# LAND SNAIL COMMUNITIES IN MEDITERRANEAN UPLAND GRASSLANDS: THE RELATIVE IMPORTANCE OF FOUR SETS OF ENVIRONMENTAL AND SPATIAL VARIABLES

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## ABSTRACT

It is difficult to define precisely determinant environmental factors that explain land snail distribution and abundance, and most variables are often interrelated. In addition, studies have generally examined only a limited number of environmental variables, yielding a partial and local habitat description. Recognised determinant factors are: climate, vegetation and soil. Competitive interactions, historical factors and spatial structure are rarely included, although they could generate biogeographic patterns on a local or regional scale. The goal of the present work is to evaluate land snail habitat complexity by examining a wide range of environmental variables. Land snails from open environments were studied in a Provence range, the Grand Luberon, characterised by low variations in pH and calcium content. Grasslands on the ridges are maintained by sheep grazing. A stratified sampling was chosen according to altitude and vegetation structure. Sites were sampled throughout the range. Different vegetation structure types were analysed, from low grasslands to shrublands. Thirty-eight environmental variables were noted for each site. They described: (1) topography and climate, (2) habitat structure, (3) flora, and (4) spatial structure of snail communities. The main analytical method used was the partial Canonical Correspondence Analysis which yielded a partition of species variation into several independent components. The four environmental variable groups were used separately. We obtained a partition of ecological variation which emphasised the predominance of habitat structure over floristic composition and the important role played by environmentally independent spatial variables. Nevertheless, it remains difficult to discriminate between the influence of climatic factors s.s., historic events and/or biotic factors within the altitudinal gradient.

## INTRODUCTION

Many studies on the distribution and abundance of land snails in relation to environment have been published since Boycott's classic review (Boycott, 1934). However, it is difficult to precisely define determinant environmental factors (Wallace, 1912), and the variables are often interrelated (Goodfriend, 1992). In addition, most studies have only examined a limited number of environmental variables (e.g. the soil), yielding a partial and local habitat description. Some authors (Bishop, 1977; Coney, Tarpley, Warden & Nagel, 1982) have analysed a wider number of variables and concluded that snail distribution and abundance are related to regional climate factors and local physical and chemical characteristics of soil. Multivariate analysis has revealed the case by case relationships between snail community organisation and environmental gradients (Dillon, 1980; André, 1982). The development of Canonical Correspondence Analysis (ter Braak, 1986) makes it possible to break down

these complex gradients into different explanatory variables (Outeiro, Aguera, & Parejo, 1994; Barker & Mayhill, 1999). However, even these explanatory variables are generally not diversified enough to reflect the true complexity of the habitat. In general, factors identified as determinant are: climate (temperature, rainfall, humidity), vegetation (floristic structure and composition) and soil (pH, calcium content and texture). Competitive interactions, historical factors and spatial structure are rarely included, although they could generate biogeographic patterns on a local or regional scale (Cameron, Down & Pannett, 1980; Magnin, 1993; Magnin, Tatoni, Roche & Baudry, 1995).

The goal of the present work is to evaluate land snail habitat complexity by examining a wide range of environmental variables. In particular, we: (1) define the respective roles of flora and habitat structure; (2) quantify climatic and topographic parameters which could be limiting factors for land snail species and (3) demonstrate the value of non-environmental factors used to explain community spatial structure. Open-environment communities were studied in a Provence range characterised by low variations in pH and calcium contents. The main analytical method used was the partial Canonical Correspondence Analysis (Borcard, Legendre & Drapeau, 1992) which yielded a partition of species variation into several independent components (Økland & Eilertsen, 1994).

## MATERIAL AND METHODS

#### Study area

The Luberon is a limestone range approximately 40 kilometres long running from east to west and located in Provence (France), 50 kilometres from the Mediterranean sea. Our study focused on the eastern side, known as the 'Grand Luberon', which reaches an altitude of 1125 m.

Due to its length, altitude, climate and orientation, the Luberon is a climatic barrier on the southern edge of the Oro-Mediterranean climate zone. There is a larger amount of precipitation than in other Provence mountains and temperatures are cooler (Livet, 1965). Mean annual temperatures for the Grand Luberon range between 11°C and 12.5° at the foot and between 7°C and 9°C at the summit. There is only one dry month (according to Gaussen's definition) and 4–5 cold months when temperatures fall below 7°C (C.N.R.S., 1975). Rainfall was estimated at 802 mm per year at the summit (Silvestre, 1977). The harsh climate is accentuated on the ridges and northern slopes by a fierce north-westerly wind ('Mistral').

The Grand Luberon's ridges are covered by a thin band of low grasslands between 900 and 1125 m. The Luberon Regional Natural Park maintains these grasslands by encouraging grazing both to create a firebreak between the two slopes and to preserve a remarkably rich biological area. The slopes themselves are highly wooded (primarily *Quercus pubescens* and *Quercus ilex* formations) and open spaces are limited to variable-sized clearings.

Soils are superficial and gravely on the ridges and slope heights with a pH between 6.8 and 7.6. CaCO3 content varies between 0 and 2%.

#### Land snail sampling

A stratified sampling was chosen according to altitude and vegetation structure. Sites were sampled throughout the range. Only open environments were studied. Different vegetation structure types were analysed, from low grasslands to *Buxus sempervirens* shrublands, including high ungrazed grasslands with or without low woody vegetation. Sites were distributed equally between 8 altitude categories, from 700 m to the summit. When possible, each different vegetation structure type was equally represented for each altitude category. A total of 80 sites was studied from March 13 to May 6, 1997.

A  $5 \times 5$  m plot was examined by two researchers at each site for 15 min. All living or fresh dead snails were sampled, then determined and counted in laboratory. A method based

on the works of Evans (1972), Puisségur (1976) and André (1981, 1982) was used to collect less than 5 mm diameter shells: vegetation, litter and surface soil down to 5 cm were sampled over a  $25 \times 25$  cm plot. Five samples were taken within the  $5 \times 5$  m square already sampled for large species. Samples were dried in an oven, then immersed in water. Floating particles were collected in a 0.5 mm mesh sieve and shells were then separated from plant material under a magnifying glass for the smallest portion. The list of species with their occurrence and abundance is given in Appendix 2.

#### Floristic and environmental records

A standard procedure of description was used, based on Godron (1968). Four variable groups were used. Variable descriptions and coding are shown in Appendix 1.

The first group (CLIMATE) consisted of 12 climatic or topographic variables: altitude, local humidity, grassland patch size, flat site, halfway up location, slope top, summit, no defined exposure, north facing, south facing, east facing, west facing.

The second set of variables (STRUCTURE) consisted of 14 habitat structure variables. Six variables describing overall soil surface cover were used: bare ground, stones, boulders, rock, litter, vegetation. Five variables described different plant layer covers: 0–5 cm, 6–15 cm, 16–25 cm, 26–50 cm, 51–100 cm. Three variables were used to describe different plant types: cryptogams, herbaceous plants, low woody plants.

The third group (FLORA) included seven of the most common dominant plant species, i.e. having the highest cover (*Buxus sempervirens* L., *Carex humilis* Leyss., *Bromus erectus* Huds., *Festuca ovina* s.l., *Helianthemum oelandicum* (L.), *Thymus vulgaris* L., *Anthilis vulneraria* s.l.).

Both floristic cover and habitat structure variables were estimated using a visual surface ratio chart (Folk, 1951).

The fourth variable group (SPACE) consisted of five variables characteristic of site position in space and compared to other sites. The first two variables were the UTM coordinates (latitude and longitude) of the sites. The other three variables described distance between sites. A Hierarchical Cluster Analysis was performed to obtain these three variables using the Euclidian distance between their coordinates. Qualitative variables were then created corresponding to the groups defined by the hierarchical cluster at different truncation levels (Dist5, Dist10, Dist20), i.e. divisions into respectively 5, 10 and 20 categories.

#### Multivariate analysis

Statistical analyses were performed using CANOCO 4.0 (ter Braak & Smilauer, 1998).

The species-sites matrix was first studied by Correspondence Analysis (CA). Abundance data were transformed logarithmically to make their distribution correspond to a normal law (Legendre & Legendre, 1984). 35 snail species were studied, but rare species abundance was down-weighted by an algorithm available in CANOCO.

The effect of environmental variables on the species matrix was then studied using Canonical Correspondence Analysis (CCA) (ter Braak, 1986). The four environmental variable groups were used separately. This made it possible both to limit the number of variables for each analysis, as suggested by Borcard *et al.* (1992) and Prodon and Lebreton (1994), and analyse all available variables.

The best descriptive variables were chosen by step-by-step selection. The significant characteristic of each variable selected and ordination axes were verified by a permutation test available in CANOCO (Monte Carlo test). The significance level was set at p < 0.05.

Partial canonical correspondence analyses were used to define the amount of variation explained by the four variable groups analysed in pairs (Økland & Eilertsen, 1994). Borcard *et al.*'s (1992) method was used. When two variable groups are analysed using this method, one is treated as a set of covariables, while the other is considered to contain explanatory variables. This made it possible to calculate variation percentages due to either one or both variable groups studied.

### RESULTS

## Ordination of land snail communities along environmental gradients

Axes 1 and 2 of the CA (Fig. 1A & B) respectively explain 21.4% and 13.5% of between-species variation. The total of eigenvalues is 1.872.

Axis 1 represents an altitude gradient. It opposes low altitude and high altitude sites. Sites at the foot of the sampled gradient at less than 800 m are at the far positive end of axis 1. The negative end of axis 1 is characterised by sites at an altitude of more than 1050 m, i.e. near the summit. There is a significant correlation between site altitudes and their rank on axis 1 of the CA (r = 0.684, p = 0.01, n = 79).

Axis 2 is a habitat structure gradient. The sites with the strongest contributions on the negative side show the highest diversity in vegetation stratification and soil cover. These are *Buxus* shrublands where the different layers are relatively equally represented with an extremely heterogeneous soil cover. On the other hand, the positive end has the sites containing low grasslands where the lowest herbaceous layer has a cover of more than 90%.

Gastropod species distribution is as follows for the two gradients (Fig. 1A):

The highest contributions to axis 1 are Trochoidea geyeri (Soós) on the negative side and Candidula uni*fasciata* (Poiret) on the positive end which are mainly responsible for the swarm's horizontal shape of the plot. These two Hygromiinae are the most common in the Grand Luberon and have altitude related distributions: T. geveri occupies the highest sites and is replaced by C.unifasciata at sites lower than 900 or 1000 m. Typical mountain species of southern France can be found on the negative end, next to T. geveri, i.e. Pupilla triplicata (Studer), Clausilia rugosa parvula Férussac and Abida secale (Draparnaud). On the positive side, C.unifasciata is associated with southern species less frequent at high elevation, i.e. Candidula gigaxii (Pfeiffer), Jaminia quadridens (Müller) and Abida polyodon (Draparnaud).



Figure 1. Correspondence Analysis (CA) of 79 land snail records on the Grand Luberon grasslands. A. Gastropod species ordination on the first factor plane (species labels as in appendix 2). B. Site ordination on the same plane.

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The negative side of axis 2 contains species such as *Zebrina detrita* (Müller), which prefers mountain shrublands, *Pomatias elegans* (Müller), which lives on loose soils and eats dead leaves, *Vallonia costata* (Müller) and *Urticicola glabellus* (Draparnaud) which are also common species in preforest habitats. Species from very open environments can be found on the positive side, such as *T. cylindrica*, *Vitrea narbonensis* (Clessin) and *T. geyeri*.

Thus the 1–2 factorial plane reveals three land snail community types:

-mountain assemblages on low grazed grasslands (with *T. geyeri*, *P. triplicata*, *T. cylindrica*),

-open Mediterranean low altitude assemblages (with *C. unifasciata, Monacha cantiana* (Montagu), *J. quadridens*),

-preforest assemblages with a more complex habitat structure from the point of view of strata and soil cover (with *Xerosecta cespitum* (Draparnaud), *A. secale*, *Cochlostoma septemspirale* (Razoumowsky), *Acanthinula aculeata* (Müller), *Punctum pygmaeum* (Draparnaud)).

Thus, two of the most important factors to explain species distribution seems to be altitudinal gradient and habitat structure complexity gradient. Variation explained by different sets of variables

CCA made it possible to precisely define the role of different groups of environmental and spatial variables determining the preceding gradients.

Seven of the initial 12 variables in the CLIMATE group were kept after a step-by-step selection (Table 1). The sum of the canonical eigenvalues of this CCA is 0.487, i.e. 26% (0.487/1.870) of species variation is explained by this variable group. The first axis (22%) of total inertia) represents an altitude gradient (Fig. 2). In fact, the altitude variable is the one best correlated with this axis which separates alpine affinity species (T. geyeri, P. triplicata, T. cylindrica) collected in altitude sites from more Mediterranean species (C. gigaxii, Solatopupa similis (Bruguière), A. polyodon) associated with lower altitude sites. Axis 2 (11.5% of total inertia) represents a gradient of patch size. The positive side is associated with sites sampled at halfway up in small clearings and young shrublands where forest affinity species were found (e.g. P. elegans and Pagodulina pagodula (Des Moulins)). The negative side is associated with sites at ridge tops and upper slopes corresponding to the largest grasslands with very open environment species (V. narbonensis, T. cylindrica, T. geyeri).

Seven of the 14 initial variables were selected from the STRUCTURE group (Table 1). The CCA yields

Variable groups	Significant variables:	Code:	Р
'CLIMATE'	altitude	ALTITUDE	0.01
	grassland patch size	SIZE	0.01
	halfway up location	M.SLOPE.	0.01
	local humidity	HUMIDITY	0.01
	east facing	E.EXPO.	0.01
	south facing	S.EXPO.	0.03
	slope top	SLOPE.T	0.05
'STRUCTURE'	vegetation layer 4 (26–50 cm) cryptogams bare ground vegetation layer 1 (0–5 cm) woody plants boulders litter	LAYER.4 CRYPTOG EARTH LAYER.1 LIGNEOUS BOULDERS LITTER	0.01 0.05 0.01 0.02 0.02 0.05
'FLORA'	Carex humilis	CHU	0.01
	Buxus sempervirens	BSE	0.01
	Bromus erectus	BER	0.01
	Festuca ovina	FOV	0.01
	Heliantemum oelandicum	HOE	0.01
'SPACE'	distance between sites (5 groups)	DIST.5	0.01
	latitude	LATITUDE	0.01
	longitude	LONGITUDE	0.01
	distance between sites (20 groups)	DIST.20	0.01

**Table 1.** Significance of environmental variables in different groups. P = significance probability in a Monte Carlo permutation test based on 99 permutations.

the sum of the canonical eigenvalues: 0.428, i.e. 22.8%(0.428/1.870) of explained species variation. Axis 1 (13.6% of total inertia) is a gradient of environmental openness (Fig. 3). It compares forest-affinity species associated with high woody cover and higher plant layer with more open-environment species associated with a 0–5 cm layer cover. Axis 2 (11.2% of total inertia) represents a gradient of habitat structure according to altitude. The sites on the far end of the negative side are located at low altitudes and have high soil



**Figure 2.** Canonical Correspondence Analysis (CCA) using the climate and topographic variable group as explanatory variables (species labels as in Appendix 2 and variable labels as in Table 1).



**Figure 3.** Canonical Correspondence Analysis (CCA) using the the habitat structure variable group as explanatory variables (species labels as in Appendix 2 and variable labels as in Table 1).

cover due to vegetation (cover > 70%) including cryptogams (cover > 15%). They are associated both with Mediterranean species (*C. gigaxii, Zonites algirus* (Linnaeus), *J. quadridens*) and forest affinity species (*Merdigera obscura* (Müller), *M. cantiana, Vitrea contracta* (Westerlund)). On the positive side, the sites for low, stony, grazed grasslands can be found, associated with high altitude open environment species (*T. geyeri, P. triplicata, T. cylindrica*).

Five plant species in the FLORA group were kept after step-by-step selection (Table 1). The CCA of the species-sites matrix constrained by these variables yields the sum of canonical eigenvalues: 0.333, i.e. 17.8% (0.333/1.870) of explained species variation. It reveals the plant species which play an important role in habitat structure (Fig. 4). The first axis represents 12.9% total inertia. The negative side is associated with B. sempervirens, the highest woody species in our sites, which provides shelter and leaf litter for forest-affinity snails (e.g. P. elegans and P. pymaeum). Plant species making up the lowest layers and snails from open environments, such as T. geveri, T. cylindrica and V. narbonensis, are on the negative side. Axis 2 (9.2% of total inertia) compares dense herbaceous formations with discontinuous grass and shrublands. Grasslands with a high herbaceous cover can be found on the negative side (B. erectus and F. ovina). The densest vegetation houses mesophilous or forest-affinity snails (Sphyradium doliolum (Bruguière), M. obscura, M. cantiana), while the least dense harbours Mediterranean open



**Figure 4.** Canonical Correspondence Analysis (CCA) using the florisitic variable group as explanatory variables (species labels as in Appendix 2).

environment species (C. gagaxii, J. quadridens, V. narbonensis). On the positive side are the extremely discontinuous high-altitude grasslands with mountain species (T. geyeri, P. triplicata, C. rugosa) and Buxus sempervirens shrublands with forest-loving species (Cepaea nemoralis (Linnaeus), P. elegans, P. pygmaeum).

The SPACE group has four selected variables (Table 1). The CCA of the species-sites matrix constrained by these variables yielded a sum of canonical eigenvalues of 0.356, i.e. 19% (0.356/1.870) of explained species variation. The first axis (17.9 % of total inertia) is strongly correlated with spatial variables based on Euclidean distance between sites, particularly Dist5 which corresponds to a classification of sites into 5 groups (Fig. 5). These site groups are well-ordinated along axis 1: on the negative side are sites sampled in the central part of the range (two groups) including species located only in this sector (i.e. Z. detrita, P. elegans, V. costata and U. glabellus). Around the origin of the axis are sites from the eastern and western ridges (one group) consisting of the most common species. Finally, the positive side contains sites from the eastern and western ends of the range (two groups), associated with southern species with a limited low-altitude distribution. The spatial pattern using the five groups best explains the species distribution pattern. If the finest grid (Dist 20) was associated with this axis, this would mean that site location in the study area has little influence on the composition of land snail community.



Figure 5. Canonical Correspondence Analysis (CCA) using the spatial variable group as explanatory variables (species labels as in Appendix 2 and variable labels as in Table 1).

Axis 2 (8.3 % of total inertia) is a latitude gradient. On the negative side are both sites from the ridges associated with mountain species (*T. geyeri*, *P. triplicata*) and same latitude sites from the eastern and western ends of the range, but at lower altitudes and associated with southern species (*A. polyodon*, *V. narbonensis*). On the positive side are sites from the northern slopes and mesophilous or forest affinity snails (*Z. algirus*, *U. glabellus*, *C. nemoralis*).

A Monte Carlo test was performed simultaneously for each of the four canonical analyses (99 permutations) on the first axis and on the first four axes together. These axes were significant in each case (p < 0.05).

Variation explained by flora and habitat structure The floristic (FLORA) and habitat structure (STRUC-TURE) variables were compared and each group was successively analysed as a covariable set. The relative importance of habitat structure and floristic composition were calculated to explain variation in the speciessites matrix. The results are shown in Fig. 6A. These two variable groups explain 31.8% of matrix variation. Nearly half (14%) is due solely to habitat structure variables which explain more than flora (8.8%). 9% of explained variation is common to both floristic and habitat structure variables.

Variation explained by climatic and spatial variables The two CLIMATE and SPACE variable groups explain a total of 36.3% of variation, i.e. more than the habitat variables (Fig. 6C). 17.3% of variation is due solely to topographic and climatic variables, 10.2% to site spatial situation and 8.8% is common to both groups.

## Partition of the variation between the four explanatory variable sets

To obtain an overall view of the relative importance of each of the four explanatory variable groups, we performed a final series of analyses where habitat description variables (FLORA + STRUCTURE) and geographic variables (CLIMATE + SPACE) were combined to form two new groups. As before, two CCAs were performed: one was constrained by geographic variables (36.3% explained variation) and the other by habitat description variables (31.8% explained variation). The amount of variation explained by each of these groups is equal to the total percentage of explained variation obtained in the first two series of partial CCAs (Fig. 6B). Two partial CCAs made it possible to calculate the amount of explained variation in the species-sites matrix due to each of these two large groups.



Figure 6. Variation partitioning of the species data matrix according to different variable groups. [a]: Amount of variation explained only by first variable group. [b]: Amount of variation explained by both variable groups. [c]: Amount of variation explained only by second variable group. [d]: Amount of unexplained variation.

The fraction of species variation explained by all variables was 54.5%. Overall, the geographic variables (CLIMATE + SPACE) explain most of the variation (22.7%). This is mainly due to species distribution according to altitudinal gradient which was demonstrated in the CA and CCA constrained by the CLIMATE variable group. Habitat description variables (STRUCTURE + FLORA) explain one-third of variation (18.2%). 13.6% of explained variables.

## DISCUSSION AND CONCLUSION

Relative importance of flora and habitat structure Axis 1 of the two CCAs constrained by floristic composition and habitat structure ordinates the sites and snail species according to a structure and vegetation complexity gradient. The results of the CCAs and partial CCAs demonstrate that floristic composition plays a much less important role in gastropod communities than habitat structure, as the latter is primarily conditioned by vertical and horizontal vegetation structure. This concurs with results obtained by most authors who indicated that habitat floristic composition is not a determinant factor in explaining land gastropod distribution. Generally, neither quantity nor quality of a plant food source influences snail distribution (Boycott, 1934). Most species have a diet essentially consisting of different kinds of dead plants, supplemented by occasional mushrooms, lichens or fresh vegetation (Mason, 1970; Wolda, Zweep & Schuitema, 1971; Williamson & Cameron, 1976). The low amount of fresh vegetation eaten can be explained by the presence, in numerous living plants, of unpalatable or chemically repulsive parts (Grime, Blythe & Thornton, 1970). Heller (1988) demonstrated that snails prefer annual plant debris in semi-arid environments over perennial plants which develop xeromorphic traits making them difficult to eat or digest. Generally, taste tests have not been very conclusive: out of 52 plant species offered to C. nemoralis, only 10 appear to be relatively palatable (Grime, MacPherson Stewart & Dearman, 1968). South (1992) also noted that variation in snail diet was dependent on food available at a particular site. Mason (1968) studied seven forest snail species and concluded that they primarily feed on dead vascular plants with differences in secondary food source choices. These differences are significant and occasional use of lichens is frequently mentioned (Mason, 1974; South, 1992) which could explain the importance of the 'cryptogams' variable in the CCA constrained by the STRUCTURE variable group. Currently, we can only note a certain selectivity for some plant species or plant families by some gastropods (e.g. Chondrinidae are lichen-feeding). It is impossible to make any conclusions about genuine associations or specialisation which could affect malacofauna distribution. The possible relationships between gastropods and plant species in a habitat are more dependent on microclimate due to vegetation structure than on species composition (Boycott, 1934; Paul, 1978; Cameron *et al.*, 1980). In the present study, *Buxus sempervirens* plays an important role: its growth in grasslands severely modifies habitat structure, through the addition of a low woody layer rich in leaf litter.

The problem arises of the overlap between floristic composition and vegetation structure variables. These two groups of variable are strongly interrelated as vegetation structure naturally depends on the species in it. This relationship is emphasised by the amount of explained variation shared in common by these two groups (9%), which was lower that the STRUCTURE group contribution (14%), but higher than FLORA (8.8%).

#### Actual complexity of the altitudinal gradient

The altitudinal gradient is the main determinant factor for land snail species distribution in the Luberon. Alpine communities can be found at higher altitudes, in particular *T. geyeri*, *P. triplicata*, *C. rugosa* and *A. secale*, which were also the basis for low-altitude land snail assemblages during the last glacial period (Magnin, 1989, 1992). The other end of the altitudinal gradient is marked by the presence of thermophilous and Mediterranean species (*C. gigaxii*, *A. polyodon*, *J. quadridens*).

Temperature decrease with altitude is definitely a limiting factor for some species. Several studies have indicated the impact of altitude (from the climatic perspective) on snail community richness and composition (Cameron & Greenwood, 1991; Dyduch-Falsniowska, 1991; Magnin, 1991). The presence of high-altitude species or combinations of species characterising land snail communities during the Pleistocene cold periods at low altitudes is generally explained by an altitudinal shift of the climatic gradient (Metcalf, 1984; Gittenberger & Goodfriend, 1992; Magnin, 1992) and these changes in distribution patterns can be used to recreate palaeoclimates (Harris, 1978; Magnin, 1992).

However, factors other than climate can explain the observed altitudinal distribution patterns. The sharing of the altitudinal gradient by *T. geyeri* and *C. uni-fasciata* raises the following problems: although there appears to be a strong climatic determinism, recent studies (Magnin, 1993) have shown that historical factors (climate changes) and competition between the two species could explain this distribution pattern.

The impact of human activities could also play an important role. The altitudinal gradient in the Luberon (as in many Mediterranean ranges) coincides with changes in landscape management styles: above 900 m, grazing by sheep has considerably changed the vertical and horizontal vegetation structure and thus reinforced an harsh microclimate.

It is difficult to clearly demonstrate the direct role of the current climatic gradient. The altitudinal gradient illustrated by our analyses could be due to a complex combination of climatic, historical and biotic factors.

#### Relative importance of spatial explanatory variables

Partial CCAs have revealed the importance of community spatial structure which is independent of the environmental variables analysed, i.e. climatic variables s.l., habitat-structure variables and grassland floristic composition. This environmentally independent spatial variation in community composition is obvious in some of the study zones where several species are strictly localised, although this localisation is not related to the particular environmental factors. This phenomenon could be due to diverse factors, such as between-species competition, low dispersal ability, undefined historic factors or a combination of several of the above factors. Particular spatial patterns, e.g. spot distribution of T. geyeri and C. unifasciata at mid altitudes, could be explained by passive dispersion caused by sheep, followed by settlement of populations maintained by local between-species competition (Pfenninger, 1997). Historical causes and low colonisation capacity could also explain localisation of species such as V. costata. However, the more or less recent history of the communities and species dispersal ability are rarely considered to explain the composition of land snail communities. When community spatial structure is analysed on any scale, it is generally linked to environmental heterogeneity (Harvey, 1974; Paul, 1978; Murray, Johnson & Clarke, 1982; Dyduch-Falniowska & Tobis, 1989; Goodfriend, 1992). When 'historical factors' are mentioned, it is usually to explain a possible temporal difference between environmental changes and the consecutive response of snail communities (Bishop, 1977; Thomas, 1985). However, Cameron et al. (1980) and Magnin et al. (1995) have demonstrated that the landscape structure and its evolution over a hundred year time period could explain part of spatial changes in snail communities. The present study confirms that historic factors have a great influence over the spatial structure of communities.

The CCAs and partial CCAs made it possible to quantify the amount of variation explained by different groups of variables which control land gastropod abundance and distribution in open mountain environments. Our results concur with accepted studies and demonstrate that habitat structure is a more important explanatory factor than floristic composition. Our analyses emphasise the important role played by non-

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environmental factors (particularly historic factors) expressed by independent spatial variables. Nevertheless, it is difficult to discriminate between the influence of climatic factors *s.s.*, historic events and/or biotic factors within the altitudinal gradient.

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## LAND SNAIL COMMUNITIES IN MEDITERRANEAN UPLAND GRASSLANDS

## **APPENDIX 1**

#### Environmental and spatial variables

#### CLIMATIC VARIABLES (12):

quantitative variables (3):
$\sim$ Altitude:
(eight 50m categories between 700 and 1100m)

$\sim I$	Humidity:	(Apparent site	humidity):
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- 1-Very dry 3- Relatively dry
- 2-Dry 4- Average site

$\sim$ Grassland patch Size:	
$1 - < 50 \text{ m}^2$	$4 - > 250m2 - < 500m^2$
$2 - > 50m^2 - < 100m^2$	$5 - > 500 \text{m}^2 - < 1 \text{ha}$
$3 -> 100m^2 -< 250m^2$	6– > 1ha

#### STRUCTURE VARIABLES (14):

Surface cover:

	•
$\sim$ Hard rock	$\sim$ Layer 1: 0–5 cm
$\sim$ Boulders(> 20 cm)	~ Layer 2: 6–15 cm
$\sim$ Broken stone (< 20 cm)	~ Layer 3: 16–25 cm
$\sim$ Vegetation	$\sim$ Layer 4: 26–50 cm
$\sim$ Litter	$\sim$ Layer 5: 51 cm–1 m

- $\sim$  Litter
- $\sim$  Bare ground
- Coding used for these 14 cover variables is:

Laver cover:

1–0–3%	3-11-25%	5-51-75%
2–4–10%	4-26-50%	6-76-100%

## FLORISTIC VARIABLES:

Cover of three dominant species for each site is coded as follows:

- 1-10-25%
- 2-26-50%
- 3-51-75%
- 4-76-100%

#### SPATIAL VARIABLES :

- $\sim$  Latitude: UTM coordinates
- $\sim$  Longitude: UTM coordinates
- $\sim$  Dist5: Division of the Hierarchical Cluster Analysis into 5 groups
- $\sim$  Dist10: Division of the Hierarchical Cluster Analysis into 10 groups
- $\sim$  Dist20: Division of the Hierarchical Cluster Analysis into 20 groups

Nominal Variables (9):

~Flat

- $\sim$ Northern exposure
- ~Halfway up location
- $\sim$ Southern exposure
- ~Upper slope
- ~Eastern exposure
- ~Summit
- $\sim$ Western exposure
- $\sim$ No defined exposure

Vegetation type cover:

- $\sim$  Low woody
- $\sim$  Grasses
- ~ Cryptogams

# CORINNE LABAUNE & FRÉDÉRIC MAGNIN

# **APPENDIX 2**

# List of the gastropod species with their abundance and occurrence (nomenclature after Kerney *et al.*, 1999)

SPECIES AND ABBREVIATIONS	NUMBER OF SHELLS	NUMBER OF SITES
CUN Candidula unifasciata (Poiret 1801)	7487	50
TGE Trochoidea geyeri (Soós 1926)	2482	48
PTR <i>Pupilla triplicata</i> (Studer 1820)	4513	44
TCA Truncatellina callicratis (Scacchi 1833)	1856	39
CAC Cecilioides acicula (Müller 1774)	281	38
GVA <i>Granaria variabilis</i> (Draparnaud 1801)	2683	38
MCA <i>Monacha cantiana</i> (Montagu 1803)	649	36
CRP <i>Clausilia rugosa parvula</i> (Férussac 1807)	1034	35
JQU <i>Jaminia quadridens</i> (Müller 1774)	267	34
TCY Truncatellina cylindrica (Férussac 1807)	880	25
XCE Xerosecta cespitum (Draparnaud, 1801)	723	21
ASE Abida secale (Draparnaud 1801)	404	18
CSE Cochlostoma septemspirale (Razoumowsky 1789)	296	17
AAC Acanthinula aculeata (Müller 1774)	76	14
PPY <i>Punctum pygmaeum</i> (Draparnaud 1801)	63	12
VCN Vitrea contracta (Westerlund 1871)	65	12
VNA Vitrea narbonensis (Clessin 1877)	101	10
PPA <i>Pagodulina pagodula</i> (Des Moulins 1830)	38	8
UGL Urticicola glabellus (Draparnaud 1801)	63	7
CNE <i>Cepaea nemoralis</i> (Linnaeus 1758)	33	6
PEL <i>Pomatias elegans</i> (Müller 1774)	86	6
MOB Merdigera obscura (Müller 1774)	13	5
LCY <i>Lauria cylindracea</i> (Da Costa 1778)	109	4
VCO Vallonia costata (Müller 1774)	996	4
CGI <i>Candidula gigaxii</i> (Pfeiffer 1850)	1135	4
PMA Phenacolimax major (Férussac 1807)	3	3
ZDE Zebrina detrita (Müller 1774)	257	3
ODO Sphyradium doliolum (Bruguière 1792)	6	2
ZAL <i>Zonites algirus</i> (Linnaeus 1758)	1	1
APO Abida polyodon (Draparnaud 1801)	1	1
CAV Chondrina avenacea (Bruguière 1792)	2	1
SSI <i>Solatopupa similis</i> (Bruguière 1792)	39	1