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Temporal differences in snail diversity responses to wildfires and salvage logging

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Summary

Species tend to peak in abundance at different times after fires. Over time, species richness (α) and landscape heterogeneity are prone to increase and lead to greater between-site diversity (β). However, post-fire salvage logging can reduce β-diversity, both directly and through its influence on succession. The as-yet understudied response of land snails to long-term habitat modification after wildfires and forest management is important for decision-making in forest restoration and conservation. We expected to detect differences in land snails and diversity in both the short and long term and between treatments in a natural park in the Mediterranean Basin. However, our results showed that post-fire management was a non-significant variable for snail community diversity, the exception being open-habitat endemic species. Plant succession and leaf litter cover were the main variables that shaped snail diversity and abundance over time after fires. Eighteen years after a fire, the land snail diversity had improved and the community composition had diversified, irrespective of the post-fire treatment, but threatened species disappeared and the total snail numbers had notably declined. To preserve threatened open-habitat species, prescribed fires and livestock grazing are recommended in combination with mature areas that can act as shelters where forest snails can recover from future disturbances.

Introduction

Fire is a key element that has a major influence on ecosystems throughout the world (Bowman et al. 2009, Pausas & Keeley 2009). Species tend to peak in abundance at different times after fires (Moretti et al. 2004), and so some authors back the idea that a matrix of fire-aged patches will maximize species diversity – the so-called 'pyrodiversity' (Parr & Andersen 2006, Kelly et al. 2015) – and favour endangered open-habitat species (Brotons et al. 2008, Santos et al. 2009, Puig-Gironès et al. 2022a). In general, greater between-site diversity (β-diversity) and landscape diversity (i.e., heterogeneity across space) are predicted to occur after fires (Hammill et al. 2018). The time elapsed since a fire may initially increase the species richness (α-diversity) as species colonize sites that now have their preferred habitat structure (Serrat et al. 2015). The effect of fire, however, varies between and within groups of species as a consequence of local factors conditioning α-diversity (Viljur et al. 2022), and subsequently a particular suite of specialized species could be favoured and so reduce the overall β-diversity (Pastro et al. 2011).

Wildfires cause soil degradation in Mediterranean forest environments due to post-fire erosion (Vieira et al. 2015) and changes in physical, chemical and microbiological properties caused by the direct loss of organic matter content (Badía et al. 2017, Alcañiz et al. 2018). Additionally, immediately after a fire, burnt trees are usually removed in a process called post-fire salvage logging (Müller et al. 2018). The ecological consequences of these management measures have been the subject of intense debate; salvage logging simplifies the habitat structure and can slow down vegetation regeneration, reduce plant and animal diversity and increase soil erosion (Thorn et al. 2018). Therefore, disturbances can reduce β-diversity, both directly and through their influence on post-fire succession. Although poorly studied to date, long-term responses under post-fire management may be relevant to post-fire soil conservation and management. If a species present in late-successional stages recovers quickly after a disturbance, its initial decline is likely to be of little relevance to its ability to persist – provided that the disturbance return time is sufficiently long for recovery to occur (Ström et al. 2009).

Despite being a major component of the soil fauna, little is known about the effects of long-term fires and salvage logging on land snails (henceforth, 'snails'), which contribute to the decomposition of forest litter, to nutrient recycling and to soil formation and productivity (De Oliveira et al. 2010). Cryptic shelters reduce the immediate effects of wildfires and salvage

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logging on these low-mobility herbivores (Kiss & Magnin 2006, Bros et al. 2011) and potentially on other soil-dwelling invertebrates (e.g., see Certini 2005, Vidal-Cordero et al. 2022). Furthermore, similar results amongst snails have been found after tree windthrow (Spelda et al. 1998) and bark beetle disturbances (Winter et al. 2015). In other highly mobile invertebrates such as wild bees, although similar abundances between salvage-logged and unlogged sites were maintained, greater bee species richness and β-diversity have been reported in unlogged sites (Galbraith et al. 2019). Epigeal invertebrates are more vulnerable to fire than hypogeal species, and their recolonization is determined more by habitat suitability than by isolation (Mateos et al. 2011). For gastropods, habitat suitability may be directly related to the amount of organic matter in the soil (Bros et al. 2011). However, little is known about the relative importance of other important environmental variables that may influence recolonization by small populations of fire survivors and by certain snail specialists (Astor et al. 2017).

The effects of salvage logging on biodiversity have mainly been studied in the short term, even though knowledge of the longer-term effects is probably more important for managers. Understanding how snails respond to long-term habitat modification due to wildfires and salvage logging is thus important for decision-making when restoring forest and improving its conservation. Given the low vagility of land snails, we expect small changes in α- and β-diversity to occur, with the exception of comparisons between short and long time period scales. The exception to this general expectation will occur if post-fire management is appropriate for snails, in which case the α-diversity will increase during the post-fire succession (Viljur et al. 2022). Therefore, we took the α-diversity to be the diversity of species at a particular site and β-diversity as the difference in the species identified between sites (Whittaker 1972, Anderson et al. 2011). For this purpose, we sampled on two occasions (2007 and 2021) 31 plots distributed in five post-fire treatment areas in the sector affected by the 2003 fire in the Sant Llorenç del Munt i l'Obac protected area in the Mediterranean Basin. Our aims were: (1) to study whether the post-fire treatment has an effect on snail diversity over time after the fire; (2) to test whether or not the time since fire and plant succession increase snail diversity; and (3) to examine which structural and ground-cover variables explain the α- and β-diversity after the fire. We predicted three possible trends: (1) diversity generally decreased over time since the fire, probably due to a series of general factors; (2) in some post-fire treatments diversity improved while in others it did not; and (3) diversity increased in all cases regardless of post-fire treatments (Fig. S1).

Materials and methods

Study area and study design

This study was performed in a burnt area in the Sant Llorenç del Munt i l'Obac Natural Park (henceforth PNSLL) in Barcelona province (north-east Iberian Peninsula; Fig. S2). The PNSLL (total area 13 694 ha) is characterized by a rugged landscape of sheer crags and unusual rock formations formed from a substrate of polymictic conglomerate rock. Its climate is subhumid Mediterranean with an annual rainfall of *c.* 600 mm that is greater in spring and autumn than in summer; its highest peaks are windier, wetter and cooler than surrounding lowland areas (Panareda & Pintó 1997). The original forest cover of the area, prone to fast-spreading fires during hot dry summers, is dominated by evergreen holm oak (*Quercus ilex* L.), Aleppo pine (*Pinus halepensis* Mill.) and Spanish black pine (*Pinus nigra* subsp. *salzmannii* (Dunal) Franco), generally with an evergreen holm oak understory (Pintó & Panareda 1995).

In August 2003, 4543 ha of the eastern part of this park (10% of its total surface area) and neighbouring areas were burnt by a wildfire (Fig. S2), which affected an area dominated by pine forest with holm oak understory. Approximately 440 ha had already been burnt in previous years (335 ha in 1970 and 105 ha in 1994). Soon after the fire and within 2 years, most of the burnt area had been completely logged using different treatments. We selected five different post-fire treatments and located several replicate sites for each treatment (Fig. S2): (1) non-managed (NM; 4 replicates), burnt in August 2003 with no post-fire treatment and removal; (2) trunk removal (TR; 13 replicates), burnt in August 2003 with complete subsequent trunk removal and all branches spread over the ground; (3) complete removal (CR; 5 replicates), burnt in August 2003 and trunk and branches removed; (4) trunk removal and subsoiling (SU; 4 replicates); burnt in August 2003 and, besides the trunk removal, the area was subsoiled (i.e., to plough or turn up the upper 20 cm of subsoil) and later replanted with pines; and (5) recurrent fires (RF; 5 replicates), corresponding to sites burnt twice, in 1970 or 1994 and in 2003, characterized by shrublands with a high percentage of bare ground and little plant cover. We only sampled areas with a pine forest that covers peripheral areas of the park to avoid the effect of forest type on snail assemblages (Kappes et al. 2006).

Snail sampling

In May–June 2007 and 2021, we used two complementary methods to search for gastropods at 31 sites inside the burnt area: (1) all snails with shell sizes over 5 mm were actively searched for in adequate microhabitats in a 10 × 10-m plot for 30 min; and (2) snails under 5 mm were collected from subsamples of soil litter from the top 5 cm of soil in four 25 × 25-cm plots. Four subsamples were randomly taken from within the larger 10 × 10-m plot and examined in the laboratory with a stereomicroscope and optical material to count and identify small snails (Santos et al. 2009). Specimens were identified to the species level; however, some species were only determined to the generic level – this is the case for *Euconulus* spp. (see Horsáková et al. 2020 for more details) and *Vitrea* spp. The same procedure was followed for *Vitrea* spp. as in Bros et al. (2011) due to the difficulty of identifying between juvenile specimens of *Vitrea contracta* and *Vitrea subrimata*.

Only fresh shells and living individuals were recorded as representative of current communities. We considered shells to be fresh (recently dead) when the periostracum was present and coloured like a living animal. Other shells were also considered to be recently dead depending on their state of preservation, their size and the microhabitat in which they were found (Pearce 2008, Cernohorsky et al. 2010). The species of which only dead specimens were collected were discarded from the analysis.

Habitat structure variables

The habitat structure and shelter in the sampling sites were characterized by recording several vegetation and ground-cover variables (Table 1). At the centre of each sampling site, the percentage of vegetation cover was recorded at points 50 cm apart along five parallel 10-m transects; thus, at each site we recorded 100 points to characterize the abundances of plant species. Vegetation variables included the extent of cover of bare soil, grass, shrubs and trees. We

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Table 1. Description of the different environmental variables used to understand snail dynamics and diversity within the burnt area.

Variable	Description
Plant cover	The first principal component (PC1, with 34.49% of explained variance) is derived from the principal component analysis of the vegetation cover that corresponded to the gradient from sites with less to more plant cover sites, mainly undergrowth
Plant succession	The second principal component (PC2) derived from the principal component analysis of the vegetation cover of ordered stations from those with germinating species characteristic of the first post-fire stages (e.g., herbaceous vegetation and *Cistus albidus*) to the stations with perennial vegetation that form the characteristic plant communities of the area (rosemary, pines and oaks)
Coarse woody debris	Mean percentage of cover provided by large woody materials such as dead trunks, stumps and wide branches, which could be used as shelter, at each point
Fine woody debris	Mean percentage of cover provided mainly by fine fallen branches on the ground, which could be used as shelter, at each point
Rocky land	Mean percentage of cover provided by rocky land and rocky outcrops at each point
Stones	Mean percentage of cover provided by large stones (>8 dm^3) at each point
Leaf litter	Mean percentage of cover provided by leaf litter on the soil at each point

performed a principal component analysis to reduce the vegetation variables that configure the habitat structure at each site (Fig. S3), where the first component corresponded to plant cover and the second ordered stations following the plant succession gradient (Table 1). The ground-cover variables also included the bare soil, coarse woody debris (CWD), fine woody debris, leaf litter (henceforth, 'litter'), rocky ground and stones (Table 1).

Statistical design

We analysed the community composition, snail abundance and diversity and, finally, the abundances of the commonest species. To assess how snail community composition was affected by time since fire and the resulting habitat structure, we explored community composition using non-metric multidimensional scaling (NMDS). Through ordination, sites could be visualized in a multidimensional space according to their similarity in species composition (Table S1). The NMDS was based on the Bray–Curtis dissimilarity index, which is less sensitive to rare species than other techniques. We also performed a permutational multivariate analysis of variance (PERMANOVA) to observe the possible differences between communities using as factors the treatment, the time since fire and their interaction. Both analyses were performed with the *vegan* (Oksanen et al. 2019) package in *R* (R Development Core Team 2017).

We used an information-theoretical approach to examine the relationships between snail α-diversity and β-diversity (response variables) and the properties of the sites (predictor variables). We used species richness as the measure of diversity: γ-diversity was the total number of snail species recorded in a sampling year (short and long time periods since the fire), α-diversity was the number of species per site and β-diversity was calculated using the Whittaker (1972) measure of β-diversity = (γ-diversity/α-diversity) − 1. We also calculated the Shannon index for each site as another measure of α-diversity.

All diversity variables were calculated for the entire pool of snail species. However, we also used four subsets of species based on moisture preferences, shelter preferences and their commonness. The moisture preferences of different species of snails were classified into two categories: xerophilous or mesophilous species (Table S2). Species were also classified into one of four shelter-preference categories: stones (walls and stones), herbaceous vegetation, shrub vegetation and humus (fallen leaves, humus and dead trunks; Bros 2006, Kemencei et al. 2014). Species were regarded as 'common' when the following two conditions were satisfied: they were captured in at least six out of the 62 sites and more than 10 individuals were present.

To test the factors related to species conservation, we classified species on the basis of their regional-range endemism and their threatened status, whereby species were scored as 0 (no endemic species nor any threatened status) or 1 (when species were an endemism or presented a threatened status). For endemism, we considered species with a restricted distribution as Catalan regional endemics, while for the threatened status we select species listed in the legislation or considered as Near Threatened, Vulnerable, Endangered or Critically Endangered on the European International Union for Conservation of Nature (IUCN) Red List (IUCN 2022). Finally, we analysed the effects of site properties on the 13 'common' selected species as response variables (Table S2).

To test the time and post-fire treatment effects on the snail community, we used generalized linear mixed models (GLMMs) with time since fire, treatment and their interaction as explanatory variables. The GLMMs had different error structures due to the origin of the data: snail abundance and β-diversity models presented a Gaussian error structure, while α-diversity (species richness), endemism species, threatened status and the abundances of 13 species were performed with negative binomial error structures and log link functions to avoid data overdispersion. Each sampled site was included as a random effect to control for possible site-based differences. GLMMs were developed using combinations of the seven environmental predictor variables (Table 1).

Before model selection, multicollinearity diagnostics and variability assessments (outliers; Zuur et al. 2010) were performed by quantifying generalized variance-inflation factors (GVIF[1/(2 df)]) for each fixed factor (Fox & Monette 1992), where GVIF values ≤ 2.5 (arbitrary threshold) suggested collinearity; however, no collinearities were found. To compare and rank models in the candidate set (Table S3), differences in Akaike information criterion for small samples (AICc) values (Δi) were calculated, where models with $\Delta i \leq 2$ had substantial support (Burnham & Anderson 2002). Then, we calculated the Akaike weights (ωi), which represent the probability that a model is the best in the set. In the absence of a clear 'best' model (i.e., $\Delta i \leq 2$ and $\omega i < 0.9$), model averaging was conducted to determine the influence of each explanatory variable. Model fit was assessed using marginal and conditional coefficients of determination (Nakagawa & Schielzeth 2013). 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 ωi values for each variable. The RIV ranges from 0 to 1, and the explanatory variable was considered robust if it had an RIV > 0.9, which it was considered as having a moderate effect for RIV values between 0.6 and 0.9 (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).

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Results

A total of 933 individuals belonging to 30 snail species were counted during the study (Table S2), 636 (68.2%) of which were found in the short time period since the fire and 297 (31.8%) were found in the long time period since the fire. Two sites had no snails in the short term, while in 2021 all sites had at least one individual. Three species (*Xerocrassa penchinati*, *Cernuella virgata* and *Xerocrassa montserratensis*) constituted 63.2% of the individuals found, of which the vast majority were found in the short term period since the fire. By 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 (in one site only). The abundance of snails was almost three times greater in the short term than in the long term, representing a significant difference in the temporal variation of the community after the wildfire.

The NMDS ordination reveals dissimilarities in the community composition (Fig. 1) corroborated by PERMANOVA ($p < 0.01$). Partitioned along the first ordination axis (Table S1), immediate vegetation after fire supported very different snail communities from those sites with a developed vegetation; vegetation variables influenced differences in community composition between short- and long-term samplings. The cover of plants, the rocky ground and CWD (arranged on the second NMDS axis) also seem to have affected the snail community composition at the sites. However, the snail communities at different sites in the short time period since the fire resembled each other more than the communities present 18 years after the fire, in which there was more dissimilarity between sites. The post-fire treatment led to some habitat differences (Fig. S4) but was not significant in PERMANOVA ($p = 0.61$) or for the time and treatment interaction ($p = 0.86$).

The GLMMs showed that, in general, treatment was a non-significant variable on snail community diversity (Table S4). However, the α-diversity of mesophilous snails had lower values in managed than in non-managed sites. β-diversity can be interpreted in such a way that the lower the β-diversity, the higher the number of species found. In this way, the β-diversity of mesophilous snails was lower after subsoiling and recurrent fires than in non-managed plots. Similarly, all humus snail components of diversity also were lower in recurrent fire plots than in non-managed plots. Conversely, endemic snails were less frequent in the non-managed sites (Fig. 2). Over time, we also saw some differences between treatments. For example, the α-diversity of the snail community in the non-treatment plots increased significantly, while in the recurrent fire plot it decreased, as did the β-diversity. Contrastingly, mesophilous and humus snails increased over time, especially in the non-managed plots, in terms of snail density and α- and β-diversity.

Plant succession and litter cover were the main variables (appearing in 12 and 11 of 21 possible models, respectively) that modelled snail diversity and abundance over time since the fire (Table 2). Plant succession had negative effects on threatened snails, while litter cover had negative effects on xerophilous snail α-diversity and herbaceous snail α-diversity (Fig. 3). Rocky ground cover increased the total abundance of snails, common snails, xerophilous snails and herbaceous snails. The reduction in stone cover had negative effects on the stone snail abundance and xerophilous snail β-diversity but increased mesophilous snail α-diversity. CWD had a positive effect on mesophilous and humus snail α-diversity.

Litter cover was the main environmental variable affecting the abundances of the 13 most common snail species (Table S5), being significant and/or with high to moderate relative importance for each variable (RIV > 0.6) for seven of these species (four with a positive relationship). In contrast, five species were affected by plant succession (three positively), three by plant cover (one positively) and three by the CWD (two positively), and one species showed a positive effect for rocky ground and stone cover values.

Discussion

Overall, our results show that in the 18 years since the fire the snail diversity improved and the community composition diversified in all cases regardless of the post-fire treatment. However, in the long term the total abundance of snails was significantly lower than in the short term. The microhabitat mosaic in burnt areas underpins a relationship between the structure and properties of the microhabitats and the diversity of snail communities. Thus, the largest changes in habitat characteristics over time drive snail community diversity. However, our results show how little the post-fire management affected the snail community over both the short and long term. Mesophilic and humus snails were more abundant and diverse in the non-managed sites, especially compared to recurrent fire sites. Plant regeneration is usually slightly slower in areas with recurrent fires than in burnt and logged areas and only becomes evident several years – rather than immediately – after a fire (Díaz-Delgado et al. 2002, Eugenio & Lloret 2004). This fact may be a consequence of the poorer capacity of the soil to recover its pre-fire characteristics and nutrient availability and because of erosion (Kishchuk et al. 2015), although these characteristics are also dependent on the geological substrate and the slope of the area. In this sense, resprouting species such as oaks may decrease in stem and total biomass and in net primary production after recurrent fires (Delitti et al. 2005). Similarly, long-lived seeder species such as Aleppo pine may be sensitive to recurrent fires that limit seed storage (Trabaud 2000, Pausas & Keeley 2014). Thus, our results support previous demonstrations that cryptic shelters in burnt areas reduce the effects of the immediate disturbance (i.e., fire) and salvage logging (Spelda et al. 1998, Kiss & Magnin 2006, Bros et al. 2011, Winter et al. 2015). Conversely, endemic snails were more present in managed sites because the endemic species found in the study area are characteristic of habitats with plenty of bare soil and stones for hiding. In both cases, the presence of these endemics is also conditioned by the vegetation succession. These species find more optimal habitat after salvage logging and in recurrent burnt areas. In contrast, the threatened species were practically absent a long time after the fire as a consequence of plant succession and the loss of suitable microhabitats.

Our study highlights the importance of considering multiple levels of diversity after fires. Although salvage logging did not directly influence the diversity of any response variable, patterns of α- and β-diversity did show how the mosaic properties of microhabitats influenced snail communities. In our study, fire and its impact on vegetation cover significantly affected the abundance and diversity of snails over both the short and long term. Thus, malacological species have significant associations with certain predictors related to vegetation cover (Müller et al. 2005). In our case, immediately after the fire, the simplification of the vegetation structure and the increase in grasses and *Cistus* vegetation were patent (Bros et al. 2011). In the long term, the recovery of a certain degree of vegetation cover due to succession and the

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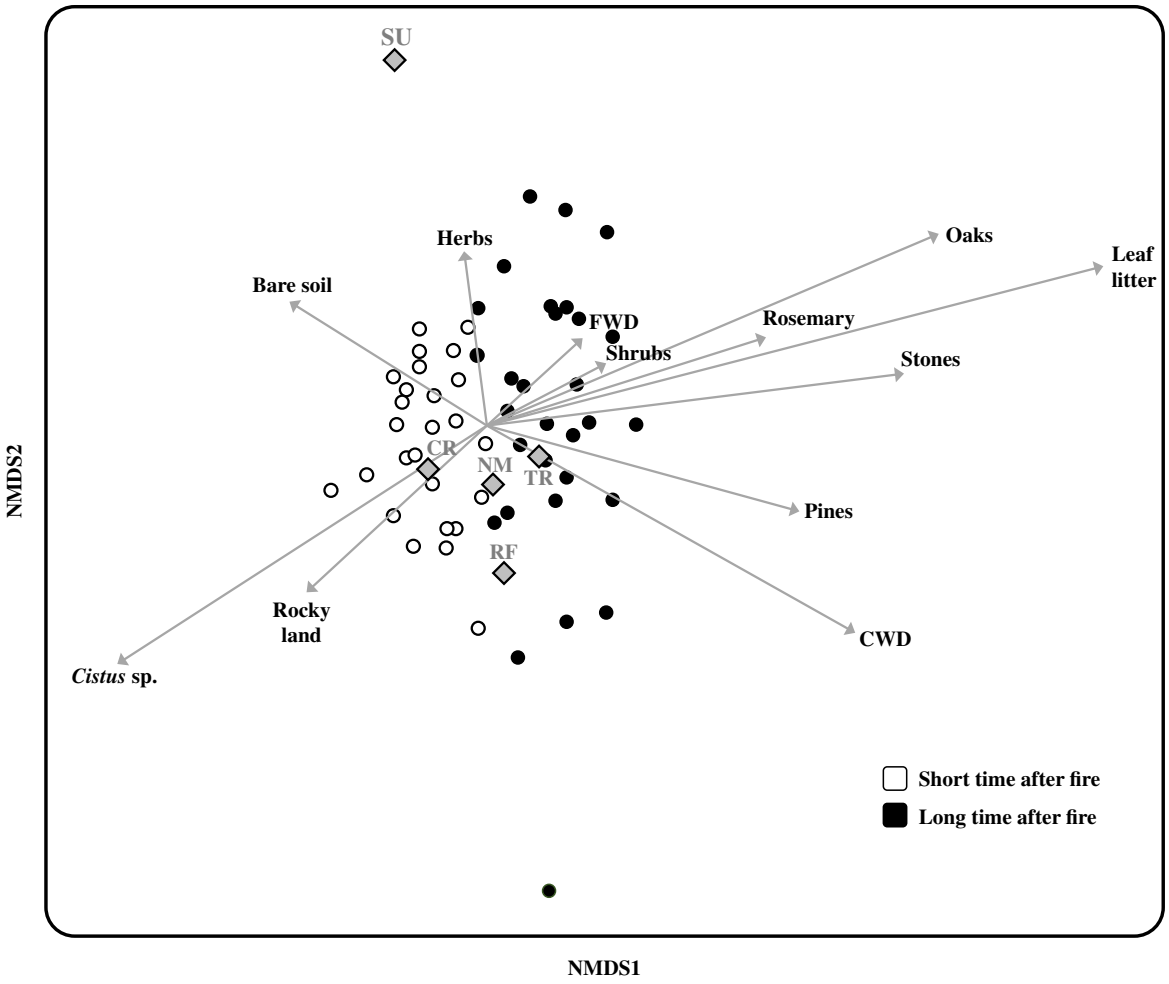


Fig. 1. The influence of time since the fire on the composition of the snail community. Ordinations represent the non-metric multidimensional scaling (NMDS) analyses on species reporting rate/cover (CDW = coarse woody debris; FDW = fine woody debris) matrices. Points represent sites, where white points correspond to a short time period and black points correspond to a long time period since the fire. Symbols represent the five post-fire treatments as factors (NM = non-managed; TR = trunk removal, CR = complete removal, SU = trunk removal and subsoiling; RF = recurrent fires). The distance between sites represents the degree of dissimilarity between the compositions of the snail communities. Arrows represent vectors of influential environmental variables. Sites without species were removed from the analyses.

increase in litter cover were the main drivers of this variation. Succession cover positively influenced the β-diversity of the total community, as well as that of mesophilous and humus snails, such that in sites with more recovered vegetation there were greater differences between communities. This increase in community differentiation may be due to the fact that these sites have greater variability in habitat structure and microhabitat, as well as having different successional pathways that may emerge as time since the fire elapsed (Taylor & Chen 2011). However, these sites also lose common species associated with open-habitat species as well as herbaceous snails. Furthermore, the increase in community differentiation in highly structured habitats was accompanied by a reduction in the number of open-habitat species (Santos et al. 2012). This decline is likely to be a consequence of a reduction in the amount of suitable open habitats, rocky ground and stone cover.

Subgroups of species based on shelter preferences are very useful for understanding patterns in α- and β-diversity to promote treatments aimed at increasing the general diversity at the scale of the burnt area. For example, as the amount of vegetation increased, the α-diversity of litter-dwellers decreased, but this value increased in shrub and humus species. These responses are related to the distribution of the shelter resources on which these species depend. Our results also suggest that while vegetation enhances total α- and β-diversity, some snail components decrease. Thus, increasing the extent of vegetation will not necessarily enhance community richness, although it may be important for individual species (Nimmo et al. 2013). Furthermore, the micro-heterogeneity induced by fires may influence snails at both the fine and broad spatial scales, as might factors such as the spatial distribution of the post-fire vegetation, its orientation, the site's aridity and the intensity of the fires (Díaz-Delgado et al. 2002, Puig-Gironès et al. 2017).

A short time after the fire, terrestrial gastropod communities appeared to be radically modified and impoverished, thereby highlighting how characteristic species from forested areas are replaced by species specialized in xeric areas (Kiss et al. 2004, Bros et al. 2011). Cryptic refuges (Kiss & Magnin 2006, Santos et al. 2009) could mitigate the impact of fire on these gastropods, allowing the conservation of a residual population that, over the years, will enable forest habitats to be recolonized. In particular, over the short term there was a sudden demographic explosion of ruderal snail species associated with herbaceous environments (*C. virgata* and, to a lesser extent, *Xerosecta cespitum arigonis* and *Cornu aspersum*, two widely distributed generalist species) that,18 years

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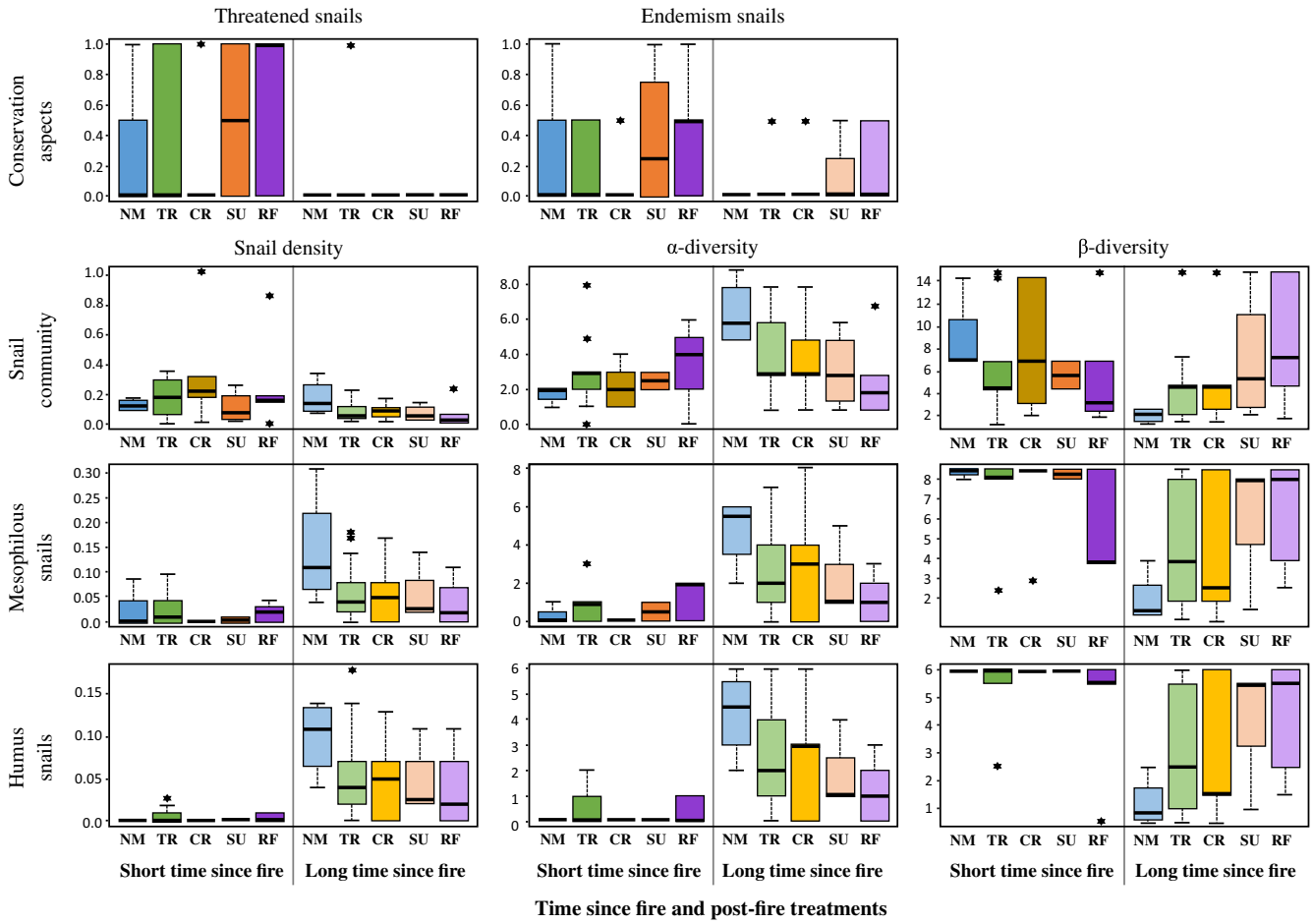


Fig. 2. Snail trends between post-fire treatments over time period since the fire. Comparison of snail conservation status (threatened and endangered snails) and the diversity, α-diversity and β-diversity of the total community, mesophilous and humus snails between management strategies (NM = non-managed; TR = trunk removal; CR = complete removal; SU = trunk removal and subsoiling; RF = recurrent fires) and time period since the fire (4 and 18 years after the fire). Boxes represent 25% and 50% quartiles of the data, while whiskers represent 0% and 75% (down and up, respectively). Asterisks show the maximum and minimum output values.

later, had become locally extinct, presumably due to changes in habitat structure. The dynamics of the spatial cover of grasses after fires in the study area appear to be very short-lived. Forest fires also favoured the population expansion of two xerophytic ground screw snail species (*X. penchinati* and *X. montserratensis*) due to the elimination of tree and shrub vegetation and the consequent expansion of the surface area of bare soil, which is suitable habitat for these two species. However, according to our results, this population expansion is limited in time due to the natural regeneration of Mediterranean forests (Santos et al. 2012, Torre et al. 2014). Thus, post-fire management can play a relevant role in species with different xerophytic preferences.

Over the long term, the local extinction of *X. montserratensis*, *C. virgata* and *X. cespitum arigonis* occurred, along with a very significant decline in the population of *X. penchinati*. Therefore, over the long term, the functional traits associated with herbaceous environments and open habitats evidently disappear or are notably reduced, losing part of the diversity and resilience of the snail community. Moreover, in the specific case of the PNSLL, this implies the disappearance of endemic and threatened species. However, our results confirm an increase in species typical of mature forests and shrub environments, namely *Cepaea nemoralis*, *Pseudotachea splendida* and *Pomatias elegans*, although *P. elegans* is a generalist species when it comes to habitat selection and is common in the pine forests of the PNSLL. The micro-mollusc community of forest humus and associated woody debris (*Acanthinula aculeata*, *Euconulus* spp., *Paralaoma servilis*, *Punctum pygmaeum*, *Truncatellina callicratis*, *Vallonia costata* and *Vitrea* spp.), which was practically non-existent immediately after the fire, increased very significantly in abundance due to the natural regeneration of the forest. According to Kappes et al. (2009), the presence of CWD on the ground is important for these organisms and for the overall proper development of this malacological community. Dead wood and dense shaving cover allows the moisture content to persist over time. Therefore, the recovery of the forest humus micro-mollusc community seems to have been related to the recovery of the vegetation and the normalization of soil microbial parameters after the fire. Furthermore, post-fire salvage logging did not seem to be a factor determining soil properties over the long term (Hedo et al. 2015). In other disturbances, such as forest clear-cutting, similar recolonization results have been observed for humus micro-molluscs that are regarded as slow-dispersing species and intolerant to microclimatic changes. Ström et al. (2009) state that population declines are transient and populations recover within a few decades. The slight increase in *Granopupa granum* and *Jaminia quadridens*, two species that are characteristic of open xerophytic environments, is surprising; it is possible that they need long-unburnt patches to increase their numbers.

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Table 2. Effect of environmental variables on land snail community. Summaries of the selected models are shown, derived from generalized linear mixed model (GLMM) analyses of total snail community (model parameter coefficient ± standard error), and the relative importance of each variable (RIV) is given in parentheses (RIV > 0.9 is a robust effect, RIV = 0.6–0.9 is a moderate effect, RIV = 0.5–0.6 is a weak effect, RIV < 0.5 shows no effect) for common snails, xerophilous snails and mesophilous snails, stone snails, herbaceous snails, shrub snails and humus snails and for conservation status. Where the variable was significant ($p < 0.05$) the parameters of the variable in question are shown in bold type.

Category	Variable	Intercept	Plant cover	Plant succession	Coarse woody debris	Fine woody debris	Rocky land	Stones	Leaf litter
Total snail community	Abundance	**0.10 ± 0.02**					**0.04 ± 0.01**		
	α-diversity	**0.76 ± 0.14**		**0.21 ± 0.09**					**0.03 ± 0.007**
	β-diversity	**14.11 ± 3.05**	−0.67 ± 0.93 (0.53)	−1.65 ± 1.89 (0.74)			0.51 ± 0.63 (0.26)	0.89 ± 1.15 (0.47)	**−0.31 ± 0.12 (0.69)**
Common snails	Abundance	**0.09 ± 0.02**					**0.04 ± 0.01**		
	β-diversity	**5.22 ± 1.03**	−0.44 ± 0.32 (0.32)	**0.88 ± 0.41 (0.73)**				0.66 ± 0.49 (0.46)	
Xerophilous snails	Abundance	0.06 ± 0.02					**0.05 ± 0.01**		
	α-diversity	**0.79 ± 0.19**	−0.11 ± 0.08 (0.37)	0.17 ± 0.14 (0.32)	−0.03 ± 0.03 (0.09)			−0.11 ± 0.09 (0.27)	**−0.02 ± 0.01 (0.90)**
	β-diversity	**5.99 ± 1.05**	0.37 ± 0.34 (0.19)	0.27 ± 0.48 (0.17)	0.26 ± 0.14 (0.24)			**1.09 ± 0.42 (1.00)**	
Mesophilous snails	Abundance	0.004 ± 0.02		**0.02 ± 0.008 (0.47)**					**0.003 ± 0.001 (1.00)**
	α-diversity	**−1.25 ± 0.36**		**0.54 ± 0.14 (1.00)**	**0.06 ± 0.03 (0.70)**		−0.08 ± 0.07 (0.25)	**0.27 ± 0.12 (1.00)**	**0.05 ± 0.01 (1.00)**
	β-diversity	**18.55 ± 1.51**	−0.27 ± 0.45 (0.18)	**−2.85 ± 0.81 (1.00)**				−0.88 ± 0.59 (0.66)	**−0.37 ± 0.06 (1.00)**
Stone snails	Abundance	**0.13 ± 0.02**						**−0.03 ± 0.007**	
Herbaceous snails	Abundance	−0.001 ± 0.02					**0.04 ± 0.009**		
	α-diversity	−0.86 ± 0.61		**−0.63 ± 0.31 (0.57)**		0.03 ± 0.03 (0.29)			**−0.06 ± 0.03 (0.63)**
	β-diversity	**3.47 ± 0.12**		**0.27 ± 0.09**					
Shrub snails	α-diversity	**−1.47 ± 0.34**		**0.38 ± 0.19 (0.79)**	0.06 ± 0.05 (0.23)		0.10 ± 0.11 (0.17)		**0.02 ± 0.01 (0.21)**
Humus snails	Abundance	0.004 ± 0.006							**0.002 ± 0.0003**
	α-diversity	**−1.34 ± 0.45**		**0.38 ± 0.17 (1.0)**	**0.07 ± 0.03 (0.73)**		−0.08 ± 0.09 (0.22)	0.24 ± 0.15 (0.50)	**0.06 ± 0.01 (1.00)**
	β-diversity	**12.83 ± 0.70**		**−1.71 ± 0.49**					**−0.28 ± 0.04**
Conservation status	Threatened snails	**−1.74 ± 0.59**		**−0.89 ± 0.38 (1.0)**	−0.06 ± 0.06 (0.33)	−0.16 ± 0.14 (0.37)			−0.03 ± 0.04 (0.11)
	Endemism	−0.39 ± 0.47		−0.25 ± 0.19 (0.29)	−0.08 ± 0.05 (0.55)	−0.14 ± 0.09 (0.57)	−0.07 ± 0.12 (0.55)	−0.21 ± 0.18 (0.20)	−0.02 ± 0.02 (0.12)

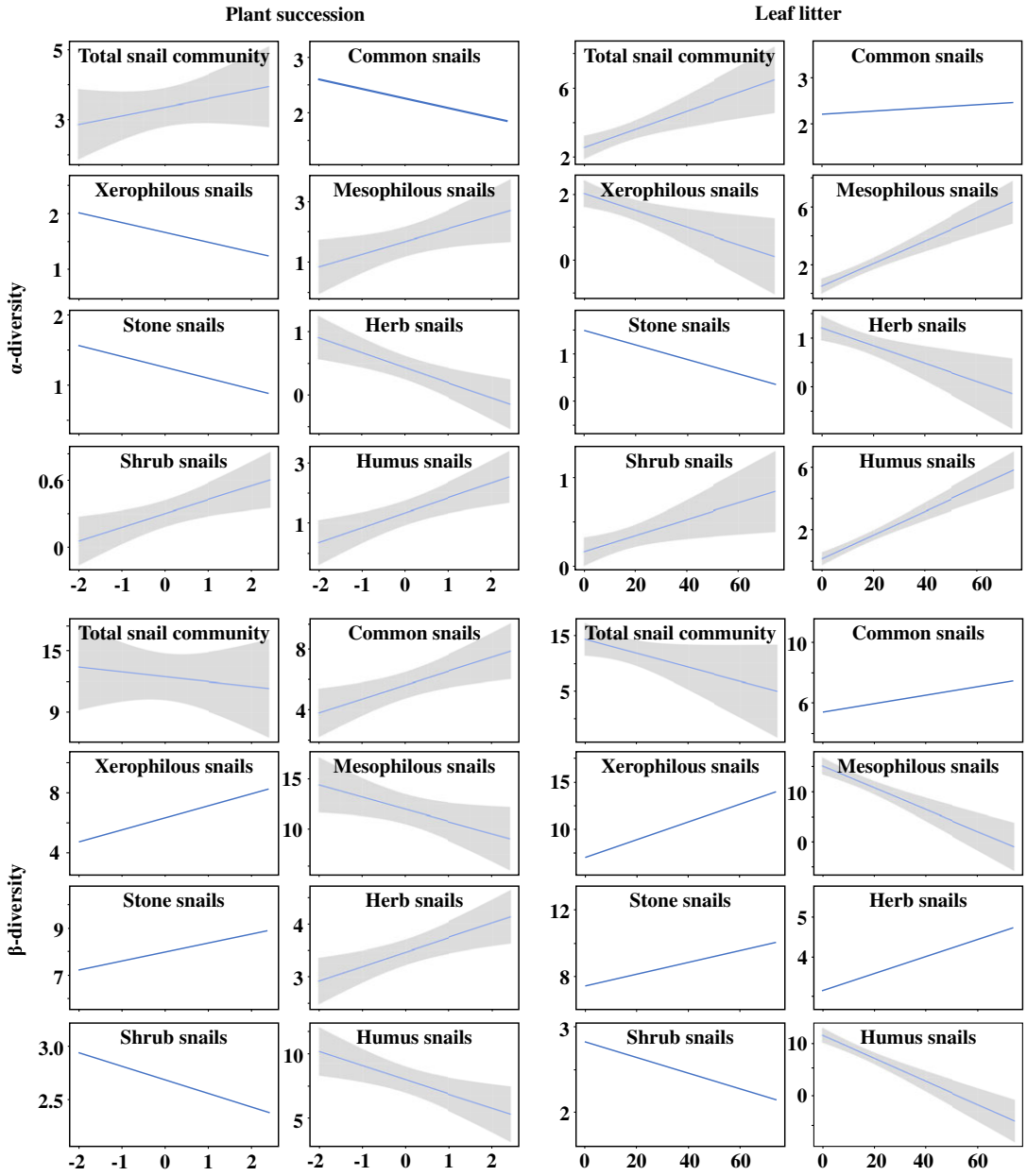


Fig. 3. Model predictions of variables over land snail β-diversity. Marginal effects (measuring the instantaneous rate of change) of the model predictors on α-diversity and β-diversity of the snails according to the plant succession variable and leaf litter cover. Trend lines and shaded standard errors (95% confidence intervals) were obtained from generalized linear mixed model (GLMM) estimates. Lines without shaded areas indicate non-significant relationships. Standard error bars are shown for the type of pre-fire habitat.

Implications for conservation and conclusions

Many authors have previously suggested that mosaic burning will benefit biodiversity conservation as it provides a variety of resources for species dependent on different fire-age classes. Fire may generate open areas that can benefit populations of endangered species (Prodon 1994, Brotons et al. 2008, Puig-Gironès et al. 2022b). This is appropriate for our threatened and endemic snail species, which increase immediately after fire but practically disappear as plant succession progresses. Over the long term, to preserve threatened and declining open-habitat species, prescribed fires and livestock grazing are recommended management tools for keeping vegetation in the early succession stages that host open-habitat species (Kiss et al. 2004, Kiss & Magnin 2006, Santos et al. 2009, Bros et al. 2011, Gaines et al. 2011). However, Greenberg et al. (2007) show how high-intensity burning with high tree mortality can be used as a management tool to increase densities of birds associated with open habitats, although this management technique may have adverse effects on species associated with the shrub strata. Therefore, low-severity fires could be applied to large, previously burnt areas to generate mosaics and increase open-habitat diversity in the focal site. If prescribed burning is used, the time window for burning should be determined. Some authors propose burning 5 or 6 years after a wildfire to manage habitats for open-habitat species (Jacquet & Prodon 2009, Puig-Gironès et al. 2022b). At a regional scale, the fire history and floristic composition will determine the recovery of each vegetation layer after fire. Furthermore, abiotic factors such as fire severity, precipitation, altitude and topography will also have important effects on such

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recovery (Díaz-Delgado et al. 2002, Puig-Gironès et al. 2017). It would also be necessary to determine the optimal size of burnt patches within the areas to be managed, which will vary according to the conservation objectives. Non-burnt or mature areas are also important for increasing mesophilous and humus-dependent species and boosting the α- and β-diversity of the focal site. This diversity will also allow future colonization processes from cryptic shelters and prevent local extinctions due to a lack of suitable sites. Along these lines, salvage logging is the most widespread post-fire practice, even though many authors postulate a negative relationship between this practice and community resilience (Thorn et al. 2018, Muñoz et al. 2021). Our results also showed a greater abundance and diversity of mesophilous and humus snails in non-managed areas. Therefore, more study of non-managed areas is still required to understand how to maximize whole-community resilience in the face of future wildfires.

Supplementary material. For supplementary material accompanying this paper, visit https://doi.org/10.1017/S0376892922000443.

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