ECOGRAPHY 26: 257–268, 2003

Identification of landscape units from an insect perspective

Guillem Chust, Joan L. Pretus, Danielle Ducrot, Anne Bedòs and L. Deharveng

Chust, G., Pretus, J. L., Ducrot, D., Bedòs, A. and Deharveng, L. 2003. Identification of landscape units from an insect perspective. – Ecography 26: 257–268.

Habitat patches vary as a function of an organism's perception. The response of species to patch mosaic may depend on the scale of observation by which the spatial pattern is perceived. A hierarchical view of landscapes is proposed to define the optimal grain of landscape affecting soil fauna (Collembola). A multilevel approach is developed to quantify the landscape grain based on the concept of contrast, that is, the magnitude of difference in measures across a given boundary between adjacent patch types. An image segmentation procedure was firstly applied to satellite images to detect edges, and this defines "homogeneous" regions at multiple contrast levels. Spatial features (number of patches, diversity of patches and edge length) were then derived from segmented images to characterise the spatial pattern that surrounds Collembola sampling sites. These landscape descriptors were computed at different levels of contrast and at three spatial scales. The statistical dependence between species occurrence and landscape descriptors was assessed by means of the Mantel test. Biodiversity, estimated by species richness and the number of endemic species, was analysed by stepwise multiple linear regression.
The multilevel approach permitted a definition of the landscape units based on the response of the assemblage to landscape heterogeneity. The effect of landscape heterogeneity was especially evident on species composition and on endemic richness when patches are defined at fine grain. The heterogeneity descriptor "number of patches", calculated at the optimal contrast level, explained 72% of the endemic richness variance. This spatial feature constituted a reliable inverse indicator of endemic richness that was extrapolated to the pixels of the image providing a spatial model.

G. Chust (chust@porthos.bio.ub.es) and J. L. Pretus, Dept d'Ecologia, Fac. de Biologia, Univ. de Barcelona, Diagonal 645, E-08028 Barcelona, Spain. – D. Ducrot, Centre d'Etudes Spatiales de la Biosphère (CNES-CNRS-IRD-UPS), 18, avenue Edouard Belin, F-31401 Toulouse Cedex 4, France. – A. Bedós and L. Deharveng, Lab. d'Ecologie Terrestre (UMR 5552 du CNRS), 18, avenue Edouard Belin, F-31401 Toulouse Cedex 4, France.

Landscapes have a hierarchical structure in the sense that regions perceived at a coarser level of detail are formed by sub-regions that we can identify at finer levels of detail. Kotliar and Wiens (1990) noted that a hierarchical mosaic of patches within patches occurs over a broad range of scales, which is a more realistic view of the classical definition of patches as "discrete and internally homogeneous entities". From a functional perspective, patches vary depending on each organism's perception (Wiens and Milne 1989). The grain of landscape perception involves two related components, the spatial resolution and the notion of contrast. Spatial resolution and the extent of the study area define the spatial scale. The concept of contrast represents the magnitude of difference in measures across a given boundary between adjacent patch types (Wiens et al. 1993) or, in general, between adjacent areas. Varying the threshold by which the contrast of neighbouring areas is considered an edge, the landscape will be described at different levels of detail, i.e. the lower the contrast level, the finer the detail with which the edges are delineated.

Accepted 5 August 2002

ISSN 0906-7590

Landscape ecologists and geographers focused their main attention on the spatial scale (e.g. Woodcock and Strahler 1987, Wiens 1989, Turner et al. 1989) for analysing the landscape pattern per se (O'Neill et al. 1991, Gardner 1998), or its effects on natural populations (Roland and Taylor 1997, Bergin et al. 2000). Few authors have dealt with the species response to the landscape at different contrast levels (e.g. Kotliar and Wiens 1990, Wiens 1992).

The present paper attempts to define the optimal grain of landscape affecting soil fauna by means of developing a multilevel approach. We characterised landscapes that surround collembolan sampling sites, at multiple levels of contrast, in order to study the influence of patch mosaic on species occurrence and on biodiversity (in particular, species richness and the number of endemic species). Empirical and theoretical work demonstrates that size, isolation and shape of habitat patches induce changes in species abundance and biodiversity (Andrén 1994, Hanski and Gilpin 1997). This patch-based approach of fragmentation effects, however, defines the patch a priori from a human-centred perspective. We characterised the landscape pattern at the landscape level (sensu McGarigal and Marks 1994) and at different levels of contrast providing a hierarchical view of the habitat (Kolasa and Waltho 1998), i.e. smaller, low-level landscape units are nested within larger, high-level units.

To characterise the landscape pattern at multiple contrast levels, we used an image segmentation procedure (Shen and Castan 1992) that detects edges defining "homogeneous" regions at a given level of contrast. Remote sensing optical imagery was selected as the source of land information because of its multispectral capabilities.

Collembola were chosen as a soil biodiversity indicator because of their high taxonomic diversity, their richness in narrowly distributed species, and their high abundance in all terrestrial habitats, especially in soils of deciduous forests where they constitute the most numerous insects (Petersen and Luxton 1982, Cassagnau 1990). The contribution of soil fauna to global biodiversity remains unclear even though, since Erwin's paper (1982), it has received considerable attention (André et al. 2002).

We explicitly distinguished the role of habitat structure from the species tolerance limits. Species tolerance limits, called here the "local" habitat, comprises those environmental variables (scale independent), such as temperature, humidity, or forest type, that directly interact with individual organisms. Habitat structure is the surrounding environment or, in other words, the spatial arrangement of landscape features, which is called here the "regional" habitat. This affects the entire assemblage by inducing changes in population cohesion and individual mobility. Regional habitat is a scale-dependent concept since the surrounding environment must be defined in relation to a given spatial scale (distance, area or volume) and to a contrast level (in relative units).

Study area

The Pyrenees constitute as a whole one of the most remarkable areas of endemism in Europe (Deharveng et al. 2000). Our study site, the Arize massif (Fig. 1), lies in the central part of the range, in a region of long forested ridges of moderate elevation. Its soil fauna has been documented in detail (Deharveng and Lek 1995, Deharveng 1996), and appears very rich in Pyrenean endemics, probably because the massif was relatively spared by quaternary glaciers. The Arize mountain reaches 1715 m a.s.l., extending on 40 km from east to west. Native vegetation consists of beech forests (*Fagus sylvatica*) above 800-900 m, and woods of different deciduous species, often dominated by oaks (*Quercus*), below 800–900 m. Lowland forest cover has been highly fragmented by agriculture. The beech zone was better preserved, but has been encroached by extensive plantations of exotic conifers during last decades. The landscape resulting from these various anthropogenic disturbance as well as from forest regeneration on abandoned pastures, is a complex mosaic of different kinds of forests, agricultural lands and small villages.

Material and methods

Satellite data

We used a high-resolution optical image, covering the area of the test site, acquired by Landsat Thematic

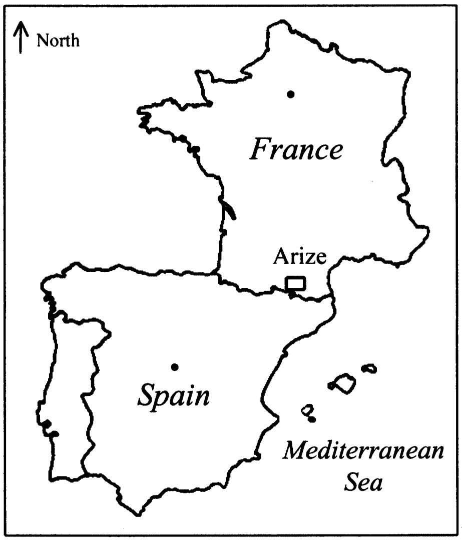

Fig. 1. Study area: the Massif of Arize (French Pyrenees).

Mapper (TM) satellite on 13 July 1990. The spatial resolution of TM images is of 30×30 m. The image has been used to generate land information concerning landscape patches by means of an image segmentation method (described in Multilevel approach: extraction of landscape descriptors) and a land cover classification.

Land cover data was derived by means of a supervised classification into 11 categories (Chust 2002): beech forest, oak forest, coniferous and mixed forest, sclerophyllous vegetation, herbaceous rangeland, ferns, cropland and pasture (2 phenological stages), urban areas, rocky habitats, streams and lakes. The classification has an overall accuracy of 90.1%, beech and oak forests have a per-category accuracy of 77.6% and 89.9%, respectively. The classification was performed with the maximum likelihood procedure using spectral bands, spectral-derived textural information and ancillary data. This land cover classification was only used to interpret and to complement the results, but not to extract landscape descriptors. An analysis at multiple spatial scales that uses land cover data and vegetation information to derive landscape descriptors was presented in Chust et al. (unpubl.).

Biological material and sampling procedures

Collembola were selected as representatives of soil fauna because they are present in dense populations in soil forest. They are easily sampled in a standardised way, and their diversity is reasonably stable along the year (Lek-Ang and Deharveng 2002).

Soil fauna was collected at 27 sites during 1998 (1 and 22 April, 5 and 6 November), between 400 and 1400 m of elevation, and in two kinds of forest habitats: 11 sites in beech forest and 16 in oak forests, over a wide range of forest fragmentation. The oak wood also includes other deciduous species (e.g. chestnut, birch, black locust-tree). Distance between neighbouring sites was at least 2.2 km in order to minimise spatial autocorrelation between biological data and between landscape descriptors. In each one of the sites, 4 samples of soil cores of 250 cm^3 each were collected within an area of ca 400 m^2. After the accumulation curves of species richness given by Deharveng (1996), 4 samples ca catch 50% of overall Collembola species richness, providing a reasonable compromise between a representative estimation of species richness of the site and the costs of the sampling effort. The soil fauna was extracted within 7–10 days, using Berlese-Tullgren funnels. A detailed description of the sampling procedures can be found in Chust (2002).

For the entire study, a total of 95 Collembola species were identified, of which 24 were endemic to the Pyrenees or to a part of the Pyrenees (Appendix 1). For each site, we estimated Species richness (S) and the number of Endemic species (E). Species richness corresponded to the average of the number of species for the 4 samples. On the contrary, endemic richness considered the total number of endemics found in the four samples. This consideration aims to give an overall measurement for the site, more than an average value from soil core samples, because endemic species were rare.

Prior to the multiscale study, we verified the homogeneity of sampling dates (April and November), concerning both species and endemic richness, by means of the Kruskal-Wallis test. This non-parametric test showed that the average values of richness measurements did not differ statistically between April and November ($p = 0.41$ for species richness, $p = 0.56$ for endemic richness), thus, the two dates could be processed together.

Local habitat versus regional habitat

We distinguish local habitat (based on topographical descriptors and forest type at the sample site) from regional habitat (here, landscape descriptors, described in Multilevel approach: extraction of landscape descriptors) in order to study their relative contribution for explaining soil fauna response.

Forest type comprises beech and oak forest. Topography comprises three variables: elevation (supposed to be related with temperature and in general with the local climate), slope (steep slopes support thinner soil substrate), and exposition (calculated as the cosine of orientation, it is then bounded between 1, i.e. exposition to north, and -1, i.e. exposition to south; this component is supposed to have a direct influence on humidity and temperature conditions).

The relationship of species richness and the number of endemics to local habitat predictor variables was tested using regression analysis.

Multilevel approach: extraction of landscape descriptors

The multilevel approach consists of 3 steps: 1) segmentation of the satellite image into relatively homogeneous regions (see below). 2) Extraction of spatial indices from the segmented land as landscape descriptors. They describe the arrangement and heterogeneity of patch mosaic in the aim of characterising species habitat and their surrounding matrix, and 3) testing the relationship between species data and landscape descriptors (described in Multilevel approach: relationship between species data and landscape descriptors).

Image segmentation is an image processing method which is based on edge detection originated by abrupt changes in intensity of neighbouring pixels. The Optimal Edge Detector developed by Shen and Castan

(1992) was applied to the TM image (spectral bands: 2,3,4,5,7). The segmentations are obtained from the edge strength map by the watershed algorithm (Vincent and Soille 1991), which is a method that gives closed, skeleton boundaries defining regions (patches). The method creates 256 levels of segmentation (here called contrast levels), where a level of segmentation corresponds to the threshold applied to the basin dynamics (Lemaréchal et al. 1998).

The segmentation process gives a description of landscape units at different degrees of edge detection. The higher the level of segmentation, the greater must be the contrast level between neighbouring areas to detect edges. The higher the contrast level, the coarser the landscape units are delimited (Fig. 2). Given that fine-grain landscape units are nested within coarse-grain units, the procedure provides a hierarchical description of landscape. This approach is equivalent to varying the maximum number of grey levels of the image (256 grey levels in Landsat TM) in the comparison of adjacent areas.

In the present work, we only considered the first 20 contrast levels. This maximum level was selected since the number of patches of the landscape decrease exponentially along the contrast levels, such that, at higher levels the number of patches represents $< 1\%$ in respect with the number of patches present at the first level; in other words, at higher levels the landscape is composed by few coarse patches involving high heterogeneous areas.

The second step of the multi-level approach consists of deriving patch-level spatial indices surrounding sampling sites from the segmented land at different contrast levels. At each level of contrast and for a defined window size centred on the sampling site, we calculated three spatial indices (Fig. 2): 1) Number of Patches (NP). It is bounded between 1 and n, where n is the number of pixels within the window. 2) Diversity of Patches (DP), based on information theory (Shannon and Wiener), it is defined as

$$DP = -\sum_{i=1}^{NP} p_i \log p_i$$

where p_i is the number of pixels of the patch i divided by n. DP is bounded between 0 and log(NP). Units are bits per patch. 3) Edge length (EL), it is the total length of all edges. EL is bounded between 0 and n. Units are given in pixels.

All three spatial indices measure landscape heterogeneity, but in different ways. The difference between NP and EL depends on the patch shape; an environment with a large and highly convoluted patch, for instance, can result on a high value of EL and a low value of NP. DP links the concepts of patch number and patch area evenness to provide a measurement of patch mosaic, called here patch diversity for analogy with the Shannon index of species diversity.

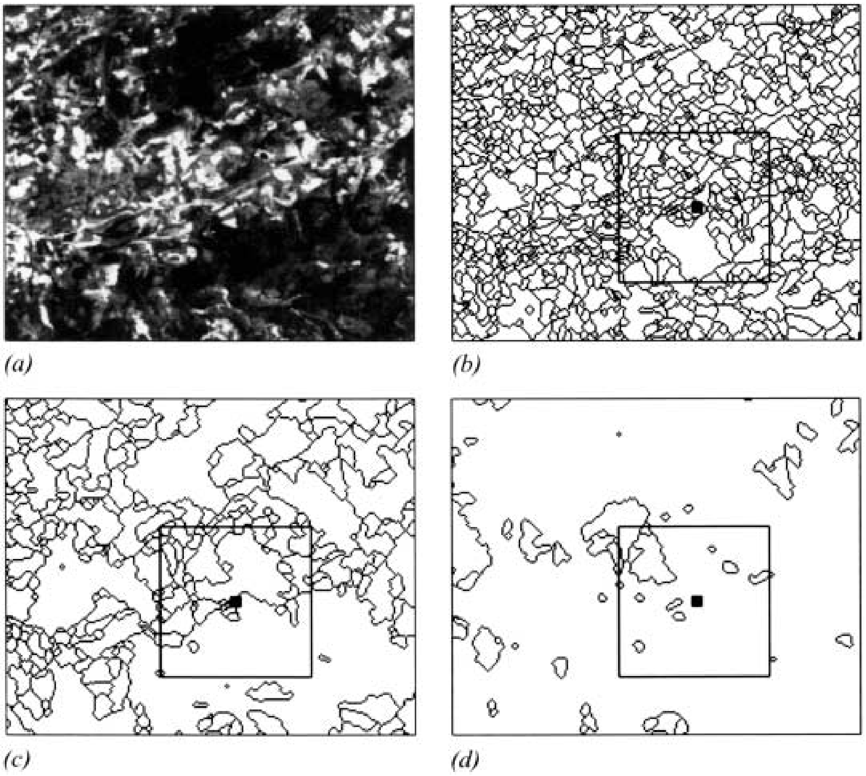

Fig. 2. Procedure to extract landscape descriptors based on the multilevel approach. A detail of the spectral band 3 of the TM image (a), segmented at increasing contrast levels. (b) Low level of contrast corresponding to fine-grain landscape perception; (c) intermediate contrast level; (d) high contrast level corresponding to coarse-grain landscape units. The large square window delimits the area in which landscape descriptors are computed. This area is centred in the sampling site (black dot) to represent the surrounding environment.

We used three window sizes: small scale (7 × 7 pixels, equivalent to 4.41 ha), intermediate scale (37 × 37 pixels, 123.21 ha) and large scale (67 × 67 pixels, 404.01 ha), in order to test the influence of spatial scales on patch statistics and on soil fauna responses.

Multilevel approach: relationship between species data and landscape descriptors

On the last step of the multilevel approach, our concern was the relationship between species data and landscape descriptors at different levels of contrast. The species occurrence was studied by means of the Mantel test; species richness measurements, by stepwise multiple linear regression analysis.

Species occurrence analysis

We used the Mantel test to determine whether the correlation between the similarity in species occurrence and the landscape resemblance differs across the contrast levels. In species matrix (m species by n sites, obtained by pooling the 4 samples of each site), each element represents the occurrence of a species at a site (i.e. a value of 0 means absence, a value of 1 means presence). The environmental matrix is a set of p variables: $\{X_1, X_2, \ldots X_p\}$, corresponding, here, to the 3 landscape descriptors (NP, DP, EL). We studied two species matrices: one for all species, the other for only the endemic species.

The Mantel test is a permutation-based non-parametric method for comparing two similarity or distance matrices, computed about the same sites (Legendre and Legendre 1998). The objective is to test the correlation between specific composition similarities and the landscape resemblance. The similarity matrix of species (n × n) was obtained from the similarity coefficient of Jaccard, an asymmetrical qualitative coefficient defined as the number of species present at the two sites, divided by the total number of species observed. The similarity matrix of environment was obtained from the Gower coefficient, which reports the landscape resemblance of environments surrounding sites. Gower's coefficient is appropriate for quantitative data and is a symmetrical coefficient (i.e. the state zero for two objects is treated in exactly the same way as any other pair of values). The simplest form of Gower coefficient (S_G) is as follows:

$$S_G(\text{site}_1, \text{site}_2) = \frac{1}{p}\sum_{j=1}^{p} S_{12j}$$

where p is the number of variables and $S_{12j} = 1 - (|X_{1j} - X_{2j}|/R_j)$, which is a normalised distance transformed into a similarity, with R_j the greatest difference of the variable. For a detailed description of similarity coefficients see Legendre and Legendre (1998). The Mantel statistic, called r_M, is a measurement of the correlation between the two matrices and results from the cross-product of the matrix elements after standardisation. It runs from -1 to $+1$ and behaves like a correlation coefficient.

The partial Mantel test estimates the correlation between similarity matrices of species and of landscape descriptors while controlling for the effect of similarity covariable matrix (here, local habitat variables). For topography we used the Gower coefficient. For forest type we used the simple matching coefficient defined as the number of sites where the forest type is the same, divided by the total number of descriptors. Since we only consider one descriptor, the simple matching coefficient only takes the values of 0 or 1.

Analysis of species richness measurements

We tested the relationship between species richness measurements (Y), i.e. species richness (all species) and number of endemic species, and landscape descriptors (X_i) by Stepwise Multiple Linear Regression (Zar 1996, Legendre and Legendre 1998) for each contrast level. Stepwise procedure tests different models by including and eliminating variables in steps, and selects the model where the multiple coefficient of correlation R is the highest and where all partial regression coefficients β are significant (i.e. $\beta \neq 0$). Therefore, we obtain a model for each contrast level l ($l = 1, 2, \ldots, n$):

$$\hat{Y}_l = B_0 + \sum_{i=1}^{m} B_i X_{i,l}$$

where B is the estimation of β, m is the total number of landscape descriptor variables included in the stepwise regression, and n is the number of levels included in the study (i.e. 20).

In order to determine the optimal contrast levels, those explaining most of the species richness variance, we performed stepwise multiple linear regression between Y and $\{\hat{Y}_1, \hat{Y}_2, \ldots, \hat{Y}_n\}$. The resulting model is as follows:

$$\hat{Y} = C_0 + \sum_{l=1}^{n} C_l \hat{Y}_l$$

where C is the new regression coefficients. This is considered the optimal model (maximal R with significant regression coefficients) to define the landscape grain that predicts diversity data. The optimal model can be extrapolated to the pixels of the image in order to obtain a spatial representation of species richness prediction.

We performed the Kolmogorov-Smirnov test of normality ($p = 0.34$ for species richness, $p = 0.19$ for endemic richness). The results indicated that dependent variables followed normal distributions, fulfilling assumptions for regression analysis.

Results

Landscape descriptors at multiple contrast levels

As a result of the multilevel procedure, landscape descriptors are highly dependent on the contrast level and the spatial scale (Fig. 3). By increasing the level of contrast, the patches will be merged monotonically, which explain the decrease of NP and EL, and in turn of DP. The curves showed that the three landscape descriptors presented low variability at higher contrast levels. The NP and EL also presented low variability for the small spatial scales. The consequences of those patterns will be discussed later in relation to the response of soil assemblages to landscape heterogeneity.

Species occurrence analysis

In order to evaluate the role of the local habitat on the species occurrence, firstly, we performed a Mantel test between the corresponding similarity matrices. This test showed that the species occurrence (all Collembola species) depended on topography (elevation, slope and orientation), $r_M = 0.42$ ($p = 0.001$), and on the forest type ($r_M = 0.36$, $p = 0.001$). In the case of endemic species, correlation with topography and forest type was lower ($r_M = 0.23$, $p = 0.003$; and $r_M = 0.15$, $p = 0.027$, respectively).

Species occurrence similarities (all Collembola species) presented different responses to landscape resemblance as a function of contrast levels and spatial scales (Fig. 4). At the scale of 4.4 ha, the correlation was very low and, in general, not significant. At the scale of 123 ha, the first 11 contrast levels were significant, presenting maximum values at 5th and at 8th levels (r_M: 0.42 and 0.41, respectively). At 404 ha scale, the curve showed a pattern similar to the one at the scale of 123 ha, but with a more defined optimal contrast level localised at the second level ($r_M = 0.44$, $p = 0.001$). Even though landscape descriptors at those three contrast levels presented different absolute values (Fig. 3), the descriptors are correlated among them (Table 1) indicating that they are actually reflecting a similar landscape pattern. Although r_M was not very high at the optimal scale, it was highly significant, indicating that ordination of species occurrence was partially affected by landscape heterogeneity when the patch was defined at fine grain and when the surrounding landscape was characterised at intermediate and large

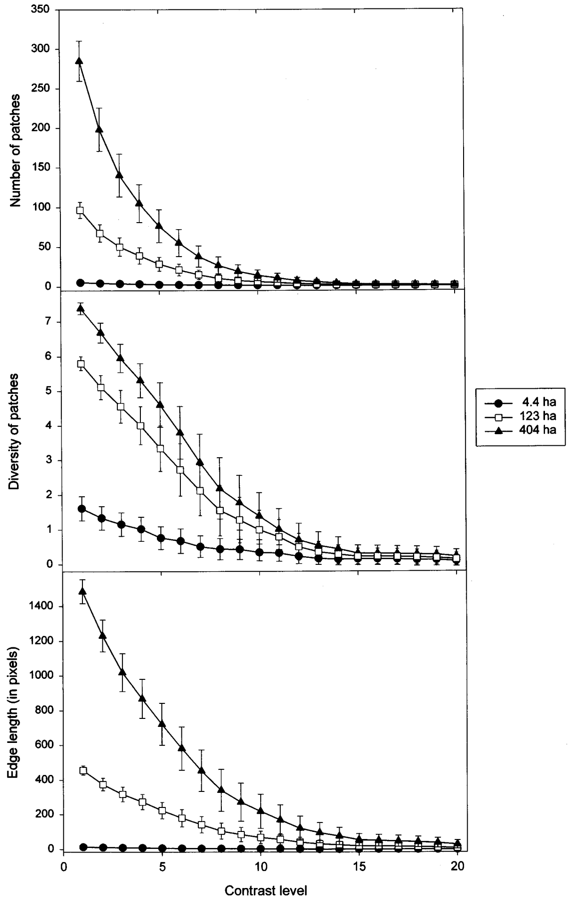

Fig. 3. Mean values and their confidence intervals (at 99%) for the three landscape descriptors of heterogeneity (number of patches, diversity of patches and edge length) as a function of the contrast level and at three spatial scales (4.4, 123 and 404 ha).

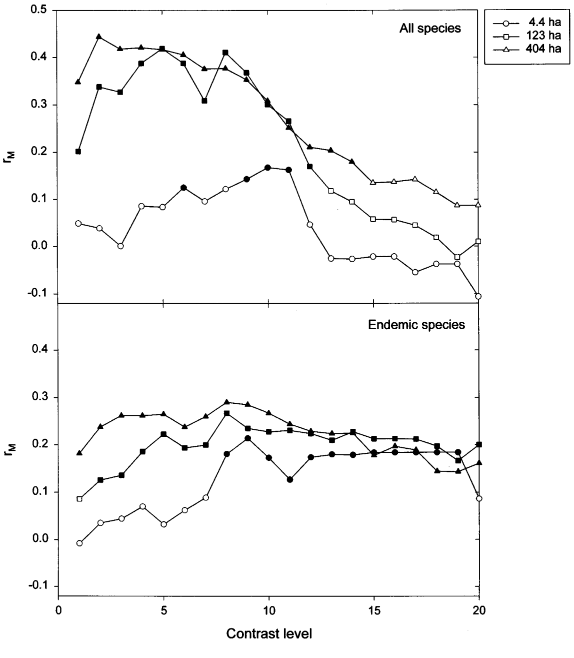

Fig. 4. Mantel correlation statistic (r_M) between species occurrence similarity and landscape resemblance through contrast levels, using three different spatial scales, for all Collembola species and for endemic species. Solid symbols (in black) indicate significant values of r_M ($p < 0.05$).

Table 1. Correlation of Mantel (r_M) between landscape descriptors resemblance at the three contrast levels (l) at which species occurrence similarities (all Collembola species) presented the highest correlation.

	l: 5 (123 ha)	l: 8 (123 ha)
l: 2 (404 ha)	0.836 ($p = 0.001$)	0.779 ($p = 0.001$)
l: 5 (123 ha)	–	0.853 ($p = 0.001$)

scales. The segmented image corresponding to this contrast level is shown in Fig. 5b; by comparison with spectral band 3 of TM image (Fig. 5a), one observes that landscape units are finely detailed in the segmented image.

The comparison between the effects of local and regional habitats on the contribution of species variance showed that topography influenced in a similar order as the landscape descriptors at the optimal contrast levels. The partition of variance was obtained by means of the partial Mantel test considering only topography since forest type was less correlated with species occurrence (Table 2). This test revealed that 23.6% of occurrence similarity variance (all species) was explained by both landscape heterogeneity and topography, where 6.25% is only explained by landscape heterogeneity and 13.5% corresponded to the interaction between both regional and local habitat. This indicates that heterogeneity and topography are partially correlated.

Concerning endemic species, matrix comparison revealed that correlation between similarity of endemic species occurrence and landscape resemblance was lower than considering all species (Fig. 4). The optimal contrast level was at the 8th level, at the large spatial scale ($r_M = 0.29$, $p = 0.001$). The small spatial scale and higher levels of contrast showed the lowest values of Mantel correlation, as in the case of all species analysis. The partition of variance also showed that interaction between heterogeneity and topography is high (Table 2).

Analysis of species richness measurements

Figure 6 illustrates the correlation between species richness measurements (species richness and number of endemic species) and spatial indices using three spatial scales at different contrast levels.

Species richness was poorly correlated with spatial indices at the three spatial scales; the optimal contrast level was at 3rd level ($r = -0.49$ with DP, at scale: 4.4 ha). Partial regression coefficients of local habitat variables (topography and forest type) were not statistically significant.

The number of endemic species was well correlated with spatial indices at the first segmentation levels (from 1 to 13) for intermediate and large scales. At the small scale, the curve was similar to the larger scales but the correlation was clearly lower. At the intermediate and larger scales the curves were similar but presented different optimal contrast levels. At the intermediate scales, the optimal level was the 4th ($r = -0.84$ with NP); see the regression fit in Fig. 7 in which the endemic richness (E) can be predicted from NP:

$$\hat{E} = -0.081\mathrm{NP}_{(4\mathrm{th},123\mathrm{ha})} + 6.142$$

At the large scale, the optimal level was the 7th ($r = -0.82$ with NP). This indicates that the degree of endemism was high in homogeneous environments (with a low number of patches) defining landscape units at fine grain. Differences between endemic response to intermediate and larger spatial scales were more quantitative than qualitative. At the optimal scale and level, partial regression coefficients of local habitat variables were not significant.

The segmented image corresponding to the optimal contrast level for endemic richness is shown in Fig. 5c; the comparison with spectral band 3 (Fig. 5a) reveals that the 4th level still conserves a high patch definition. In the segmented landscape, one can discriminate heterogeneous regions, corresponding to a mosaic of bright patches contrasted with a dark matrix, from homogeneous areas corresponding to dark surfaces. Given that NP, calculated at this contrast level and for intermediate spatial scales, explained 72% of the variance, this spatial index constituted a reliable inverse indicator of endemic richness that was extrapolated to the pixels of the image (Fig. 5d). In fact, estimates of endemic richness can only be predicted on the land corresponding to beech and oak forest, where the accuracy of the estimates depends on the error of the regression function and on the error of the land cover classification.

The small spatial scale and higher levels of contrast presented the lowest values of multiple correlation, as in the case of species occurrence analysis. This fact must be associated with the low variability observed of the descriptors at those scales of observation, in other words, the landscape pattern was not properly discriminated by patch statistics in those situations.

Ecological interpretation of landscape heterogeneity

Results showed that species occurrence was ordinated by landscape heterogeneity and endemic richness was negatively correlated by the number of patches. This indicates that, whatever the landscape heterogeneity represents, it can indirectly report important features of soil communities. One may ask, however, which land-

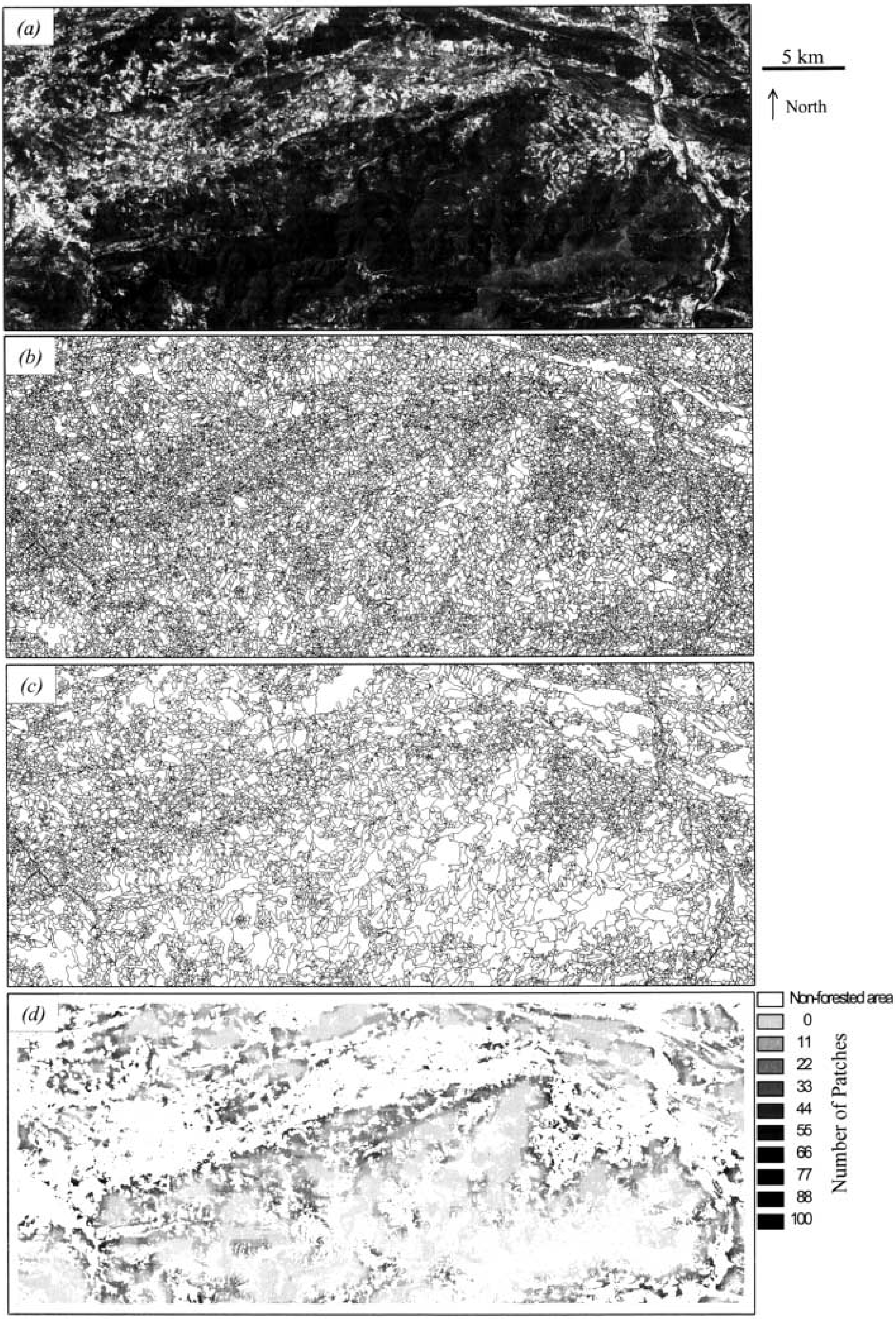
(a)
5 km
North
(b)
(c)
(d)
Non-forested area
0
11
22
33
44
55
66
77
88
100
Number of Patches

Fig. 5.

Table 2. Partition of variance between habitat variables to explain similarity of species occurrence based on the partial Mantel test. Values are given in percentages. Landscape descriptors are calculated at the optimal contrast levels and scales, i.e. l: 2, 404 ha for all species; and l: 8, 404 ha for endemic species.

	Landscape descriptors	Topography	Interaction	Total
All species	6.25	3.85	13.5	23.6
Endemic species	3.73	0.83	4.68	9.24

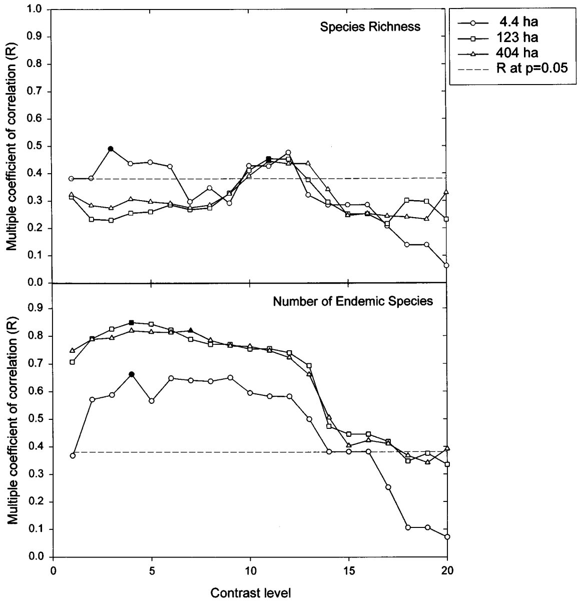

Fig. 6. Multiple correlation coefficient (R) between species richness measurements (species richness and the number of endemic species) and spatial indices using stepwise multiple linear regression analysis, at different contrast levels and using three spatial scales.

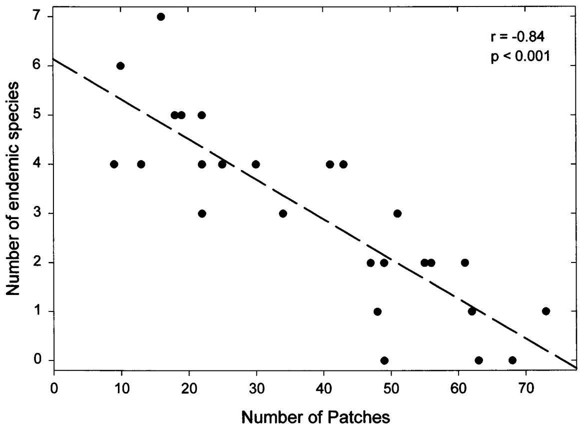

Fig. 7. Number of endemic species against number of patches at the optimal contrast level (4th) and the optimal spatial scale (123 ha), r = − 0.84 (p < 0.001). See also the corresponding Fig. 5c showing the definition of patches at this optimal contrast level, and the landscape descriptor (Fig. 5d).

scape elements conform heterogeneity to be the main cause of impoverished degree of endemism.

The knowledge of Arize and the visual comparison between segmented maps and raw images suggested that agricultural areas and villages conformed heterogeneous regions. To confirm this hypothesis we plotted the percentage of each land cover (derived from the supervised classification) against heterogeneity of the landscapes which surround sampling sites (Fig. 8). As heterogeneity depends on the scale and the contrast level used, it was defined as the number of patches at the optimal contrast level (i.e. 4th) and scale (i.e. 123 ha) for endemic richness. Fig. 8 confirmed that heterogeneous landscapes comprised an important representation of agricultural and urban areas in the study area, indicating that the process of forest fragmentation was mainly responsible for the resulting landscape heterogeneity. In such heterogeneous areas, then, the size and connectivity of forest fragments tend to take lower values. The small size of the forest patches and their relative proximity to agricultural and urban areas could be associated with a higher presence of human activities on forest. All this leads us to suspect that the effects of forest fragmentation on endemic soil fauna are explained by factors that are well known to affect diversity (such as patch size, patch connectivity, human frequentation, and grazing). The fact that effects of these factors are particularly apparent for narrowly distributed species reflects the usual sensitivity of these species to environmental changes.

Discussion and conclusions

The effect of landscape heterogeneity was especially evident on species occurrence and on endemic richness for collembolans. The multilevel approach defined the contrast level and spatial scale of landscape heterogeneity which affected Collembola. For the species occurrence analysis, this grain determined the regional

Fig. 5. a) Spectral band 3 of the TM image of Arize. b) Segmented image at the 2nd contrast level that correspond to the optimal response of species occurrence, from Mantel test. c) Segmented image at the 4th contrast level that correspond to the optimal response of the number of endemic species, from multiple regression analysis. d) Number of patches calculated from the segmented image which is showed in Fig. 5c; since this landscape descriptor was correlated with endemic richness (r = − 0.84, p < 0.001), it served as an inverse indicator of endemic richness.

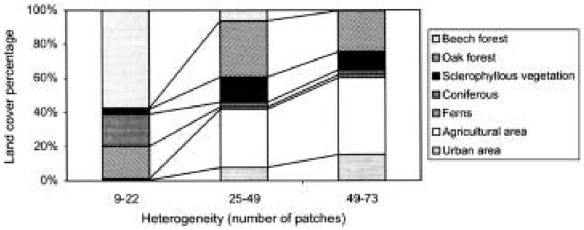

Fig. 8. Land cover percentage against landscape heterogeneity. Landscape heterogeneity is represented here by the number of patches at the 4th contrast level. The subdivision in three degrees of landscape heterogeneity is such that each one of these classes considers an equal number of landscapes surrounding the sampling site. See text for a detailed explanation.

habitat of the assemblage, in other words, the manner in which collembolan assemblages respond to landscapes.

Remotely sensed imagery was found to be adequate for landscape description that partially explained valuable parameters of collembolan assemblages. At present, there is increasing interest in testing the reliability of assessing biodiversity by satellite images (Stoms and Estes 1993, Innes and Koch 1998, Turner et al. 2001). A strength of our approach is that the multilevel procedure uses unsupervised land information, that is, it is not necessary to produce interpreted land information (such as land cover classification) reducing the length and costs of analysis. Moreover, the regression model can be extrapolated to the overall image in order to map the degree of endemism by means of the number of patches because this is an inverse indicator of endemic richness. Such spatial models can be useful to propose central boundaries for conservation areas on a scientific basis and at minimal cost (Hudson 1991, Jennings 2000, Stoms 2000).

Our results indicated that the lowest spatial scale did not properly evaluate patch statistics and thus yielded in a low correlation at all contrast levels. The scale of 123 ha gave similar results of 404 ha indicating that landscape pattern at intermediate scale contained the major part of spatial variance of the larger scale, though the area of intermediate scale only represented a 30% of the larger scale. This indicates that the definition of spatial scales to characterise landscape heterogeneity is of primary importance to detect the community response. The use of higher-resolution satellite sensors (e.g. IKONOS, SPOT-5 HRG) may help to identify optimal spatial scales; however, a microhabitat spatial analysis at the stand scale might also reveal finer optimal scales, where other levels of organization could play the main role.

Ongoing research (Chust et al. unpubl.) is directly dealing with the scale problem to define the optimal spatial scales of influence and the use of the derived models to predict biodiversity values. In that study, landscape descriptors were based on vegetation and land cover classification at multiple spatial scales, and therefore, the processing of multispectral images was larger. Working with the same Collembola data, they also found that heterogeneity, measured as the standard deviation of a radiometric vegetation index in a defined range of spatial scales, affected negatively endemic richness. The multiscale and multilevel approaches are conceptually different; while the first approach seeks to estimate the area of influence, the second attempts to identify the grain of landscape unit definition by which assemblages and biodiversity are affected. However, the landscape pattern may converge in a defined range of scales and contrast levels, in particular in that range where fauna is affected. For Collembola species in the Arize, the optimal models explained a similar amount of variance, ca 72%, for both multiscale and multilevel approaches, indicating that, in this case, the reliability of the two spatial models is similar.

In contrast with the multiscale approach, another potential application of the multilevel analysis, based on remote sensing, is the production of a land cover classification based on arthropod-centred perspective. The method of image segmentation has been applied to land cover classification (e.g. Lobo 1997), where the segmentation level is selected from human-centred perspective. We suggest that landscape units could be defined through the multilevel approach for land cover classification by selecting the community's optimal level. Arthropod-centred classifications of habitat types might be more useful to designate reserve networks than are current human-centred cartographies.

Acknowledgements – The authors wish to acknowledge the contribution of A. Lopès and R. Fjørtoft for their valuable technical support in image segmentation. Guillem Chust was supported by a grant from the Univ. of Barcelona (Spain).

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Appendix 1. List of Collembola species, and their habitat preferences, collected from the massif of Arize.

Species	Habitat	Species	Habitat
Anurida sp.*	FS	*Monobella grassei*	FL
Anurida granaria	OH	*Monobella pyrenaica**	FSF
Arrhopalites sp.	FL	*Mucrella acuminata**	FSF
Bilobella aurantiaca	FL	*Neelus murinus*	L
Brachystomella parvula	OH	*Neonaphorura duboscqi*	S
*Cassagnaudina coiffaiti**	FLB	*Oncopodura crassicornis*	S
Ceratophysella armata	FL	*Onychiurus ariegicus**	FS
Ceratophysella denticulata	OH	*Onychiurus* gr. *minutus* 1*	FS
Cryptopygus debilis	FLF	*Onychiurus* gr. *minutus* 2*	FSF
*Deutonura deficiens**	FL	*Onychiurus* gr. *minutus* 3*	FSF
Dicyrtomidae sp.	-	*Onychiurus* gr. *minutus* 4*	FSQ
Dicyrtomina ornata	L	*Onychiurus insubrarius*	FS
Dicyrtomina sp.	L	*Onychiurus pseudogranulosus*	FL
Entomobrya nivalis	V	*Paratullbergia callipygos*	FS
Entomobrya sp.	V	*Parisotoma notabilis*	Ub
Folsomia quadrioculata	L	*Protaphorura* gr. *armata*	Ub
Folsomia candida	Ub	*Pseudachorutes parvulus*	FL
Folsomia decopsis	FLF	*Pseudisotoma* sp.1	FL
Folsomia manolachei	Ub	*Pseudisotoma* sp.2	FLF, FSF
Folsomia multiseta	FL	*Pseudosinella duodecimoculata*	FLF, OH
Folsomia sensibilis	FLF	*Pseudosinella alba*	FL
Folsomia sp.1*	FSF	*Pseudosinella decipiens*	FL
Folsomia sp.2*	FSF	*Pseudosinella* sp.*	FLF
*Friesea cauchoisi**	FSF	*Rusekella peyrei**	FLF
*Friesea troglophila**	FSQ	*Schaefferia ariegica**	FLF
*Friesea truncata**	Ub	*Schaefferia subcaeca**	FLF
Heteromurus major	FLQ	Sminthuridae sp.1	FLQ
Heteromurus nitidus	OH, FL	Sminthuridae sp.2	FLQ
Hymenaphorura sp.*	FSF	Sminthuridae sp.3	FLQ
Isotoma viridis	OH	Sminthuridae sp.4	FLQ
Isotomiella minor	FL	Sminthurides sp.	OH
Isotomodes cf. *quadrisetosus*	S	*Sminthurinus aureus*	OH
Isotomurus cf. *palustris*	Hy	*Sminthurinus niger*	FL
*Isotomurus nebulosus**	Hy	*Sminthurinus signatus*	OH
Isotomurus prasinus	Hy, OH	*Sminthurinus* sp.1	FLQ
Kalaphorura cf. *burmeisteri*	FLQ	*Sminthurinus* sp.2	FLQ
Lepidocyrtus curvicollis	FL	*Sminthurus* sp.	-
Lepidocyrtus cyaneus	FL	*Sphaeridia pumilis*	Ub
Lepidocyrtus lanuginosus	FL	*Stenaphorura quadrispina*	S
Lepidocyrtus lignorum	FL	*Superodontella* sp.	S
Lepidocyrtus sp.	-	*Tetracanthella ariegica**	FLF
Lipothrix lubbocki	FL	*Tetracanthella recta**	FLF
Megalothorax minimus	FL	*Tomocerus flavescens*	FLQ
Megalothorax sp.*	FL, Hy	*Tomocerus minor*	Ub
Mesaphorura sp.	S	*Willemia aspinata*	FL
Micranurida sp.1	S	*Willemia* cf. *anophthalma*	FL
Micranurida sp.2	S	*Xenylla* sp.	FL
*Monobella edaphica**	FSF		

* Endemic species from the Pyrenees

Abbreviations: OH – open habitat, FL – forest litter, FS – forest soil, FLF – forest litter (*Fagus sylvatica*), FSF – forest soil (*Fagus sylvatica*), FLQ – forest litter (*Quercus*), FSQ – forest soil (*Quercus*), V – on vegetation, Ub – ubiquist, S – soil, Hy – hydrophilic, L – litter, – – not applicable (collective taxon).