2006). How community structure and function change after fire is key for understanding the processes that drive patterns of biodiversity in burnt areas (Gosper et al., 2013; Henry et al., 2022) and, ultimately, for implementing suitable biodiversity management strategies.

The structural modification of habitats in the aftermath of wildfires has a serious impact on animal recolonization given that animals need to take advantage of the food, thermal and shelter resources associated with post-fire changes in vegetation (Auclerc et al., 2019; Puig-Gironès et al., 2018). Consequently, wildfires have the capacity to filter the species that are best adapted to post-fire environmental conditions (Pausas and Verdú, 2008). Fire can have a dramatic direct impact on both the soil fauna living in leaf litter and on vegetation (Whelan, 1995), above all on those species – ranging from microorganisms to millipedes, gastropods and earthworms – that have little chance of escaping (Bardgett, 2005). Nevertheless, some components of the soil fauna may survive in cryptic shelters and recolonize burnt areas from unburnt micro-patches or the subterranean layer (Kiss and Magnin, 2003). Thus, understanding the response of species to environmental changes is a vital task in biodiversity conservation and management. Currently, trait-based approaches are still relatively novel in animal ecology, partly because of the lack of reliable or relevant trait data for many groups (Moretti et al., 2017). As a result, few studies have ever demonstrated consistent links between environmental factors and soil fauna traits (e.g. Astor et al., 2017; Auclerc et al., 2019; Makkonen et al., 2011).

Land snails are one of the major component of the soil fauna. They are key members of ecosystems and carry out a wide array of important functions including nutrient cycling, the decomposition of forest litter, soil formation and productivity, predation and/or scavenging (De Oliveira et al., 2010; Nyffeler and Symondson, 2001). Snail species are limited by environmental conditions (Martin and Sommer, 2004), vegetation and leaf litter characteristics (Gheoca et al., 2021), and are particularly sensitive to the structure, humidity and shade of their micro-habitats (Kemencei et al., 2014). Fire abruptly transforms habitat structure (i.e. openness) and environmental conditions. Fires can have both direct and indirect impacts on the survival of land snails. Direct impacts include mortality during the fire event (Nekola, 2002), while indirect impacts include the reduction of wood, litter, and mulch layers on the soil surface (Nicolai and Ansart, 2017). Fire can also alter the microclimate for snails by reducing or modifying sources of nutrition, buffering, and shelter such as organic substrates and residues (Knapp et al., 2009). In the short- and med-terms since fire,

land snails have to respond to these changes since shrub and young tree layers may become dominant (Capitaniao and Carcaillet, 2008). Few individuals of mesophilous, forest or litter snail species survive wildfires (Kiss and Magnin, 2006) due to the loss of available resources and the increase in soil surface temperature (Ray and Bergey, 2015) but opportunistic and xerophytic species may increase (Bros et al., 2011; Santos et al., 2009). Thus, post-fire macro- and microhabitat changes will shape post-fire land snail communities (Puig-Gironès et al., 2022) and functional community composition. Despite the importance of terrestrial invertebrates in ecosystem functioning, they are often understudied (Braby, 2018; Cardoso et al., 2011) and there is a significant gap in our understanding of their response to fire disturbances (Decker et al., 2023). This lack of research extends to land snail populations and traits, as their responses to wildfire events are largely unknown.

In this study, we examine and compare the long-interval taxonomic and functional changes occurring in a snail community after the 2003 fire in Sant Llorenç del Munt i l'Obac Natural Park. The snail community was sampled four (2007) and eighteen (2021) years after this fire. Long-interval monitoring (e.g. two monitoring periods separated in time after a disturbance) allows us to capture how the faunal composition changes both taxonomically and functionally in relation to a disturbance, and to highlight how the magnitude of a disturbance has an impact on communities. Taxonomically, we had previously noted that in the mid-term since the 2003 fire, the land snail diversity (alpha and beta) had increased at burnt sites and that its community composition had diversified. However, 18 years after the fire certain threatened species had disappeared and the relative abundance of snails had declined notably (Puig-Gironès et al., 2022).

The aim of this new study was to describe the long-interval functional changes occurred in two sampling periods along the post-fire succession in the snail community from this natural park. Accordingly, we explored the following hypotheses: (a) despite the limited mobility of snail species, there is a taxonomic replacement between the two sampling periods (4 and 18 years since fire). We expect that this replacement is driven by the functional traits displayed by the commonest snail species found at each sampling period (Kiss et al., 2004; Bros et al., 2011). Consequently, we predict that the functional traits found in the community will be shaped by the habitat features found during each sampling period. (b) Given the habitat transformation along the postfire succession from open (less vegetated) to closer landscape, we expect that snail functional groups would shift from traits linked to open habitats (i.e. higher radiation, drier conditions), to those linked to moist and mature habitats (i.e. moist environments). (c) Fire simplifies the structure of the habitat which tend to return to pre-fire (more complex) conditions along the post-fire succession. Thus, eighteen years after the fire a more complex habitat structure is expected to allow for a greater functional diversity of snails compared to a more simplified habitat in the short term (Puig-Gironès et al., 2022). Accordingly, we predict that snail functional diversity would be higher in the mid-term.

2. Material and methods

2.1. Study area

The study area (13,694 ha) is located in the Sant Llorenç del Munt i l'Obac Natural Park (henceforth PNSLL) in Barcelona province (NE Iberian Peninsula, Fig. 1). Its geological substrate is composed of polymictic conglomerates dominated by rugged crags and unusual rock monoliths, all within a landscape characterized by forest patches. The climate is

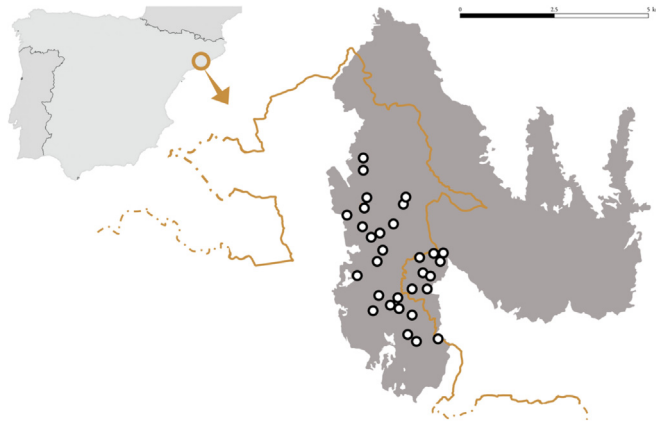


Fig. 1. Study area and sampling location.

Location of Sant Llorenç del Munt i l'Obac Natural Park in Catalonia (north-east of Iberian Peninsula) and the situation of the 31 sampling stations (dots) in the 2003-burnt area (grey). Orange line corresponds to Natural Park limits. (grey). Orange line corresponds to Natural Park limits.

subhumid Mediterranean (average annual rainfall of around 600 mm) with windier, wetter and cooler conditions on peaks than in lowland areas and more rain in spring and autumn than in summer. The original forest cover is dominated by evergreen holm oak (*Quercus ilex* L.) and Aleppo (*Pinus halepensis* Mill.) and Spanish black (*Pinus nigra* subsp. *salzmannii* (Dunal) Franco) pines, generally with an evergreen holm oak understorey (Puig-Gironès et al., 2022). The area is prone to fast-spreading fires during the hot dry summers. In August 2003, 4543 ha of the eastern part of this natural park (10 % of its total surface area) and neighbouring areas were burnt by a wildfire (Fig. 1). The burnt landscape had previously been covered by a pine forest with a holm oak understorey. After the fire, burnt areas were occupied by dense shrubland dominated by grey-leaved cistus (*Cistus albidus* L), rosemary (*Salvia rosmarinus* Spenn), badassi (*Lotus dorycnium* L), elm-leaf blackberry (*Rubus ulmifolius* Schott) and redoul (*Coriaria myrtifolia* L). 18 years later, the habitat has experienced significant differences in habitat structure and composition, doubling the amount of wood debris and leaf litter, although it has lost weeds and bare soil (Fig. S1).

2.2. Gastropods sampling and functional assignation

In May–June 2007 and 2021 we searched for gastropods at 31 sites inside the burnt area (Fig. 1) using two complementary methods. (1) All snails with a shell size over 5 mm were actively searched for in suitable microhabitats for 30 min in 10 × 10-m plots; (2) snails <5 mm were collected from four 25 × 25-cm subsamples of litter from the top 5 cm of soil. Four subsamples were then randomly taken from within the larger 10 × 10-m plots and examined in the laboratory with a stereomicroscope and optical material to count and identify small snails (Santos et al., 2009). Specimens were mostly identified to species level, although some were only determined to generic level. Due to the persistence of dead shells in the field, only fresh shells and living snails were counted as representative of current communities (see Bros et al., 2011 for more details). The species of which only dead specimens were collected were excluded from the analysis.

To perform a functional classification, we grouped all the snail species found into six ecologically relevant traits that represent the most important ways in which these species interact with the environment. We utilized information from the Kerney et al. (1999) and Falkner et al. (2001) trait database, a comprehensive resource for soil fauna and commonly used in snail trait studies (e.g. Astor et al., 2017; Dahirel et al., 2015). Additionally, for some Mediterranean species, we also employed a local knowledge approach (Bros, 2000; Bros, 2006). Thus, the ecological traits comprised a total of 17 functional classes (Table 1) related to life-history (shell size), dispersal ability (shell shape), habitat preferences (macro and microhabitat), tolerance to abiotic conditions (moisture preference) and biogeographical distribution.

Table 1

Snail functional-trait description.

Description of the different categories and functional classes of land snails in Sant Llorenç del Munt i l'Obac Natural Park.

Category	Functional classes	Description
Biogeographic distribution	Wide distribution	Includes snail species with a wide distribution, Palearctic or Holarctic.
	European	Relates a species with a centre and western European distribution.
	Mediterranean	Species characteristics of the Mediterranean basin distribution.
Moisture preferences	Xerophilous	Species with highest affinity for dry sites.
	Mesophilous	Species with highest affinity for moist sites.
Macrohabitat	Forest	Species of snails that mostly inhabit forests.
	Open areas	Snail species that occur in mostly open and/or sparsely vegetated habitats.
	Generalists	Snail species that do not show preferences for any type of habitat.
	Herb	Snail species found among herbs.
Microhabitat	Shrub	Snail species found among shrubs.
	Stones	Snail species found in walls or sheltering under stones.
	Humus	Snail species that live among fallen leaves or in decomposing dead trunks.
Snail size	Small	Small shell volume (from 0 to 25 mm ³).
	Medium	Medium shell volume (from 25 to 1000 mm ³).
	Large	Large shell volume (>1000 mm ³).
Shell form	Spherical	Corresponds to categorical classification of snails with the spherical form of its shell.
	Cone	Corresponds to snails with cone-form shell.

- 1) The distribution patterns of land snails follow Welter-Schultes (2012): species were classified as having either a wide distribution (WD), or a central and western European (E) or Mediterranean (MD) distribution.
- 2) Moisture preference: species were categorised as either xerophilous (X) or mesophilous (M) following Bros (2000), Bros (2006).
- 3) The macrohabitat categories follow the classification used by Bros (2000) from the same area: forest (F), open area (OA) or generalist (G) species.
- 4) The predominant microhabitat categories also follow Bros (2006): herbs (HB), shrubs (SH), stones (ST) or humus (HM).
- 5) The average snail shell size, extracted from animalbase.org (AnimalBase Project Group, 2022), was used to calculate the body volume (mm³) using the cone formula ($V = \pi r^2 h / 3$, where r corresponds to shell radius and h to its height). Snails were classified as either small (SL), medium (ME) or large (L) (e.g. Emberton, 1995).
- 6) Finally, the shell form was classified as spherical (SP) or cone-shaped (CN).

Although biogeographical distribution is not strictly a functional trait, species with different distributions can evolve divergent life-history traits. Indeed, some authors have demonstrated that differing faunal responses to fire are related to biogeographical origin (Ferreira et al., 2016; Prodon, 1993). Moisture preference is associated with snail tolerance to dry conditions, as humidity is an important abiotic factor influencing snail abundance and diversity (Martin and Sommer, 2004). Macrohabitat provides insight into the specific environmental conditions necessary for snail survival and reproduction, such as soil type, temperature, and light levels. Microhabitat occurrence reflects where the species prefer to live at a small scale, such as on trees, in the litter layer or on mosses. Small-scale species can potentially interact and compete, which can lead to niche partitioning (Hax and Golladay, 1993). Shell size and shape can be constrained by environmental factors and habitat structure (Schamp et al., 2010) and have been found to be involved in competition and niche differentiation. Body size has been linked to niche partitioning through specialization on different resources (Bowers and Brown, 1982), while shell shape also indicates preferred microhabitats (Cameron and Cook, 1989).

2.3. Environmental variables

At the centre of each sampled site, the vegetation and ground-type covers were recorded at points 50 cm apart along five parallel 10-m transects, separated by 1 m. We thus used 100 points to characterize the structure of the habitat at each sampling site. During the two sampling periods and at each point, six environmental predictor variables describing the vegetation structure (two variables) and shelter availability (four variables) were recorded. On both occasions, sampling was carried out in the same places by the use of geo-references.

The vegetation structure was characterized by defining six vegetation-type covers (grass, grey-leaved cistus, rosemary, other shrub species, oaks or pines). Cistus and rosemary are medium-sized shrub species (height: 40–120 cm) and are very abundant in the study area. Their particular structures provide snails living on the ground below these shrubs with special micro-environmental features. For this reason, these two-plant species were considered separately. Percent cover of each vegetation type was quantified visually as plot size is small. We arcsine-transformed cover percentages, and reduced these vegetation types to two main components by a principal component analysis (PCA). The first component (PC1, henceforth plant cover, with 34.49 % of explained variance) corresponded to the gradient from less to more bare-soil cover sites, mainly undergrowth. The second component (PC2, henceforth plant succession, with a 24.41 % of explained variance) ordered sites from those with germinating species characteristic of the first post-fire stages (e.g. *Cistus* spp.) to sites with perennial vegetation characteristic of long-unburnt plant communities (rosemary, pines or oaks) (Fig. S2). PC1 and PC2 scores were extracted from vegetation-type covers, and used as explanatory variables in further analyses (view [Data analyses](#) section).

Shelter availability was estimated by measuring at each point the bare-soil cover and the abundance of three structures that are used as shelter by snails: (a) cover provided by large woody materials such as dead trunks, stumps, wide branches and fine fallen branches on the ground, hereafter

referred to as necromass; (b) the percentage of cover provided by stones (over 8 dm³); and, finally, (c) the percentage of cover provided by leaf litter on the soil.

Based on the vegetation structure and shelter availability recorded at each point, we calculated the average values for each sampled site and created a matrix of environmental variables for each sampled site and period (2007 and 2021).

2.4. Data analyses

Each snail species was characterized by a functional class within each ecological trait ([Table 1](#)). Accordingly, the abundance of each snail species per sampled site (matrix of taxonomic abundances) and its functional classification ([Table 2](#)) were linked to generate a matrix of functional abundances for each sampled site, i.e. the number of individuals for each functional class was quantified. The matrices of taxonomic and functional abundances, plus the matrix of environmental variables, were used in further analyses. First, we compared the functional and environmental matrices using generalized linear mixed models. Then, we compared subsamples of functional abundances with PERMANOVAs. Finally, we associated the three matrices using Redundancy analyses.

2.4.1. Modelling snail functional classes and comparing functional abundances

Functional abundances for each sampled site were used as dependent variables and were modelled with generalized linear mixed models (GLMMs) using a negative binomial error structure and log link function to avoid data overdispersion. Each sampled site was included as a random effect to control for possible site-based differences and the independence. These models were performed using combinations of the seven-predictor variables (time since fire, plant cover, plant succession, bare soil, leaf litter, rocky land and necromass).

Before the model selection, multicollinearity diagnostics and variability identification (outliers) were performed ([Zuur et al., 2009](#)).

Table 2

Snail species functional attributes.

List of the functional attributes for each species found in the 2003-burnt area of Sant Llorenç del Munt i l'Obac Natural Park. Distribution: wide distribution (WD), European (E) and Mediterranean (MD). Moisture preferences: xerophilous (X) and mesophilous (M). Macrohabitat: forest (F), open-areas (OA) and generalists (G). Microhabitat: stones (ST), shrub (SH), herbs (HB), humus (HM). Shell size: small (SL), medium (ME) and large (L). Shell form: spherical (SP) and cone (CN).

Species	Acronym	Distribution	Moisture	Macrohabitat	Microhabitat	Shell size	Shell form
<i>Abida cylindrica</i>	Abicyl	MD	M	F	ST	ME	CN
<i>Abida polyodon</i>	Abipol	MD	M	G	ST	ME	CN
<i>Acanthinula aculeata</i>	Acaacu	WD	M	F	HM	SL	SP
<i>Aegopinella</i> spp.	Aegsp	E	M	F	HM	ME	SP
<i>Cepaea nemoralis</i>	Cepnem	E	M	F	HM	L	SP
<i>Ceruella virgata</i>	Cervir	E	X	OA	HB	L	SP
<i>Cornu aspersum</i>	Corasp	E	M	G	HB	L	SP
<i>Discus rotundatus</i>	Disrot	E	M	F	HM	ME	SP
<i>Euconulus</i> spp.	Eucsp	WD	M	F	HM	SL	SP
<i>Ferussacia folliculum</i>	Ferfol	MD	X	OA	SH	ME	CN
<i>Graniberia braunii</i>	Grabra	MD	X	G	ST	ME	CN
<i>Granopupa granum</i>	Gragra	MD	X	OA	ST	SL	CN
<i>Helicigona lapicida</i>	Hellap	E	M	F	ST	L	SP
<i>Jaminia quadridens</i>	Jamqua	E	X	OA	ST	ME	CN
<i>Monacha cartusiana</i>	Moncar	E	X	OA	HB	L	SP
<i>Montserratina bofilliana</i>	Monbof	MD	M	F	ST	ME	SP
<i>Otala punctata</i>	Otapun	MD	X	OA	SH	L	SP
<i>Oxychilus courquini</i>	Oxycou	MD	X	F	ST	ME	SP
<i>Oxychilus draparnaudi</i>	Oxydra	E	M	G	HM	L	SP
<i>Paralaoma servilis</i>	Parser	WD	M	F	HM	SL	SP
<i>Pomatias elegans</i>	Pomele	E	M	F	HM	L	CN
<i>Pseudotachea splendida</i>	Psespl	MD	X	OA	SH	L	SP
<i>Punctum pygmaeum</i>	Punpyg	WD	M	F	HM	SL	SP
<i>Rumina decollata</i>	Rumdec	MD	X	G	HM	L	CN
<i>Truncatellina callicratis</i>	Trucal	MD	M	G	HM	SL	CN
<i>Vallonia costata</i>	Valcos	WD	M	G	ST	SL	SP
<i>Vitrea</i> spp.	Vitsp	WD	M	F	HM	SL	SP
<i>Xerocrassa montserratensis</i>	Xermon	MD	X	OA	ST	L	SP
<i>Xerocrassa penchinati</i>	Xerpen	MD	X	OA	ST	ME	SP
<i>Xerosecta cespitum arigonis</i>	Xerces	MD	X	OA	HB	L	SP

Multicollinearity was detected by quantifying variance-inflation factors (VIF) and generalized variance-inflation factors (GVIF[1/(2df)]) calculated for each fixed factor (Fox and Monette, 1992). Large VIF or GVIF values (arbitrary threshold of ≤ 2.5 suggesting collinearity) were sequentially dropped from further analysis. To calculate the difference between the best model and all others in the candidate set, differences in Akaike AICc values (Δ_i) were calculated. Models with $\Delta_i \leq 2$ had substantial support (Burnham and Anderson, 2002). We also calculated Akaike weights (ω_i), which represent the probability that a model is the best in the set. In the absence of a clear 'best' model, model averaging was conducted to determine the influence of each explanatory variable. Model fit was assessed using marginal and conditional coefficients of determination (Nakagawa and Schielzeth, 2013). A predictor variable was considered to influence the response variable (diversity measures) when the coefficient $\pm 95\%$ confidence intervals did not overlap with zero. In addition, to interpret the magnitude of each variable in the average final model, the relative importance of each variable (RIV) was weighted based on the sum of ω_i for each variable. The RIV ranges from 0 to 1 and the explanatory variable was considered robust when $RIV > 0.9$; a moderate effect between 0.6 and 0.9; a weak effect between 0.5 and 0.6; and no effect below 0.5 (Chiaradia et al., 2016; Kennedy et al., 2013). These analyses were performed using the *lme4* (Bates et al., 2015) and *MuMin* (Bartoń, 2016) packages in R (R Development Core Team, 2017).

We employed a permutational analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities to analyse the effects of time since fire and environmental variables on the taxonomic and functional composition of the land snail community. This analysis was conducted using 999 permutations to establish robust results. To understand the relationships between these variables, we also employed Redundancy Analysis (RDA). In the RDA, time since fire (a categorical variable) and environmental variables (continuous variables) were included as explanatory variables. The significance of each explained variance in the RDA was calculated by ANOVA-like permutation tests (9999 permutations), using the *vegan* (Oksanen et al., 2019) packages in R (R Development Core Team, 2017). Thus, this analysis allowed us to identify and summarize linear relationships of the taxonomic and functional composition of communities and the explanatory variables.

2.4.2. Functional diversity analyses

Based on the abundance of each functional class within each ecological trait, four functional diversity (FD) indices were calculated for each sampled site: functional richness, functional evenness, functional divergence (Villéger et al., 2008) and functional dispersion (Laliberté and Legendre, 2010). Functional richness (FRic) measures the total volume at each site, corresponding to the number of functional classes. Functional evenness (FEve) measures the equality between the abundances of the functional classes within each ecological trait. High evenness implies effective use of the entire functional space, while low values imply that parts of the functional space are underutilized (Mason et al., 2005). Functional divergence (FDiv) measures the overlap between the ecological niches. High divergence implies low overlap and thus less competitiveness between species (Mouillot et al., 2013). Finally, functional dispersion (FDis) is very similar to functional divergence and measures community specialization (Laliberté and Legendre, 2010). Functional diversity indices for each site were calculated using the *dbFD* function in the *FD* (Laliberté et al., 2014) package in R (R Development Core Team, 2017). Initially, the *FD* package uses the functional abundance dataset to calculate a Gower inequality matrix, and then performs a principal coordinate analysis (PCoA) to obtain the axes that serve as new traits for calculating the functional diversity indices.

Paired *t*-test were performed to detect effects of time since fire on the four FD indices. In addition, generalized additive mixed model (GAMMs) were used to evaluate the non-linear relationship between FD indices and the most relevant environmental variables (i.e. plant succession, leaf litter and stone cover), with the sampled site as a random effect. We performed these generalized additive mixed models (GAMMs) using the *gam4* (Wood and Scheipl, 2014) R package.

3. Results

During the study, a total of 933 individuals belonging to 30 snail species were recorded. Of these individuals, 636 (68.2%) were found in the short-term period since the wildfire, while 297 (31.8%) were found in the mid-term period. Notably, two sites had no recorded snails in the short-term period, but all sites had at least one individual present in 2021. Three species (*Xerocrassa penchinati*, *Ceruellia virgata* and *Xerocrassa montserratensis*) made up 63.2% of the individuals found, with the majority being found in the short-term period since the wildfire. In contrast, fewer than five live individuals were found for nine species. In terms of species richness, at 45 sites (72.6%), fewer than four species were recorded. The maximum number of species found at one site was nine (at a single site only). The abundance of snails was almost three times greater in the short-term period compared to the mid-term period, indicating a significant difference in the temporal variation of the community after the wildfire due to significant differences in habitat structure and composition (Fig. S1).

Modelling the abundance of functional classes using GLMM (Table S1) demonstrated how plant succession and leaf litter cover influence several snail functional attributes (Fig. 2). Of the seventeen snail functional classes, 10 were affected by plant succession (Table S2), six positively and four negatively. The GLMM analysis also showed that 11 functional classes were significantly related to leaf litter cover, seven positively and four negatively. Wide distributions, mesophilous, forest macrohabitat, humus and shrub microhabitat, and small size species increased in plots with more complex vegetation structure, as well as in plots characterized by greater leaf litter cover (Table S2). Conversely, xerophilous, open-area macrohabitat, herb microhabitat and large-sized species were less abundant with greater leaf litter cover. Four functional classes (wide distribution, mesophilous, humus microhabitat and small-sized species) were positively affected by stone cover. Although spherical-shaped species decreased with vegetation succession, they were more present with leaf litter. The European, Mediterranean, under stones, and medium shell-size functional classes did not generate any reliable model since they did not differ from the null model (Table S1).

The taxonomic composition of the land snail community was greatly influenced by time since fire (PERMANOVA: F -value = 63.73, p -value = 0.001, $R^2 = 0.35$), as well as by plant cover ($F = 27.59$, $p = 0.001$, $R^2 = 0.16$), plant succession ($F = 7.72$, $p = 0.001$, $R^2 = 0.04$), leaf litter ($F = 9.93$, $p = 0.001$, $R^2 = 0.05$), stones ($F = 2.58$, $p = 0.04$, $R^2 = 0.01$) and necromass ($F = 11.65$, $p = 0.001$, $R^2 = 0.07$). The taxonomic RDA revealed that the community composition differed with time since fire and with the five environmental variables (Fig. 3a). The biggest differences were related to time since fire on axis 1 (eigenvalue = 0.12, explained proportion = 0.7) and its association with open-habitat species such as *Xerocrassa penchinati*, *X. montserratensis*, *Ceruellia virgata* and *Cornu aspersum*, the commonest species at a short time since fire. The second axis (eigenvalue = 0.03, explained proportion = 0.17) discriminated between wide or European distribution, mesophilous and forest snail species (*Vitrea* spp., *Pomatias elegans*, *Cepaea nemoralis*, *Euconulus* spp., *Vallonia costata* and *Punctum pygmaeum*) as opposed to Mediterranean, xerophilous and open-area species (*Jaminia quadridens*, *Ferussacia folliculum*, *Oxychilus courquini* and *Granopupa granum*).

The abundance of land-snail functional classes was influenced by time since fire (PERMANOVA: $F = 38.82$, $p = 0.001$, $R^2 = 0.31$), as well as by plant cover ($F = 13.42$, $p = 0.001$, $R^2 = 0.11$), plant succession ($F = 4.33$, $p = 0.002$, $R^2 = 0.03$), leaf litter ($F = 4.48$, $p = 0.001$, $R^2 = 0.04$), stones ($F = 2.53$, $p = 0.03$, $R^2 = 0.02$) and necromass ($F = 5.27$, $p = 0.001$, $R^2 = 0.04$). Here, the functional RDA also had a significant association with time since fire, as did the environmental variables with particular functional classes (Fig. 3b). The first axis of the RDA (eigenvalue = 0.1, proportion explained = 0.83) discriminated between functional groups associated with habitat complexity variables derived from time since fire. Several functional classes, namely, Mediterranean distribution, xerophilous preference, open-area macrohabitat, stone microhabitat, and medium-size were related to a short time since fire. By contrast, wide distribution, mesophilous preference, forest

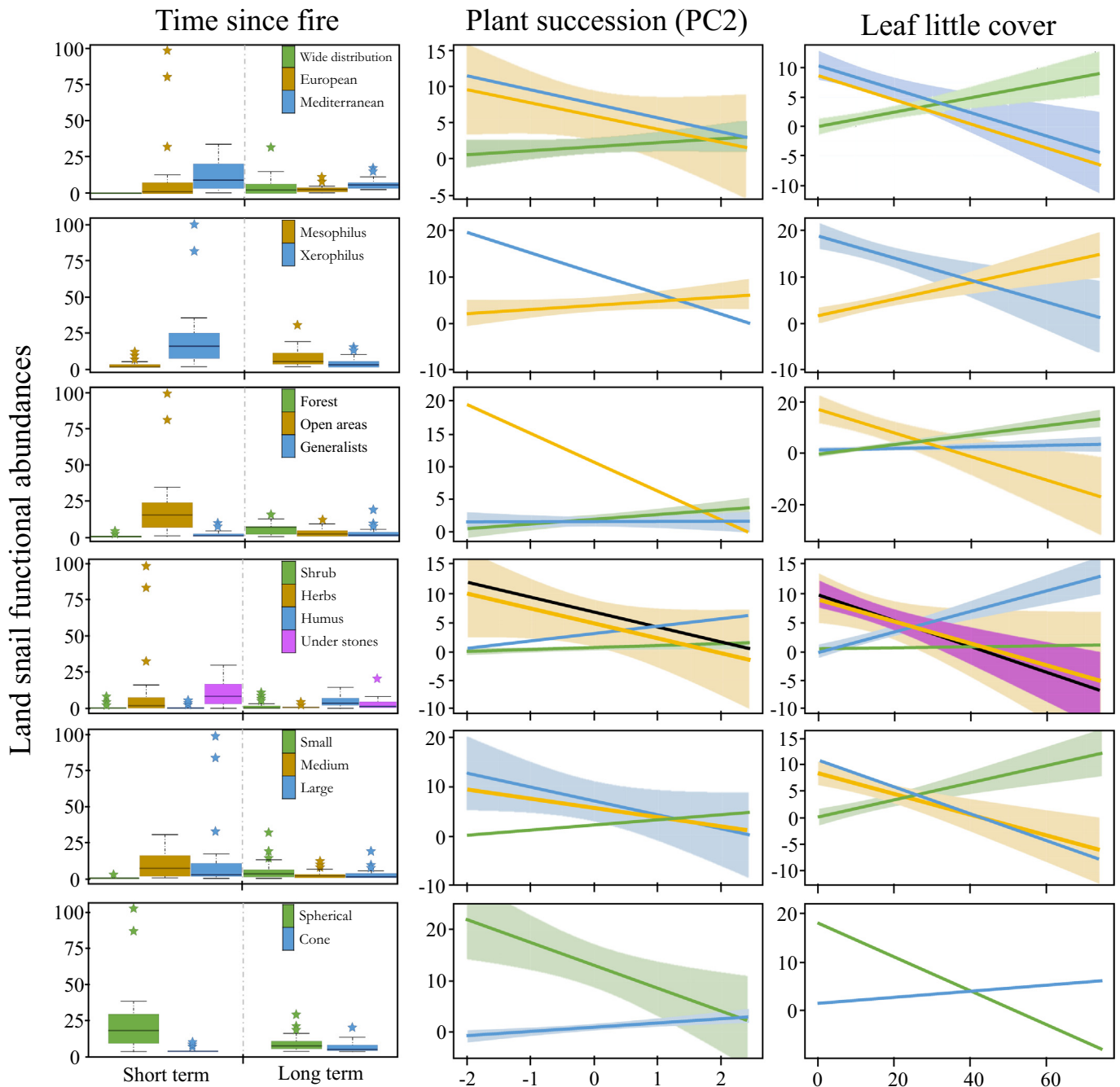


Fig. 2. The influence of variables on trait group occurrence. Influence of time since fire, plant succession (PC2) and leaf litter cover on the distribution of snail trait group occurrence in Sant Llorenç del Munt i l’Obac burnt area. Boxplot represent data distribution on each time since fire category (short and mid). Lines are fitted from generalized linear mixed models of number of species per site within each functional group. Shaded areas represent 95 % confidence intervals. Lines without shaded areas indicate non-selected variables, i.e. Akaike weights (ω_i) ≥ 0.5 and p value ≤ 0.05 . Forest, open areas and generalists correspond to macrohabitat category trait group occurrence; stones and humus to microhabitat; small and mid to snail shell size; spherical and cone to snail shell form; wide distribution to biogeographic distribution.

macrohabitat, hummus microhabitat, cone-shaped shell and small size were related to a mid-time since fire and associated habitat structure variables. The second axis (eigenvalue = 0.01, proportion explained = 0.12) discriminated between large and herb-preferring species, on the one hand, and cone-shaped shells and medium- and small-sized species, on the other (Fig. 3b).

Based on the functional indices calculated for snails in each sampling unit, there was significant variation in the functional richness (paired t -test: = 4.1, $df = 30$, p -value ≤ 0.001), functional evenness ($t = 2.51$,

$df = 30$, $p = 0.02$), functional divergence ($t = 2.22$, $df = 30$, $p = 0.03$) and functional dispersion ($t = 5.26$, $df = 30$, $p \leq 0.001$) between short and mid times since fire (Fig. 4); i.e. functional diversity indices were greater eighteen years after the fire. In general, the GAMMs showed that the functional indices were significantly higher with greater leaf litter cover (Table S3). Functional richness was also greater in the complex vegetation structure that is characteristic of the vegetation succession. Functional evenness did not relate to any environmental variable except time since fire; stone cover was not related to any functional index.

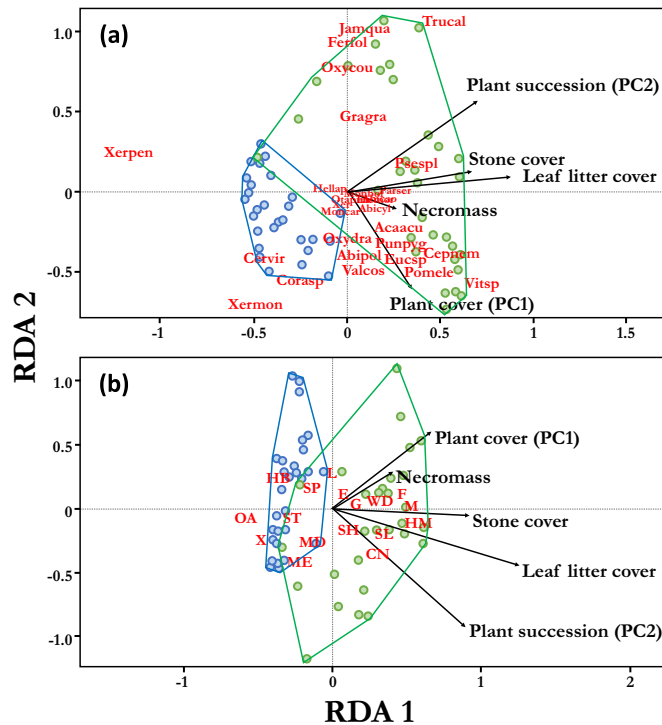


Fig. 3. Redundancy analysis. Redundancy analysis plots on the (a) taxonomic diversity and (b) functional traits of the land snails in de Sant Llorenç del Munt i l'Obac Natural Park. Blue and green circles correspond to short and mid time since fire, respectively. Acronyms for species: *Abida cylindrical* (Abicyl), *Abida polyodon* (Abipol), *Acanthinula aculeata* (Acaacu), *Aegopinella* sp. (Aegsp), *Cepaea nemoralis* (Cepnem), *Cermuella virgata* (Cervir), *Cornu aspersum* (Corasp), *Discus rotundatus* (Disrot), *Euconulus* sp. (Eucsp), *Ferussacia folliculum* (Ferfol), *Graniberia braunii* (Grabra), *Granopupa granum* (Gragra), *Helicigona lapicida* (Hellap), *Jamiania quadridens* (Jamqua), *Monacha cartusiana* (Moncar), *Montserratina bofilliana* (Monbof), *Otala punctata* (Otapun), *Oxychilus courquini* (Oxycou), *Oxychilus draparnaudi* (Oxydra), *Paralaoma servilis* (Parser), *Pomatias elegans* (Pomele), *Pseudotachea splendida* (Psespl), *Punctum pygmaeum* (Punpyg), *Rumina decollata* (Rumdec), *Truncatellina callicratis* (Trucal), *Vallonia costata* (Valcos), *Vitrea* sp. (Vitsp), *Xerocrassa montserratensis* (Xermon), *Xerocrassa penchinati* (Xerpen) and *Xerosecta cespitum arigonis* (Xerces). Acronyms for the functional traits: wide distribution (WD), central and western European (E), Mediterranean (MD); xerophilous (X), mesophilous (M), forests (F), open areas (OA), generalists (G), herbs (HB), shrub (SH), stones (ST), humus (HM), small-size (SL), medium-size (ME), large-size (L), spherical-form (SP) and cone-form (CN). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

In this study, we examined how a land snail community changed in two particular periods (short- and mid-term) after a wildfire. We modelled changes in functional classes, compared taxonomic and functional community composition, and examined changes in functional diversity indices. In a previous study, we had demonstrated that there had been a taxonomic replacement of the dominant species in the short- (three years) to mid-term (18 years) since fire (Puig-Gironès et al., 2022); in the current study, we show that this taxonomic replacement was caused by the environmental preferences of the dominant snail species during these two periods. In accordance with our predictions, the variation in community composition between post-fire ages can be attributed to species traits and the successional changes occurring in habitat conditions. Our results thus show that land snail communities respond functionally to fire. The main effects of time since fire on the snail functional groups were driven by the post-fire development of the structure of the understorey vegetation and the availability of shelter. Snail species that need mesophilous conditions such as humus and shrub cover were more abundant in mid-term successional vegetation

once the plant cover had recovered, whereas snails that prefer xerophilous open-areas – as well as herb specialists on the ground – were more abundant in the first few years since fire while the ground-layer habitat was still open.

At taxonomic level, we observed contrasting responses in the time since fire and habitat variation during the succession: snail turnover shows strong species decreases and increases between short and mid time since fire. These contrasting responses to fire have been reported previously in other snail communities and are consistent with the great and diverse dependence of these organisms on changing vegetation and shelter structures during post-fire succession (Kiss and Magnin, 2003; Kiss et al., 2004; Santos et al., 2012). Functional-trait replacement over time suggests that species adapt their particular habitat requirements. At a functional level, our results also show that snails with xerophilic and mesophilic preferences have different relevant importance after fire and are highly affected by post-fire microhabitat complexity. Xerophilous-related snail traits were more abundant immediate after the fire when leaf litter were scarce but, after successional plant recovery, mesophilous-related traits became more abundant. Moretti et al. (2009) showed that the functional response of bees was notable in temperate regions but more stable in the Mediterranean due to the replacement of functionally similar species. Immediately after fires in the Mediterranean region, xerophilic-related traits are more stable after perturbations (i.e. high resistance and resilience to disturbance) due to the more severe evolutionary selection provoked by the recurrence of wildfires. Humidity is one of the main factors that affect land snail species richness and community composition (Hoffmann et al., 2011). The majority of land snail taxa have a preference for humid microhabitats and little tolerance of dry environmental stress (Astor et al., 2017). However, xerophilous snails have strategies and mechanisms for coping with water stress (Schweizer et al., 2019) that allow them to overcome climatic constraints and be abundant after fire. On the other hand, the rapid response after fire by herb specialists (many of them large-sized with spherical shells) may be attributable to the great diversity of herbaceous plants that appear immediately after fire (Vilà et al., 2001). We can thus argue that the climatic features that make the Mediterranean Basin a fire-prone region (dry and hot summers) are also strong drivers that filter particular functional traits.

As time elapsed after the 2003 fire, the habitat became more complex, with more plant cover and leaf litter. These conditions are associated with the presence of land snail forest-related traits such as wide distributions, humus microhabitats and small sizes. Our results reinforce the importance of local environmental conditions including habitat and vegetation characteristics (Bros et al., 2016; Müller et al., 2005) and soil architecture (Nekola, 2003) in the distribution of land snails in burnt landscapes. Suitable microhabitats ensuring snail survival and protection – irrespective of forest age – are required to maintain land snail diversity and abundance (Barbato et al., 2020). They allow land snails to respond to adverse climate stressors by selecting appropriate microhabitats to minimize the risk of dehydration (Moreno-Rueda et al., 2009).

Four years after fire, spherical shell forms (flat shells) are more abundant given that cone-shaped (tall) shells need more time to increase in burnt areas, due possibly to the functional link between snail locomotion and shell form. The spiral index, defined as the shell height divided by its diameter, shows a bimodal distribution in land gastropods with two predominant types: high- or low-spiralled (Cowie, 1995; Emberton, 1995). Tall shells are generally active on steep or vertical surfaces and gastropods, whereas flat shells are more active on flatter or even horizontal surfaces (Cook and Jaffar, 1984). It has been suggested that this is due to the mechanics of shell balance during locomotion on different substrates (Okajima and Chiba, 2009), so the increased presence and variability of vertical structures eighteen years after the fire may explain – at least in part – this functional change in shell forms.

In accordance with our final prediction, we detected significant differences in land snail functional indices according to the time since fire. The variation in microhabitat complexity driven by leaf litter cover and plant succession could lead to more ecological opportunities for a larger number

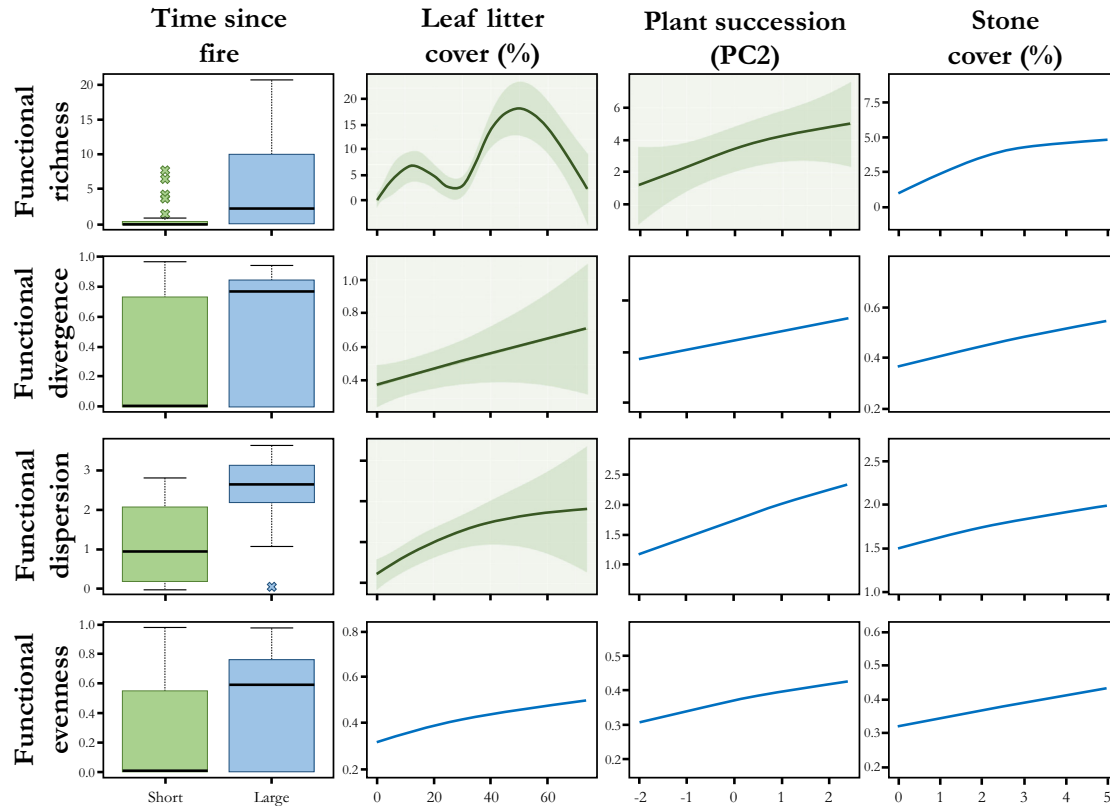


Fig. 4. The influence of variables on functional diversity indices.

The influence of time since fire, plant succession (PC2), leaf litter and stone cover on the distribution of snail functional diversity indices in Sant Llorenç del Munt i l'Obac burnt area. Boxplot represent data distribution on each time since fire category (short and mid). Lines are fitted from generalized additive mixed models; where shaded areas represent 95 % confidence intervals and their absence indicate non-significant relationships.

of land snail species, and may explain the differences found in functional richness, evenness, divergence and dispersion. The greater heterogeneity in land snail traits in the long-interval since fire seems to permit a more stable functional community to rebuild after fire. This community may be enhanced by greater local functional richness since more strategies and niches are available that can be exchanged (Kosicki and Hromada, 2018), thereby provoking a shift in species composition but not in the functional assemblage (Petchey et al., 2007). However, in our case there were both changes in the species and in the functions, they perform in the environment. Beetle communities in the burnt areas also were more functionally diverse in terms of the traits associated with habitat, feeding and phenology but were less diverse in terms of the traits associated with climatic conditions, habitat specificity and woody decay (Moretti et al., 2010). However, the few differences in the functional metrics of evenness, divergence and dispersion may have been caused by beetles' poor discriminative ability when identifying functional changes in a fire-related community.

5. Conclusions and conservation remarks

Our functional analysis indicated that the short term since fire provides a time-window for certain Mediterranean xerophilous snail species specialized in early successional habitats (Smith, 2018) that use stones and herbs in open landscapes, and have spherical medium-sized or large shells. In the mid-term, however, plant succession will allow for the recovery of species negatively affected by fire including European mesophilous species, characteristic of forest habitats, that inhabit humus and shrubs, are small and have conical snails.

Fire regimes are currently changing in the Mediterranean Basin with an increased frequency of big fires (Pausas, 2022). How snail species will face this fire regime shift is still unknown, although the absence of long-unburnt forests by the increased frequency of fires could impede the establishment

of species that need moist, mature and complex habitats. Our study can help to understand which snail functional traits are selected during post-fire succession, and this is critical for understanding the taxonomic and functional resilience of communities to disturbances such as fire (Mateos et al., 2011; Moretti et al., 2009; Rainsford et al., 2022; Rhee et al., 2022; Santos and Cheylan, 2013). Our results suggest that a large proportion of species with specific requirements can take advantage of the new habitats created by wild-fire. Three main mechanisms explain the change in community and functional composition. a) Fire and post-fire conditions release new resources (e.g. open habitats and rapid herb grow) that attract communities dominated by pioneer species (Moretti and Legg, 2009; Pausas, 2006); b) altered post-fire conditions select for species with narrow climatic requirements, i.e. xerothermic species (Pausas and Verdú, 2008); and c) mid-term post-fire conditions increase the range of plant sources (types, sizes and decay stages) and, consequently, the number the niche spaces, thereby benefiting forest and mesophilic species and adding to the functional richness.

Therefore, time since fire plays an important role in the functional turnover of the selected land snail functional classes. This is probably also true for other soil groups with life histories and life forms that are similar to those of land snails. Surprisingly, we found that this low-mobility group had a high turnover – both taxonomically and functionally – since fire that was similar to high-mobility groups such as birds (Santos et al., 2014). Consequently, our results support the idea that functional traits underlie the response of organisms to environmental changes caused by fire. This is relevant because as primary consumers gastropods aid forest decomposition processes and contribute to nutrient cycling, and soil formation and productivity (De Oliveira et al., 2010). They are an important food source for a vast number of species (Nyffeler and Symondson, 2001) and, furthermore, their shells are the primary calcium source for the eggs of some bird species (Graveland et al., 1994). Therefore, they underpin ecosystem functioning during succession.

On the other hand, functional redundancy could occur when there are taxonomic differences between the short and long-intervals, although this will not lead to changes in the functional traits of the community. Our results inform about no redundancy, i.e. species made functions strongly different between short and mid-term after fire. Consequently, time since fire is the main driver that makes snail communities richer in functional diversity to future fires. Therefore, fire should also be seen as a beneficial disturbance for biodiversity when homogeneous forest systems with little taxonomical or functional biodiversity are affected. To maintain or promote biodiversity in burnt areas, micro- and macrohabitat heterogeneity promotion is the best strategy for increasing functional richness and ensuring the resilience of biota, i.e. unburnt microhabitats with different times since fire should be preserved if regular prescribed burns are used. This will ensure that there will be different communities at different sites, thereby increasing the gamma diversity and resilience. However, although here we use a great number of functional classes, improved knowledge of the functional traits of snail species and communities is still required, especially in the case of the understudied but still key components of ecosystems such as the main diet components of land snail species.

CRedit authorship contribution statement

Roger Puig-Gironès: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Xavier Santos:** Supervision, Methodology, Writing – original draft, Writing – review & editing. **Vicenç Bros:** Supervision, Methodology, Writing – original draft, Writing – review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.162677>.

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