Contrasting responses of two xerophilous land snails to fire and natural reforestation

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Abstract

Land-use change is considered the main disturbance in landscape structure and composition, directly affecting faunal distribution and species richness worldwide. Wildfires and natural reforestation alter habitat structure in terms of vegetation cover and also in soil composition and moisture; these processes hence trigger habitat transformations that act as opposing forces at small spatial scales. We have explored the contrasting effects of wildfires and natural reforestation on two land-snail species of the genus *Xerocrassa*, which are endemic in the western Mediterranean. Snails were sampled in pine and Holm oak forest, stony bare slopes and burnt sites. Both species followed a similar pattern: they were present in more than 75% of the stony bare slope sites and around 50% of the burnt sites, but were almost absent in Holm oak forests. The comparison of aerial photographs from 1956 and 2003 showed that stony bare slopes were significantly larger in 1956, this indicating that the natural reforestation might close these habitats, and consequently threaten the viability of the *Xerocrassa* populations. Given their limited mobility, the presence of *Xerocrassa* at burnt sites suggests that these species live in small and cryptic populations within the forest, surviving fire and expanding their distribution due to the appearance of adequate habitats. Our study shows that natural reforestation and fire play opposing roles in conserving *Xerocrassa* populations. The preservation of stony bare slopes as well as other open areas is a key management guideline to maintain landscape mosaics and help future conservation of species of open habitats such as these vulnerable endemic gastropods.

Contents

Introduction

Over one-fifth of the land area of the globe has been converted to human-dominated uses (Hoekstra *et al*., 2005). Land-use change is considered the main process disturbing the structure and composition of the landscape, directly affecting the faunal distribution and species richness in many taxonomic groups (Parody *et al*., 2001; Dupouey *et al*., 2002; Ribeiro *et al*., 2009). The Mediterranean basin has been altered by human activities for at least 5,000 years (Bottema *et al*., 1990; Blondel *et al*., 2010), and the impact of these activities has caused transformation, fragmentation, degradation, and loss of natural habitats, which have threatened at least 15% of all endemic animals and plants (Brooks *et al*., 2002). Thus, land-use change is considered the factor with the strongest impact on the loss of biodiversity in Mediterranean ecosystems (Sala *et al*., 2000).

A particular case of habitat alteration is fire. Wildfires are natural disturbances that have shaped vegetation structure and influenced associated faunas in almost all regions in the world (Bond *et al*., 2005). In Mediterranean ecosystems, wildfires are common natural perturbations, and a fundamental element for understanding the functioning and structure of these ecosystems (Moreno and Oechel, 1994; Trabaud and Prodon, 2002). Fire affects natural animal communities by causing direct mortality during fire and indirect deaths by changes in post-fire habitat structure (Whelan, 1995; Broza and Izhaki, 1997; Buddle *et al*., 2006). However, a mosaic of different post-fire succession

stages promotes habitat heterogeneity, and this in turn facilitates biodiversity conservation (Bradstock *et al.*, 2005; Driscoll *et al.*, 2010). Given that species greatly diverge in habitat requirements, a heterogeneous landscape driven by fire-mosaic dynamics may support high biodiversity with a number of species adapted to different stages of postfire succession (Moretti *et al.*, 2004; Driscoll and Henderson, 2008; Santos and Poquet, 2010). Understanding mechanistic causes of this heterogeneous response is a conservation concern for the management of wildlife reserves heavily affected by fire (Driscoll *et al.*, 2010).

Terrestrial gastropods are an appropriate model group for evaluating their response to fire as they are highly sensitive to changes in vegetation structure due to their dependence on moisture (Cook, 2001; Heller, 2001). This dependence make snails extremely vulnerable to wildfires and provokes major diver-

sity losses after fire (Nekola, 2002; Kiss *et al.*, 2004; Severs, 2005; Kiss and Magnin, 2003, 2006; Santos *et al.*, 2009; Bros *et al.*, 2011). Although most snail species from temperate regions depend on moisture (Kerney and Cameron, 1999), some are adapted to dry habitats. For example, during the first post-fire years, when habitat structure is very simple, dominant snails in burnt localities from southern France are xerophilous species (Kiss *et al.*, 2004). In boreal American dry forests, prescribed fires have resulted in fine-scale mosaics acting as refuges for the endemic mountainsnail genus *Oreohelix* (Gaines *et al.*, 2011); this management restores mountainsnail habitats and avoids large and severe fires. Thus, through post-fire succession, contrasting responses are expected from land-snail species in parallel to changes in habitat structure.

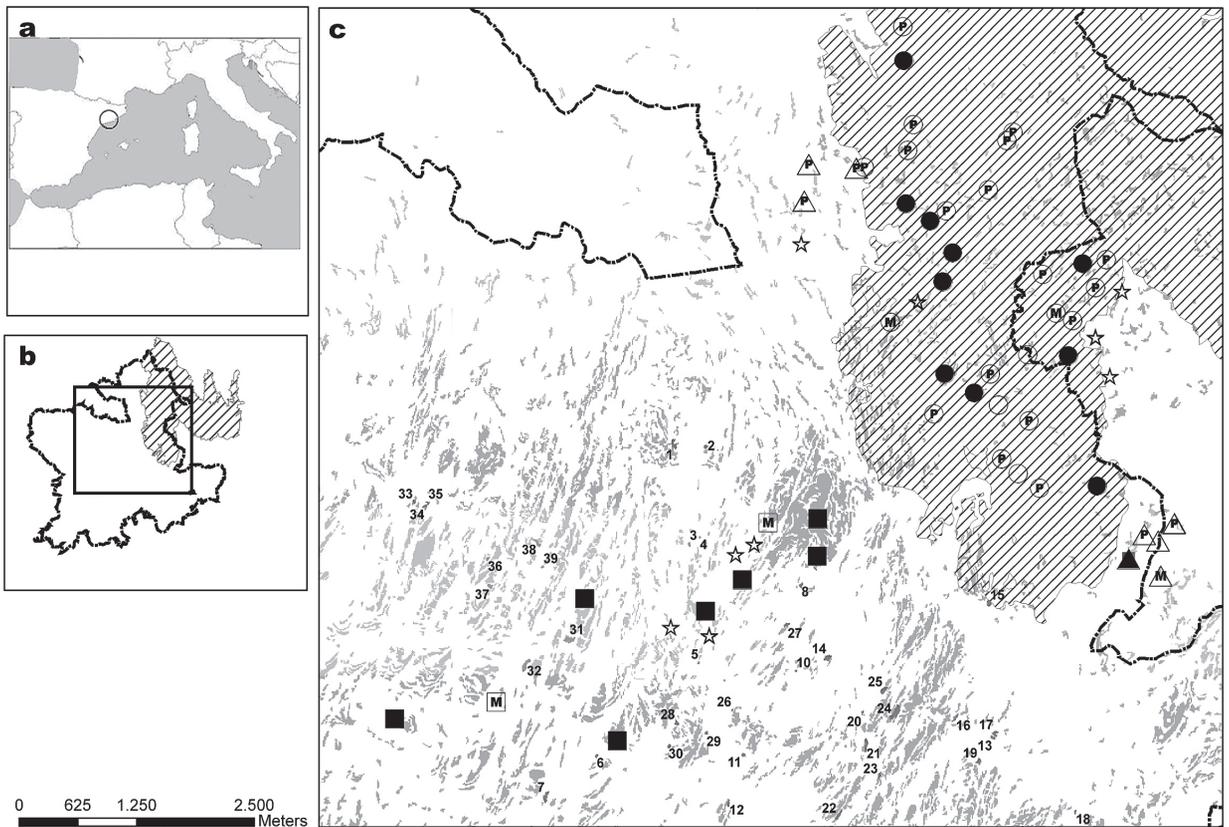We have investigated this issue in a Mediterranean

Fig. 1. Geographic location of the study area in southwestern Europe (a), area burnt in 2003 (grey area) with respect the Natural Park perimeter (dotted line) (b) and distribution of sites sampled (c). In (c), the grey areas show the distribution of stony bare slopes in the park, whereas numbers represent slopes measured from aerial photographs in 1956 and 2003. Symbols of the sites are: Holm oak forest (circles), pine forest (stars), stony bare slope (triangles) and burnt sites (rhomboids). Open symbols represent sites without snails, black symbols those with both species, and M and P those with the presence of only *X. montserratensis* or *X. penchinati*, respectively.

reserve severely affected by summer fires. The objective of our study was to examine the response of two xerophilous species of the genus *Xerocrassa* to fire and natural reforestation in Sant Llorenç del Munt i l'Obac Natural Park. We have specifically sought to identify the factors of the habitat structure that determine presence/absence of these snails in forest, open, and burnt sites. Such information may help explain the mechanistic responses of these species to fire and natural reforestation and may aid managers in making decisions to enhance biodiversity conservation in fire-prone areas (Driscoll *et al.*, 2010). The two endemic *Xerocrassa* species in the park are valuable in terms of conservation, and these results will be relevant to evaluate threats related to natural perturbations, and to propose management guidelines for the correct conservation of their populations.

Material and methods

Study site

The study site was located in St Llorenç del Munt i l'Obac Natural Park, Barcelona province, north-eastern Spain (Fig. 1A). This reserve, located in the Catalan Pre-coastal Mountain Range, has a total area of 13,694 hectares. The landscape of the park is rugged, with prominent conglomerate crags and monoliths. The highest peak is La Mola (1,104 m). The lithology of the park is very uniform, namely a polymictic conglomerate ground composed by a deposition of pebbles from a varied origin later being cemented by an argillaceous matrix. Calcareous conglomerates are much less abundant and differentiated by the whitish colour due to dominance of calcareous matter (Badia *et al.*, 2009). The erosive action on these types of rock gave the park its unique relief, characterised by narrow valleys, and stony bare slopes and monoliths surrounded by a Holm oak forest. The climate of the study area is subhumid Mediterranean with annual rainfall of around 600 mm (Panareda and Pintó, 1997). Rainfall is higher in spring and autumn than in summer. Thus, the area is prone to fast-spreading fires during hot, dry summers.

The original forest tree in the park is Holm oak *Quercus ilex* L., 1753, in some parts mixed with *Q. Coccifera* L., 1753 and *Q.* x *cerrioides* Willk. & Costa, 1859. Peripheral lowland areas were covered by vineyards during early 20th century, and after the *Phylloxera* plague the grapevines were replaced by pines *Pinus halepensis* Mill., 1768 and plantations of *Pinus*

nigra Arnold, 1785. The pine forest has Holm oak underbrush. In August 2003, 10% of the park burned during a summer fire that affected 4,443 ha with 1,778 ha of this lying inside the park (Fig. 1B). Impelled by wind, the blaze spread quickly, burning the entire area in just one day (10th August 2003). Almost all the burnt area was dominated by a pine forest with Holm oak underbrush. After the fire, charred areas were occupied by dense scrub dominated by Mediterranean shrub species such as *Cistus albidus* L., 1753, *Rosmarinus officinalis* L., 1753, *Dorycnium pentaphyllum* Scop., 1771, *Rubus ulmifolius* Schott, 1818, *Genista scorpius* (L., 1805), *Pistacia lentiscus* L., 1753, and *Coriaria myrtifolia* L., 1753. Resprouter trees such as *Arbutus unedo* L., 1753 and other plants such as *Echium vulgare* L., 1753, *Convolvulus arvensis* L., 1753, *Aphillantes monspeliensis* L., 1753, *Anagallis arvensis* L., 1753, *Helianthemum oelandicum* (L., 1802), *Leontodon taraxacoides* (Vill.) Mérat, 1831, *Ononis natrix* L., 1753, *Psoralea bituminosa* L., 1753, *Linum* sp., and *Euphorbia* sp. were found in the underbrush but increased their abundance after fire due to their reprouting or seedling capacity, a common trait in many Mediterraean plant species. Grasses such as *Brachypodium phoenicoides* Roemer & Schultes, 1817 and *Brachipodium retusum* (Pers.) Beaur., 1812 also were commonly found in burnt areas.

One the most characteristic habitats in the Park are stony bare slopes, called 'codines' in Catalan. This xerophilous habitat is found usually on hills and mountain tops over 700 m altitude, and it has thin soil layer. Usually this habitat shows a patchy and isolated distribution, with rupicolous vegetation surrounded by Holm oak forest. This habitat occupies 590 ha of the park (4.3% of the Park surface), although it holds a particular fauna and flora, which significantly contributes to the biodiversity of the entire Natural Park (Badia *et al.* 2009). The plant community is composed by species such as *Arenaria conimbricensis* Brot. 1800, *Erodium foetidum* ssp. *glandulosum* (Cav.) Willd., 1800, *Sedum album* L., 1753*, Narcissus assoanus* Dufour, 1830*, Dipcadi serotinum* (L.) Medicus, 1790, and *Thymus vulgaris* L., 1753 (Panareda & Pintó, 1997; Badia *et al.*, 2009).

Study species

The gastropod community in Sant Llorenç del Munt i l'Obac Natural Park includes more than 90 terrestrial and freshwater species, forest and rupicolous specialist species being dominant (Bros, 2000). The gastropod
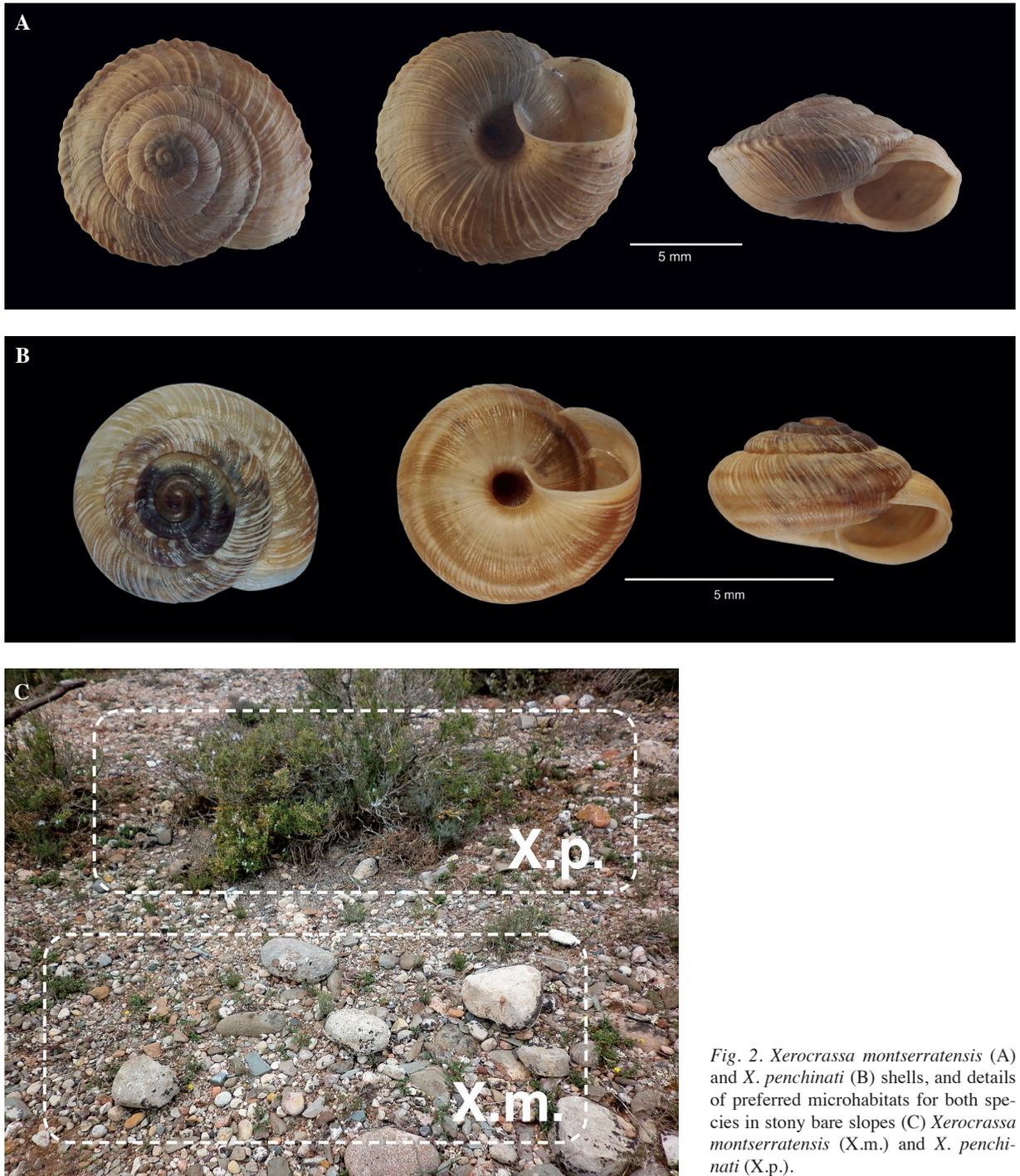
Fig. 2. Xerocrassa montserratensis (A) and *X. penchinati* (B) shells, and details of preferred microhabitats for both species in stony bare slopes (C) *Xerocrassa montserratensis* (X.m.) and *X. penchinati* (X.p.).

community includes two species of the genus *Xerocrassa* Monterosato, 1892 (Gastropoda, Hygromiidae). In the Iberian Peninsula, this genus is represented by 20 endemic species and often with very restricted distributions (Bank, 2011). The study site is occupied by two species of this genus: *X. montserratensis* and *X. penchinati*.

Xerocrassa montserratensis (Hidalgo, 1870) is a small snail (shell diameter: 7-12 mm) with a polymorphic and heavily striated shell, 5-6 spire whorls

(Fig. 2A), and occupies xerophilous habitats (Bros, 2000). Our preliminary studies reported that this snail prefers habitats with abundant medium-sized loose rocks produced by the erosion of the conglomerate substrates (Bros, 2006). This species has a restricted distribution, being found exclusively in three nearby mountainous natural parks: Montserrat, Sant Llorenç del Munt i l'Obac, and Serralada de Marina (Martinez-Ortí and Bros, 2011). Based on its restricted distribution, habitat fragmentation, and low ability to recolonize restored habitats, it is listed as Endangered in the IUCN Red List of threatened Species (Martínez-Ortí, 2011).

Xerocrassa penchinati (Bourguignat, 1868) shows morphologic and ecologic traits similar to those of *X. montserratensis*. This is also a small snail, with a delicately striated shell of 5-6.5 mm in diameter and 4-5 spire whorls (Fig. 2B; Kerney and Cameron, 1999; Clanzing and Bertrand, 2000; Bragado et al, 2010). This snail prefers habitats that include calcareous soil with scarce vegetation, Mediterranean shrub, degraded pine forests, and open areas with abundant grass and stones. In these habitats, the species is found in several ground microhabitats such as under stones larger than 20 mm in diameter (Clanzing and Bertrand, 2000) and near the scrub roots during the summer dry periods (V. Bros, pers. obs.). This snail is endemic of the northwestern Iberian Peninsula, with isolated populations in some Mediterranean coastal sites at Southern France (Clanzing and Bertrand, 2000).

Site selection and gastropod sampling

In May-June 2007, four years after the summer fire, we started a stratified sampling at 62 sites (Fig. 1C) including Holm oak forest ($n = 11$), pine forest ($n = 9$), stony bare slopes ($n = 9$), and burnt areas ($n = 33$). Holm oak and pine sites were selected as representative of major woodland habitats in the park, whereas stony bare slopes had been previously reported as adequate habitats for *Xerocrassa* species in the park (Bros, 2000, 2006). All the burnt sites were pine forests before the 2003 fire.

All the sites were selected in polymictic conglomerate ground, flat areas, and similar slope orientation (from southwestern to southeastern). In a subsample of 20 out of 62 sites (stony bare slopes were not examined), we did not find differences in soil pH, electrical conductivity (dS m^{-1}), %C, and %N (Kruskal-Wallis test H = 2.29, $P = 0.51$; H = 3.86, $P = 0.28$; H = 4.49, $P = 0.21$; H = 0.98, $P = 0.81$, respectively; Tere Sauras, unpublished data). Charcoal remains after the fire are expected to produce increased carbon content in soil (Kappes *et al.*, 2012), although in our study area, %C did not vary between unburnt and burnt sites four years after the fire (Tere Sauras, unpublished data), probably because post-fire logging removed a significant part of charcoal.

Site selection was limited by the distribution of each habitat type in the Park, although sites were selected in order to avoid spatial autocorrelation on snail occurrence and abundance. For example, most stony bare slopes are in the center of the park and hence some Holm oak sites were selected close to them, whereas the 2003 fire occurred in the eastern part of the Park and consequently some pine and Holm oak sites were selected in the fire edge (Fig. 1C).

At each site, *Xerocrassa* snails were actively searched for by hand for 20 min within a 15 x 15 m square, turning over stones and coarse woody debris. According to Ward-Booth and Dussart (2001), this sampling method is appropriate for snail species with shells larger than 3 mm and *Xerocrassa* species in the natural park are over 3 mm of shell size.

Vegetation structure has been shown to influence snail abundance and diversity (Coppolino, 2010). Thus, habitat structure of sampling sites was characterized by recording several vegetation and ground-cover variables along a longitudinal 50-m transect that crossed the 15 x 15 m squares used for snail searches. We recorded the extent of four vegetation types (Holm oak [HOLM] and pine [PINE] trees, extent of shrubs [SHRUB] and grass [GRASS]) and three groundcover types (leaf-litter from tree and shrub species [LITTER], bare ground [BARE] and refuges [REFUGE]) at points 50 cm apart along that transect. Thus, each vegetation and groundcover type is measured as the number of contacts along transects and consequently represents their relative abundances on transects. Any kind of stone larger than 10 cm in diameter, or any dead trunk was considered a refuge, since these are the preferred microhabitats for *Xerocrassa* species (Bros, 2006). Habitat structure was characterized with these vegetation and groundcover variables since their influence on the abundance and diversity of snail communities in the Mediterranean basin has been reported by several authors (*e.g.* Magnin *et al.*, 1995; Ondina and Mato, 2001; Labaune and Magnin, 2002).

Changes in open stony bare slopes between 1956 and 2003

Given that stony bare slopes are very suitable for *Xerocrassa* species (Bros, 2006), the temporal dynamics

Fig. 3. A famous site in the natural park called 'Morral del Drac' circa 1910 and in 2008. In the more recent photograph, it is possible to discern the incremental growth of Holm oak forest.

(degree of reduction or amplification) of these narrow habitats were estimated for the last 50 years in the park by comparing aerial photographs taken in 1956 and 2003. The 1956 photo was the first aerial photo taken in this region. Both photographs were geo-referenced, and 39 open-rocky points were randomly selected (Fig. 1C) and their surface areas were measured with ArcGIS tools. Stony bare slopes were selected randomly across the park although selection was constrained by the quality of the photograph made in 1956; those points with high slope and especially those without clear limits in the photograph made in 1956 were excluded to avoid mistakes in surface estimate. Differences in the surface areas of these sites between 1956 and 2003 were compared by a Wilcoxon Matched Pairs Test.

Statistical analysis

The relationship between the vegetation variables and the four habitats defined were analysed using CANOCO for Windows (version 4.55; ter Braak and Šmilauer, 2002). The linear or unimodal relation between variables and habitats was tested by a Detrended Correspondence Analysis (DCA). We found that the largest DCA gradient was 2.957, indicating that the distribution was linear, since a Canonical Correspondence Analysis (CCA), which assumes unimodal distribution of the data, is not adequate when the length of gradient (estimated with a DCA) is smaller than 4 (ter Braak and Šmilauer, 2002; Lepš and Šmilauer, 2003). Therefore, we analysed the relation between vegetation and groundcover variables and habitats by a Redundancy

Analysis (RDA), statistically testing the relationship between the axes and variables by a permutation Monte Carlo test (ter Braak and Šmilauer, 2002).

How vegetation and groundcover variables affected the presence and abundance of *Xerocrassa* species was examined in two steps. In the first step, we tested whether the vegetation and groundcover variables differed between samples with presence and absence of the *Xerocrassa* species by using Student's t-test or Mann–Whitney U-test (M–W U-test) when variables did not fit normality and homoscedasticity of variances. In the second step, we used Generalized Linear Models (GLZ) to analyse the effect of the vegetation and ground-cover variables on *X. montserratensis* and *X. penchinati* abundances using Poisson error distributions and a log link function, due to the number of sites without snails. From the GLZ, we regarded the standardized regression coefficients of variables to see the sign of their effects on the abundance of *Xerocrassa* species. Before the analyses, the variable LITTER was removed as it was heavily correlated with HOLM. The other variables were maintained as $r < 0.60$ in all the pairwise correlations, and therefore it is improbable that multicollinearity affected the statistical results.

Assumptions of parametric tests (normality, homoscedasticity of the variances) were tested for each variable before the analysis. Observed versus expected frequencies in the presence-absence of *Xerocrassa* sp. in the four habitats sampled were compared by χ^2-tests. Mean values are followed by ± standard error, and we set alpha equal to 0.05 for significance in all tests. Analyses were performed with STATISTICA (version 6.0).

We tested for non-random patterns of *Xerocrassa* species co-occurrence with EcoSim 7.0 (Gotelli and Entsminger, 2001). The input for the co-occurrence analysis is a presence-absence matrix. As there are a number of sites without both *Xerocrassa* species, we decided to use a degenerate matrix procedure which accepts empty sites in the analysis. We calculated the Variance ratio (V-ratio) which in fact is an index of variability in species richness per site; when niche limitation constrains the number of coexisting species, the variance in species richness among sites will be small relative to the null model (*i.e.* V-ratio = 1.0 as species are distributed independently and sites are equiprobable). V-ratio < 1.0 means that there is a strong negative covariance between species pairs (*i.e.* species tend to exclude), whereas V-ratio > 1.0 means that there is a positive covariance between species pairs (*i.e.* species tend to co-occur) (Gotelli and Entsminger,

2001). From our presence-absence matrix, Ecosim performed 1000 simulations and empty sites were included in the process. We compared our observed V-ratio score with the distribution of the V-ratio scores obtained from simulations.

Results

After measuring the surface area of 39 stony bare slopes in the aerial photographs from 1956 and 2003, we detected 30 samples that had larger surface areas in 1956 and nine samples for which this was the case in 2003. Stony bare slopes had larger surface areas in 1956 (Wilcoxon $Z = 3.32$, $n = 39$, $p = 0.0009$) as the canopy of the Holm oak forest surrounding these areas increased over time. The reduction of stony bare slopes was on average 15.18% of surface area. Differences in the extent of Holm oak forest were significant when old and recent photographs of some of the most popular monoliths in the natural park were compared visually (Fig. 3). According to the presence of *Xerocrassa* in the four habitats sampled (see below), temporal variation in stony bare slopes in detriment to Holm oak forest is expected to reduce the availability of preferred habitats for *Xerocrassa* snails.

The redundancy analysis (RDA) showed significant differences in the vegetation and soil structure among habitats (trace = 0.795, *F*-ratio = 75.00, $p = 0.0001$). The greatest differences were between Holm oak forest and burnt sites, with a clear and significant discrimination on axis 1 (eigenvalue = 0.591, *F*-ratio = 83.66, $p = 0.0001$), whereas axis 2 also proved significant (eigenvalue = 0.139, *F*-ratio = 29.94, $p = 0.0001$) and discriminated between pine forest sites and open bare slope sites (on-line supplementary material S1). Accordingly, several vegetation and groundcover variables were associated with habitats. For example, on axis 1, burnt sites were characterized by greater grass coverage, and Holm oak sites by a greater amount of litter. On axis 2, open rocky areas had more refuges and bare ground (on-line supplementary material S1). *Xerocrassa montserratensis* was recorded at 24 (38.7%) sites, whereas *X. penchinati* was found at 41 (66.1%). Their presence differed according to the habitats (*X. montserratensis*: $\chi^2 = 16.33$, *df* = 3, $p = 0.001$; *X. penchinati*: $\chi^2 = 8.80$, *df* = 3, $p = 0.03$) as both species were uncommon or absent at Holm oak forest and *X. montserratensis* also in pine forest, but common in open areas (stony bare slope and burnt sites) (Fig. 4). Accordingly, Student's t- /Mann–Whitney U-tests showed

	Mean Presence	Mean Absence	t-value df = 60	Z
X. montserratensis				
HOLM	2.33±0.76	23.03±5.59		2.69 **
PINE	3.00±1.68	11.95±3.36		1.9 *
SHRUB	25.96±3.81	32.37±2.03	1.62	
LITTER	3.29±1.74	23.37±4.96		2.62 **
BARE	37.33±4.49	19.74±2.33		3.13 **
GRASS	23.96±2.35	17.05±2.17	2.09 *	
REFUGE	8.00±0.97	8.47±1.14	0.29	
X. penchinati				
HOLM	2.37±0.52	39.71±8.56		3.86 **
PINE	6.73±2.70	11.90±3.85	1.11	
SHRUB	31.29±2.38	27.14±3.41	1.01	
LITTER	4.00±1.45	38.24±7.30		4.08 **
BARE	32.27±2.72	15.38±4.16	3.5 **	
GRASS	21.61±1.82	16.05±3.29	1.61	
REFUGE	9.10±0.99	6.71±1.26	1.44	

Table 1. Student's t-test or Mann-Whitney U-test comparisons of abundance in vegetation and groundcover types between sites with (presence) and without (absence) *Xerocrassa montserratensis* and *X. penchinati*. Values are means ± SE.

Variables	Estimate	S. E.	Wald Stat.	p
X. montserratensis				
Intercept	-1.446	2.053	0.496	n.s.
HOLMOAK	-0.089	0.041	4.814	*
PINE	-0.046	0.022	4.182	*
SHRUB	0.010	0.022	0.187	n.s.
BARE	0.041	0.022	3.504	n.s. (0.06)
GRASS	0.043	0.021	4.240	*
REFUGE	-0.017	0.026	0.449	n.s.
X. penchinati				
Intercept	-1.488	1.200	1.539	n.s.
HOLMOAK	-0.065	0.018	12.639	**
PINE	-0.005	0.007	0.404	n.s.
SHRUB	0.046	0.013	12.443	**
BARE	0.031	0.013	6.032	*
GRASS	0.020	0.012	2.712	n.s.
REFUGE	0.059	0.013	19.560	**

Table 2. Results of the GLZ models for *X. montserratensis* and *X. penchinati* abundances and effects of the vegetation and groundcover variables measured in the sites sampled. See list of all variables in the Methods section.

that both species were present at sites with a low abundance of Holm oaks (and leaf-litter) and a high abundance of bare ground (Table 1).

According to the GLZ results, the contribution of vegetation and groundcover variables on the abundance of the two *Xerocrassa* species demonstrated that Holm oak affected the abundance of both species negatively, and pine affected *X. montserratensis* abundance negatively. Moreover, grass cover increases the abundance of *X. montserratensis*, whereas extent of shrub, bare ground and number of refuges increases the abundance *X. penchinati* (Table 2).

The two species were absent from 16 out of 62 sites (26%), only one species was found in 27 sites (44%) and both species in 19 sites (31%). The co-occurrence analysis showed that the observed V-ratio was 1.2188, whereas the V-ratio mean after 1000 simulations was 1.0039 (variance 0.0164), which means that the two *Xerocrassa* species do not tend to exclude one to other.

Discussion

This study identifies the habitat requirements of two endemic and xerophilous gastropods, *Xerocrassa montserratensis* and *X. penchinatti*, in a protected

Mediterranean area. Our results indicate that the two *Xerocrassa* species avoided Holm oak forest, common in the park and in many Mediterranean ecosystems, which often forms a very dense canopy. In addition, *X. montserratensis* appears to be more demanding in the habitat structure since the expansion of pines and scrubland has a negative impact on its presence.

Our co-ocurrence analysis indicates that the species do not mutually exclude. In fact, both species are absent in Holm oak forest although they cohabit in stony bare slopes where both species select particular microhabitats in accordance to their habitat requirements, namely bare ground and pebbles for *X. montserratensis*, and shrub for *X. penchinati* (Fig. 2C). GLZ results confirm these microhabitat preferences as *X. montserratensis* appears to be primarily dependent on open areas, whereas *X. penchinati* is more demanding in particular habitat structures such as the presence of shrubs and refuges. Despite the lack of information on basic ecological traits of both species (*e.g.* diet, activity patterns or physiological tolerance to drought), morphological variation in shell morphology (striation, size and number of spire whorls) might give insights on adaptive abilities to different microhabitats (Goodfriend, 1986; Schilthuizen, 2011). In fact, *X. montserratensis* and *X. penchinati* slightly differ in shell striation (deep and highly striated, and moderately striated), carene (present and absent) and form (more and less plane, respectively). These differences would be in accordance to more strict xerophilous microenvironments occupied by *X. montserratensis* (Giokas, 2008; Moreno-Rueda, 2011).

Many land-snail communities are very sensitive to plant community structure and soil properties (Dedov *et al.*, 2006; Kappes *et al.*, 2006), avoid habitats without detritus on the ground (Cook, 2001; Heller, 2001), and are highly diverse and rich in wet microhabitats with abundant vegetation and humus (Watters *et al.*, 2005). However, the two *Xerocrassa* species analysed here are habitat specialists, preferring open areas with scarce vegetation. Specialization in life-history traits can make species vulnerable to extinction (McKinney, 1997; Davies *et al.*, 2004; Santos *et al.*, 2006), this pattern being even more critical for *X. montserratensis* due to its small distribution range (ICHN, 2008; Martinez-Ortí, 2011). For this reason, changes in the abiotic and biotic characteristics of the preferred habitats for the *Xerocrassa* species (*e.g.* increment of canopy, reduction of refuges) may affect the viability of their populations.

This study demonstrates that *Xerocrassa* snails pre-

fer stony bare slopes. These rocky spots, originated by the erosive action of the water on the conglomerate matrix, are among the most distinctive geomorphological features of the Natural Park, and important biodiversity hotspots due to their particular fauna and flora with several species of conservation interest (Fig. 5; Badia *et al.*, 2009). Stony bare slopes are found basically on hilltops, preferably at altitudes over 700 m, and occupy 590 hectares, representing 4.3% of the surface of the natural park. Such rocky spots are often small and isolated, and frequented by park users (Bros, 2011), these factors increasing the vulnerability of snail populations. The comparison of stony bare slopes by aerial photographs and subsequent analyses indicates that these habitats have shrunk in the last 60 years, with a natural expansion of Holm oak reforestation. Plant succession in stony bare slopes starts by increasing the thickness of the leaf litter layer with the accumulation of litter from the nearby forest; over time, this process continues with the establishment of shrub species such as *Cistus albidus* and *Rosmarinus officinalis,* which in turn retain more soil and eventually allow the establishment of some arboreal species. This phenomenon is less noticeable in more sloped stony bare slopes where soil retention is not significant.

In the Mediterranean basin, the forest surface area has increased in the last century (Barbero *et al.*, 1990). This is due in part to the abandonment of traditional agricultural activities, giving rise to subsequent natural revegetation (Lasanta and Vicente-Serrano, 2007; Moreira and Russo, 2007), as well as the extensive forestry usually made with allochthonous species such as eucalyptus and conifers. Although greater forest cover improves the quality of the habitat for most terrestrial Palaearctic gastropods considered to be intolerant to drought (Kerney and Cameron, 1999; Ström *et al.*, 2009), this pattern does not fit certain species that prefer habitats with low vegetation cover such as many *Xerocrassa* species (*e.g.* Hermony *et al.*, 1992; Graack, 2005).

Surprisingly, we also found *Xerocrassa montserratensis* and *X. penchinati* at burnt sites. These areas harbouring the two *Xerocrassa* species are precisely those with the lowest gastropod diversity and species richness in the park due to the fire impact on the land-snail community (Bros *et al.*, 2011). Indeed, in our study area, wildfires drastically reduced snail-species richness and facilitated a shift of dominant species in favour of open-space species, this pattern leading to a juxtaposition of two different assemblages in burnt
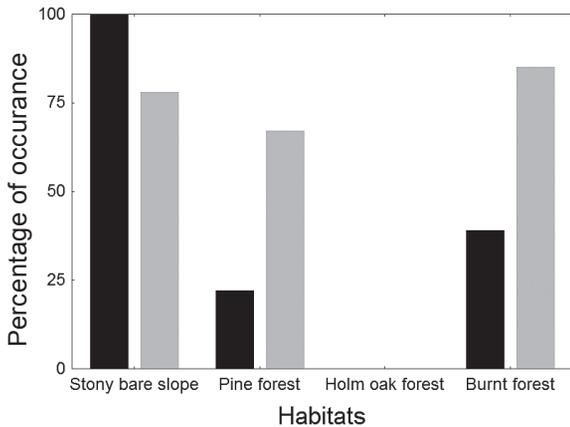
Fig. 4. Percentage of occurrence of *X. montserratensis* (black columns) and *X. penchinati* (grey columns) in Holm oak forest, pine forest, burnt, and stony bare slope sites.

and non-burnt areas (Santos *et al.*, 2009). The severe impact of fire on land snails has been widely reported and is related mainly to changes in several environmental features of the habitat such as changes in vegetation structure, soil moisture, and pH, as well as the loss of the leaf-litter layer (Nekola, 2002; Severs, 2005; Santos *et al.*, 2009; Hylander, 2011; Bros *et al.*, 2011). In Mediterranean areas where the fire regime has persisted over decades or centuries, land-snail communities appear highly altered and composed mainly of Mediterranean and xerophilous species (Kiss *et al.*, 2004).

The presence of the two *Xerocrassa* species at burnt sites is noteworthy, given that before the fire in 2003, most of the burnt areas were dense pine and Holm oak forests. Therefore, the way in which *Xerocrassa* species colonize the burnt areas is still an open question, especially considering the low recolonization rates of gastropods from the unburnt edge of the fire (Santos *et al.*, 2009). A plausible explanation is the existence of suitable microhabitats inside the forest for xerophilous species such as *Xerocrassa* snails. After the fire, the availability of cryptic refuges (Kiss and Magnin, 2003, 2006) facilitates the survival of snail populations. The environmental conditions at burnt sites contribute to the maintenance of xerophilous and open-area snails to the detriment of forest snails. This pattern has been previously highlighted in Mediterranean vertebrate groups (Herrando *et al.*, 2003; Moreira and Russo, 2007) and bears extraordinary importance in terms of conservation, since many open-area species are threatened (*e.g.* Law and Dickman, 1998; Pino *et al.*, 2000) and are endemic to the Mediterranean basin (Perevolotsky, 2006).

In summary, fire and natural reforestation may act as contrasting stressors for the presence of *Xerocassa* species due to differences found in vegetation and groundcover among habitats. Natural reforestation is closing stony bare slopes, thus reducing the most favourable habitats for xerophilous snails in the park, whereas wildfire seems to favour their population recovery. These results contribute significantly to our understanding of how natural processes mould Mediterranean communities, and consequently, our results

Fig. 5. Stony bare slopes in the Montcau, one of the most famous peaks in the Sant Llorenç del Munt i l'Obac Natural Park. Steep- and shallow-sloped stony bare slopes are surrounded by Holm oak forest.

may have important implications for management and conservation. The natural dynamics in a natural park is clearly natural reforestation, although *Xerocrassa* is negatively responding to increased cover. For this reason, it is essential to consider several management approaches to control this tendency such as grazing or tree/brush cutting (although grazing has been recognized to have negative effects for land snails in nutrient-poor pastures, Boschi and Baur, 2007). In fact, several management measures have been started in the last 7 years in the natural park to mimic past land uses (*e.g.* grazing and logging in abandoned fields, Lobo *et al.*, 2007). The final objective of this management is to enhance biodiversity by the maintenance of landscape mosaics (*i.e.* spatial heterogeneity) to avoid a uniform forest canopy (Lobo *et al.*, 2007; Pino *et al.*, 2000; Bartolomé *et al.*, 2000, 2005). Management of low-slope stony bare slopes, the preferred habitat for *Xerocrassa*, can be especially important, and future studies should examine spatiotemporal changes in *Xerocrassa* presence and abundance in these habitats. Pintó and Panareda (1995) reported that stony bare slopes are the last step of forest degradation due to the human exploitation of Holm oak trees for wood, or the degradation of abandoned cropland and subsequent soil erosion. Over the long term, there is a natural revegetation process of low-slope stony bare slopes. Due to their importance, monitoring and conservation of stony bare slopes should be a priority management practice in the park. Accordingly, our study may give valuable insights into the management practices which may be applied to recover favourable habitats of threatened species such as *Xerocrassa* snails.

Reforestation practices throughout the Mediterranean have long relied on procedures borrowed from pine forestry (Pausas *et al.*, 2004; Rey *et al.*, 2009). Our results show that xerophilous species such as *X. montserratensis* may be harmed by this practice. In fact, extensive pine forests as a result of forestry processes seem to be low-quality habitats for several arthropod communities (Vance *et al.*, 2007; Mateos *et al.*, 2011). Extensive pine forests reduce habitats for open-area species in the Mediterranean basin (Preiss *et al.*, 1997; Stefanescu *et al.*, 2004). However, pine forests are prone to burning, and wildfires, though catastrophic for several components of the biota, provide new open areas and consequently facilitate the recolonization of open-space species (Herrando *et al.*, 2003; Santos *et al.*, 2009, Santos and Poquet, 2010). Future climate conditions are expected to increase fire frequency and extent (McKenzie *et al.*, 2004), and the response of xerophilous and a priori drought-resistant snail species to repeated-fire regimes is unknown. In the present scenario, a balance between different environmental stressors may promote landscape heterogeneity, thereby increasing biodiversity at a regional scale (Plotnick and Gardner, 2002; Possingham *et al.*, 2005). Wildlife reserves as Sant Llorenç del Munt i l'Obac Natural Park are suitable localities to apply management practices intended to produce landscape mosaics, hence facilitating the conservation of particular and sensible habitats for endangered species such as *Xerocrassa* land snails.

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On-line supplementary material

S1. Redundancy analysis plot of the association between vegetal plus soil variables and the four habitats sampled.