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FRANCE, 2004

Changes in Collembola richness and diversity along a gradient of land-use intensity: A pan European study

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KEYWORDS

Collembola; Land-use intensity; Landscape diversity; Bioindicators

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Summary

Changes in Collembola richness and diversity along a land-use intensity gradient were studied in eight European countries (Portugal, Spain, France, Switzerland, Hungary, UK, Ireland and Finland). In each country a set of six 1 km² land-use units (LUUs) were selected forming a gradient ranging from natural forest to agricultural dominated landscapes, passing through mixed-use ones. In addition to data on Collembola, detailed information regarding landscape diversity and structure was collected for each LUU. A total of 47,774 individuals were identified from 281 species. Collembola reacted not only to changes in the diversity of the landscape, but also to the composition of that diversity and the area occupied by each land-use type at each LUU. Although species richness patterns were not concordant among the different countries, the total number of species per LUU (landscape richness) was generally higher in natural forests and mixed-used landscapes, and lower in agricultural dominated landscapes. Moreover, high richness and diversity of Collembola at each LUU were associated with a diverse landscape structure, both in terms of number of patches and patch richness. Despite this comparable species richness between mixed-use landscapes and those dominated by natural forests, average species richness on forested areas (local richness) decreased along the gradient, showing that forest patches on mixed-use landscapes support a lower richness than in landscapes dominated by forest. This aspect is important when addressing the role of native forests in structuring biodiversity in disturbed and fragmented landscapes. Although a diverse landscape can support a high biodiversity, the results suggest that intensive fragmentation should be avoided with the risk of collapsing local species richness with the consequent result for regional biodiversity.

Introduction

Land-use change is one of the primary factors determining patterns of biodiversity of soil organisms at local and regional levels (Lavelle et al., 1997; Bengtsson, 2002). Human-induced disturbances connected to land-use practices, which often result in different levels of soil use intensity, may influence biodiversity positively or negatively, although those which have been used over the last century are usually connected with a loss of species (Bengtsson et al., 2000).

Understanding the impact on biodiversity due to changes in land-use practices over spatial and temporal scales is essential for the development and implementation of effective measures to preserve biodiversity in human-disturbed landscapes. Only through the existence of appropriate monitoring programmes comprising a

‘good set’ of biodiversity and ecological indicators and adequate sampling schemes can this knowledge be acquired and refined (McGeoch, 1998; Niemela, 2000).

Collembola can be considered good candidates to be included as biodiversity indicators among soil fauna in an “indicator shopping basket” (Stork, 1995). Not only they are well represented in the soil system in terms of diversity, but they also respond to a variety of environmental and ecological factors, like changes in soil chemistry, microhabitat configuration, and forestry and agricultural practices (Hopkin, 1997).

Despite the existing valuable information, most previous studies were conducted at relatively small spatial-scales, often at the ‘habitat’ level, which makes it difficult to extrapolate these findings to large-scale landscape scenarios. Studies aiming to evaluate the degree of change in Collembola diversity patterns induced by land-use intensification at the landscape scale are scarce (Chust et al., 2003a, b; Ponge et al., 2003), highlighting the need for further information on the response of soil fauna to land-use at this spatial level.

As a part of a broader EU-funded project (‘Biodiversity assessment tools—BIOASSESS’, EVK4-1999-00280), this study helps to fill this gap, by analysing the response of Collembola communities to a gradient of land-use units (LUUs), ranging from forest to agricultural-dominated ones, established in eight European countries representing different biogeographic regions. Specifically this paper aims to (i) analyse if the response pattern of biodiversity descriptors along the established gradient is similar between countries and (ii) to detect what are the main landscape features related to land-use explaining patterns in Collembola diversity.

Materials and methods

Study areas, experimental design and sampling

Sampling was conducted in eight European countries representing different biogeographical regions: Mediterranean (Spain and Portugal), Continental (France), Alpine (Switzerland), Pannonic (Hungary), Atlantic (UK and Ireland) and Boreal (Finland). In each country, a set of six 1 km² LUU1–6 were selected in an area where the characteristic vegetation type of the biogeographical region was represented. Each set of LUUs formed a gradient of land-use intensity ranging from forest-dominated LUUs to ones dominated by agriculture. The percentage cover of forest and open areas (agricultural crops, grassland/pastures) in each LUU per country are indicated in Fig. 1.

At each LUU a grid of 16 sampling points, separated 200m from each other, was established. At each sampling point Collembola were sampled by taking a soil core (5 cm diameter) including the organic horizon (when present) plus 5 cm in depth of the mineral soil. Collembola were extracted using dynamic behavioural methods (i.e., Berlese or Macfadyen) and they were identified to the species level. Sampling was done in the spring of 2001 (France) or spring of 2002 (other countries).

Data analyses

Biodiversity patterns and relationships with landscape metrics were analysed at the LUU level (sum of the 16 samples inside each LUU). Biodiversity descriptors estimated were: species richness, Shannon, Evenness, Margalef, Simpson, Log a, Jack Knife and Whittaker β -diversity. A concordance analysis (Zar, 1996) was performed to compare the pattern of each descriptor among countries.

Landscape variables were obtained by remote sensing techniques using fused images derived from a Landsat 7 ETM satellite image with good spectral information and an IRS (1C or 1D, depending on the availability) image with good spatial resolution (5m re-sampled). Both the multispectral and panchromatic images were chosen from a timeframe to cover the main vegetation period between end of May and September. The 5m resolution fused product was visually interpreted and digitised using the software ArcView (version 3.x, ESRI, US) to extract the following land-use classes: coniferous, broadleaved, mixed forest with closed, open, and very open stands, agro-forestry, artificial surfaces like cities and roads, open spaces with no vegetation, agricultural crops, agricultural and natural grasslands, shrub land and heath land, wetland, and water bodies. These land-use classes followed a standardised protocol developed for the BioAssess project to ensure comparability of the results across the countries. Landscape structure in each LUU was quantified using four metrics: **NP**—number of patches of each land-use class existing in the landscape, **AREA**—percentage of area covered by each class; **AREA_MN**—mean patch area of each class, **PR**—patch richness, i.e., represents the number of classes in the landscape. All metrics were calculated using Fragstats (version 3.3, UMASS, US).

Relationships between biodiversity descriptors and landscape metrics were determined using partial correlation values, using country as a covariable (to account for biogeographic and country level variance when looking at the relationship with land-use). The visualisation of these relationships was achieved with a partial Redundancy Analysis (RDA) also using country as a co-variable. Furthermore, a GLM modelling of each

biodiversity descriptor, using sample scores from RDA axis 1 as explanatory variable, was performed; the quadratic function and the Log as link function were used in the analyses (Leps and Smilauer, 2003).

All classical statistical analyses were done using STATISTICA 6.0 software package (StatSoft, 2001) and all multivariate analyses and GLM modelling were done using CANOCO 4.5 software (Ter Braak and Smilauer, 2002).

Results

Biodiversity patterns along the land-use gradient

A total of 47 774 specimens were collected and identified into 281 species. Changes in the number of species and other species richness measures (Margalef, Log α and Jack Knife) along the land-use gradient did not follow a clear similar pattern in every country (Table 1). However, with the exception of Spain, there was a tendency for mixed-use landscapes (LUU3–4) to present similar or even higher number of species when compared to LUU1. Low species numbers tended to occur in forest plantations (mainly displayed in LUU2) or in agricultural dominated areas. This trend is visible in the concordance analysis (Fig. 2a), although no significant differences were obtained, indicating that the pattern was not statistically similar among the countries.

Species diversity descriptors (Shannon and Simpson), although less discriminative than richness measures, showed an oscillating pattern, with a tendency to increase along the gradient (Table 1). Concordance analysis showed this trend, but no significant differences were obtained here either (Fig. 2b). Whittaker beta diversity presented lower values on forest dominated LUUs and higher values on those LUUs representing mixed-use and agricultural dominated landscapes (e.g., LUU4–6) (Table 1). The similarity of this pattern among all countries is given by the significant differences ($P < 0.01$) found on concordance analyses (Fig. 2c).

Landscape features governing biodiversity along the land-use gradient

Partial correlations with land-use metrics. The decrease of forested area along the land-use gradient (Fig. 1) showed no significant relation with the number of species identified at each LUU (Table 2). The possible loss of 'forest' species in LUUs dominated by grassland areas is partially compensated for, if not surpassed, by

the number of species more common in open habitats. This was a feature common to all countries (although less marked in Portugal and Finland – where the percentage of forested areas is high in most of the LUUs), with the proportion of species typical of open habitats increasing along the land-use gradient.

This pattern was confirmed by significant positive partial correlation values between the average number of species on forested or open sampling points with the percentage of area covered by the corresponding land-use type at each LUU (Table 3). Concordance analysis also reflected this trend, with a decrease of the average species number in forest habitats along the land-use gradient and the simultaneous increase of the average number of species on open habitats (Fig. 2d). Significant differences were found on both concordance analyses, indicating that both patterns were similar among countries. However, and except for Hungary, this increase in species richness in open habitats along the gradient was more evident on grassland or pasture areas than on arable fields. This is confirmed by the significant negative correlation between the percentage of agricultural area with the total number of species (Table 2).

RDA and GLM. The relationship between biodiversity descriptors and the calculated land-use metrics can be visualised from the biplot resulting from the partial RDA (Fig. 3a). Land-use metrics explained 24.8% of total variability of the response data (inter-sample variability was 20.5% and country explained 54.7% of total variation), and the significance of this relationship was given by the result of the Monte Carlo permutation test (Axis1 – eigenvalue = 0.186, $F = 18.77$, $P < 0.01$).

It is possible to observe an increase in the number of patches and in the area covered by grassland/scrubland and the associated decrease in the forest cover area from right to left along Axis 1 (Fig. 3a). This is accompanied by an increase in land-use richness, thus contributing to a general increase in most Collembola richness and diversity measures. With the exception of β -diversity, all these biodiversity descriptors were not associated to the area covered by arable fields, positioned along Axis 2.

GLM fit of the different descriptors (Figs. 3b,c), using sample scores from Axis 1 of RDA as explanatory variable, allows a better visualization and interpretation of the relationship between the two sets of variables. All models were significant (Table 4) and the “optimum” values for all descriptors presented a negative score, showing the positive association with the increase of the area and number of patches of open land-use types.

Discussion

Collembola diversity across the land-use gradient

Changes operated on the landscape across the selected land-use gradient significantly influenced Collembola richness and diversity patterns. In each country, differences across the LUUs reflected, among other features, changes in the dominant land-use type or types. Therefore differences in Collembola diversity when comparing the several LUUs were expected since this group of organisms is known to react to changes in land-use (Ponge, 1993; Filser et al., 1996; Lauga-Reyrel and Deconchat, 1999).

The pattern observed on the several biodiversity descriptors along the land-use gradient was not common to all countries. Despite the tendency for LUUs dominated by natural non-managed forest (LUU1) and/or mixed-used landscapes to have the highest species richness at LUU level, the absence of a significant concordance in the patterns along the gradient can be attributed mainly to site-specific variation within each country. Although site-selection was done following the same criterion, the unavoidable geographical differences in landscape configuration led to discrepancies in the spectrum of land-use cover along the gradient in each country. As a consequence, those LUUs having higher percentage cover of land-use types often associated to impoverished Collembola communities, namely crop areas, presented a decrease in species richness. The low number of species in arable areas has been reported by several authors (Heisler and Kaisser, 1995; Alvarez et al., 2000, 2001), a fact connected to the type and frequency of management-induced disturbances occurring on these areas. In this study the situation in Ireland can be used to illustrate this point: LUU4, being a mixed-use unit, would be expected to have a higher species number; however, since crop areas occupy almost 50% of the area (Fig. 1), species richness dropped to a level similar to that found in LUU6 (Table 1).

Landscape features driving Collembola diversity

This study indicates that the change in species richness at LUU level along the gradient was not simply related to the percentage of forest cover, which prompts the question of which landscape related factors might regulate Collembola diversity at this larger and more complex spatial scale. In relation to the total species richness at each LUU, the reduction in the number of species on forested areas associated to the decrease in the percentage cover of this land-use type was, in most cases analysed, compensated by the increase in the number

of species appearing in open areas. As reported by Sousa et al. (2004) for a Mediterranean cork-oak system, these could be not only those “forest” species having a broad distribution, with a better dispersal capability and able to adapt to open environments, but also unique “open habitat” species. This balance contributes to the similar, or even higher, species richness occurring in mixed-use landscapes in most countries, when compared to those dominated by native forests. This could be expected, and was corroborated by the consistent pattern of a higher β -diversity in mixed-used LUUs, since more land-use types increase the diversity of microhabitats, thus being able to support the existence of a richer community with species having different ecological and habitat requirements (Rusek, 2001). However, it is important to identify which type of land-use represents those open areas in those mixed-use LUUs. Redundancy and GLM analyses indicate that grasslands, pastures and scrublands are more important than arable fields in supporting a high Collembola richness. This agrees with a previous study that considers grasslands as biodiversity “hot spots” within intensive agroecosystems (Gardi et al., 2002). These findings indicate that not only the diversity of land-use types, but also the composition of that diversity, the area occupied and the number of patches of each land-use type, are among the landscape features governing Collembola richness and diversity at larger spatial scales. This is in agreement with Dauber et al. (2003) who found that landscape diversity and percentage cover of certain land-use types could act as indicators for species richness of bees and ants at the landscape scale.

Despite this increase, or “levelling off”, of total species richness in mixed-used LUUs when compared to the corresponding LUU1, results obtained also show that the average species richness at landuse level decreases on those mixed-use landscapes. This indicates that when the landscape is fragmented (often the case in mixed-use landscapes), species richness at habitat level tends to be lower than when the landscape is dominated by that single land-use type. This was evident in several countries, particularly in forested areas, and is similar to the result obtained by Ponge et al. (2003), also for woodland areas. These authors attributed this phenomenon to a collapse of Collembola populations rather to the meaningful extinction of species, although Lauga-Reyrel and Deconchat (1999) found that forest fragmentation led to a loss of forest specialist species. In this case both situations occurred; the average number of individuals on forested areas showed also a tendency to decrease along the gradient, indicating a possible collapse of certain populations, but the loss of some forest species was also observed in some countries (Sousa, personal information). This aspect is of paramount importance, namely when considering the fragmentation of native forests and when analysing their role in structuring regional biodiversity (Chust et al., 2003a, b) and acting as main donor areas in managed landscapes, improving spatial resilience in case of disturbance (Bengtsson, 2002; Bengtsson et al., 2003).

All these observations stress the importance of being cautious in interpreting and generalizing the relationships between biodiversity and landscape composition and structure, and also indicate that country specific (or region specific) information regarding, e.g., climate, management and land-use history, should be taken into account when doing so and incorporated when developing predictive models. Nevertheless, the data presented here revealed solid trends over an extended biogeographical range, indicating that diverse landscapes (composed of several land-use types) support a similar (in some cases, higher) regional (landscape level) Collembola richness when compared to native forests.

However, this does not imply that all landscapes should be transformed into heterogeneous mosaics, since the possible maintenance or increase in species richness at landscape level could be done at cost of a decrease in habitat species richness. The important is that all this information should be considered when addressing landscape planning and land management and its effect on the conservation of soil fauna and, ultimately, the soil system as a goods and services provider (Bolger, 2001). When managing extensive and homogeneous areas (production forests, grasslands or crop areas), the maintenance of remnant patches (native vegetation), corridors or even the introduction of other patch types could be considered and implemented as active measures to improve diversity at landscape level (Samways, 1995). However, a compromise solution has to be achieved in order to avoid intensive fragmentation with the risk of collapsing local species richness with the consequent result for regional biodiversity.

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References

Alvarez, T., Frampton, G.K., Goulson, D., 2000. The role of hedgerows in the recolonisation of arable fields by epigeal Collembola. *Pedobiologia* 44, 516–526.

- Alvarez, T., Frampton, G.K., Goulson, D., 2001. Epigeic Collembola in winter wheat under organic, integrated and conventional farm management regimes. *Agr. Ecosyst. Environ.* 83, 95–110.
- Bengtsson, J., 2002. Disturbance and resilience in soil animal communities. *Eur. J. Soil Biol.* 38, 119–125.
- Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *For. Ecol. Manage.* 132, 39–50.
- Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., Nystrom, M., 2003. Reserves and resilience and dynamic landscapes. *Ambio* 32, 389–396.
- Bolger, T., 2001. The functional value of species biodiversity—a review. *Biology and environment. Proc. R. Irish Acad.* 101B, 199–224.
- Chust, G., Pretus, J.L., Ducrot, D., Bedos, A., Deharveng, L., 2003a. Identification of landscape units from an insect perspective. *Ecography* 26, 257–268.
- Chust, G., Pretus, J.L., Ducrot, D., Bedos, A., Deharveng, L., 2003b. Response of soil fauna to landscape heterogeneity: determining optimal scales for biodiversity modeling. *Conserv. Biol.* 17, 1712–1723.
- Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A., Wolters, V., 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agr. Ecosyst. Environ.* 98, 321–329.
- Filser, J., Lang, A., Mebes, K.-H., Mommertz, S., Palojarvi, A., Winter, K., 1996. The effect of land use change on soil organisms – an experimental approach. *Verh. Ges. Ökol.* 26, 671–679.
- Gardi, C., Tomaselli, M., Parisi, V., Petraglia, A., Santini, C., 2002. Soil quality indicators and biodiversity in northern Italian permanent grasslands. *Eur. J. Soil Biol.* 38, 103–110.
- Heisler, C., Kaiser, E.-A., 1995. Influence of agricultural traffic and crop management on collembola and microbial biomass in arable soil. *Biol. Fertil. Soils* 19, 159–165.
- Hopkin, S.P., 1997. *Biology of the Springtails*. Oxford University Press, Oxford.
- Lauga-Reyrel, F., Deconchat, M., 1999. Diversity within the Collembola community in fragmented coppice forests in south-western France. *Eur. J. Soil Biol.* 35, 177–187.

- Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., Heal, O.W., Dhillon, S., 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. *Eur. J. Soil Biol.* 33, 159–193.
- Leps, J., Smilauer, P., 2003. *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press, Cambridge.
- McGeoch, M.A., 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biol. Rev.* 73, 181–201.
- Niemela, J., 2000. Biodiversity monitoring for decision making. *Ann. Zool. Fennici* 37, 307–317.
- Ponge, J.-F., 1993. Biocenoses of Collembola in Atlantic temperate grass-woodland ecosystems. *Pedobiologia* 37, 223–244.
- Ponge, J.-F., Gillet, S., Dubs, F., Fedoroff, E., Haese, L., Sousa, J.P., Lavelle, P., 2003. Collembolan communities as indicators of land use intensification. *Soil Biol. Biochem.* 35, 813–826.
- Rusek, J., 2001. Microhabitats of Collembola (Insecta: Entognatha) in beech and spruce forests and their influence on biodiversity. *Eur. J. Soil Biol.* 37, 237–244.
- Samways, M.J., 1995. *Insect Conservation Biology*. Chapman & Hall, London.
- Sousa, J.P., Gama, M.M.da, Pinto, C., Keating, A., Calh a, F., Lemos, M., Castro, C., Luz, T., Leit o, P., Dias, S., 2004. Effects of land-use on Collembola diversity patterns in a Mediterranean landscape. *Pedobiologia* 48, 609–622.
- StatSoft Inc, 2001. *STATISTICA (Data Analysis Software System), Version 6*. Tulsa, OK, USA.
- Stork, N.E., 1995. Measuring and monitoring arthropod diversity in temperate and tropical forests. In: Boyle, T.J.B., Boontawee, B. (Eds.), *Measuring and Monitoring Biodiversity in Tropical and Temperate Forests*. Center for International Forestry Research, Bogor, pp. 257–270.
- Ter Braak, C.J.F., Smilauer, P., 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5)*. Microcomputer Power, Ithaca, NY.
- Zar, J.H., 1996. *Biostatistical Analysis*, third ed. Prentice-Hall International, London.

Legends of figures

Figure 1. Percentage of area occupied by the major land-use types (forest, shrubland, grassland/pasture, agricultural crops and others) at each land-use unit. Values calculated using remote sensing information based on patch-type data.

Figure 2. Sum of ranks for the several biodiversity descriptors along the land-use gradient based on the concordance analyses (see text for details). (a) No. of taxa, Margalef, Log Alfa and Jack-Knife indices; (b) Shannon and Simpson diversity indices; (c) Whittaker Beta diversity and (d) average number of species on sampling points from forested or open habitats. Significant differences for the concordance analysis (P-value) are indicated in the corresponding lines.

Figure 3. Graphical representation of the results from the partial Redundancy Analysis performed on the “LUU vs biodiversity descriptors” and “LUU vs land-use metrics” matrices. (a) Biplot representing biodiversity descriptors and land-use metrics; (b) GLM fit for Margalef, Log Alfa, Shannon, Simpson and Whittaker Beta diversity indices; (c) GLM fit for no. of taxa and Jack-Knife richness. See text and [Table 4](#) for details.

Table 1. Biodiversity descriptors along the land-use gradient for each country

| | No of species | | | | | | | | Abundance | | | | | | | | |
|-----------------------------|---------------|-----------|-----------|------------|-----------|-----------|-----------|-----------|--|-------------|--------------|-------------|--------------|-------------|------------|-------------|-------------|
| | PT | SP | FR | CH | HU | UK | IR | FIN | PT | SP | FR | CH | HU | UK | IR | FIN | |
| LUU1 | 35 | 56 | 43 | 54 | 22 | 7 | 28 | 26 | LUU1 | 1103 | 4004 | 1682 | 1727 | 459 | 78 | 681 | 897 |
| LUU2 | 11 | 33 | 42 | 53 | 33 | 10 | 25 | 24 | LUU2 | 312 | 4512 | 2097 | 2317 | 551 | 152 | 600 | 911 |
| LUU3 | 25 | 38 | 51 | 44 | 27 | 16 | 25 | 30 | LUU3 | 272 | 1246 | 2065 | 1578 | 900 | 76 | 665 | 887 |
| LUU4 | 28 | 23 | 44 | 54 | 21 | 16 | 13 | 29 | LUU4 | 611 | 548 | 1014 | 1612 | 373 | 34 | 333 | 775 |
| LUU5 | 30 | 22 | 42 | 46 | 34 | 11 | 23 | 27 | LUU5 | 352 | 1060 | 1478 | 1395 | 695 | 46 | 210 | 683 |
| LUU6 | 21 | 22 | 47 | 46 | 35 | 10 | 9 | 25 | LUU6 | 1689 | 472 | 1402 | 1657 | 1241 | 25 | 46 | 251 |
| All LUUs | 58 | 79 | 88 | 104 | 67 | 32 | 43 | 47 | All LUUs | 4339 | 11842 | 9738 | 10286 | 4219 | 411 | 2535 | 4404 |
| Species diversity (Shannon) | | | | | | | | | No unique species (occurring only at a single LUU) | | | | | | | | |
| LUU1 | 3.70 | 3.31 | 3.45 | 3.83 | 3.51 | 1.19 | 3.59 | 3.01 | LUU1 | 9 | 17 | 3 | 7 | 5 | 1 | 3 | 1 |
| LUU2 | 1.16 | 2.07 | 3.74 | 3.69 | 3.72 | 1.15 | 2.77 | 3.06 | LUU2 | 0 | 2 | 1 | 4 | 6 | 3 | 5 | 1 |
| LUU3 | 3.55 | 3.41 | 3.98 | 3.82 | 3.00 | 2.77 | 3.02 | 3.40 | LUU3 | 5 | 9 | 4 | 1 | 2 | 3 | 2 | 1 |
| LUU4 | 3.26 | 2.73 | 4.13 | 3.82 | 2.89 | 3.45 | 1.03 | 3.25 | LUU4 | 3 | 3 | 3 | 8 | 1 | 5 | 0 | 3 |
| LUU5 | 3.63 | 1.44 | 3.88 | 4.10 | 4.00 | 2.87 | 3.13 | 3.62 | LUU5 | 1 | 2 | 2 | 3 | 7 | 2 | 3 | 2 |
| LUU6 | 2.24 | 1.94 | 4.02 | 3.99 | 3.85 | 3.02 | 2.48 | 3.62 | LUU6 | 4 | 0 | 9 | 6 | 2 | 2 | 0 | 4 |
| Evenness (Pielou) | | | | | | | | | Species richness (Margalef) | | | | | | | | |
| LUU1 | 0.72 | 0.57 | 0.64 | 0.67 | 0.79 | 0.42 | 0.75 | 0.64 | LUU1 | 4.85 | 6.63 | 5.65 | 7.11 | 3.43 | 1.38 | 4.14 | 3.68 |
| LUU2 | 0.34 | 0.41 | 0.69 | 0.64 | 0.74 | 0.34 | 0.60 | 0.67 | LUU2 | 1.74 | 3.80 | 5.36 | 6.71 | 5.07 | 1.79 | 3.75 | 3.38 |
| LUU3 | 0.76 | 0.65 | 0.70 | 0.70 | 0.63 | 0.69 | 0.65 | 0.69 | LUU3 | 4.28 | 5.19 | 6.55 | 5.84 | 3.82 | 3.46 | 3.69 | 4.27 |
| LUU4 | 0.68 | 0.60 | 0.76 | 0.66 | 0.66 | 0.86 | 0.28 | 0.67 | LUU4 | 4.21 | 3.49 | 6.21 | 7.18 | 3.38 | 4.25 | 2.07 | 4.21 |
| LUU5 | 0.74 | 0.32 | 0.72 | 0.74 | 0.79 | 0.83 | 0.69 | 0.76 | LUU5 | 4.95 | 3.01 | 5.62 | 6.21 | 5.04 | 2.61 | 4.11 | 3.98 |
| LUU6 | 0.51 | 0.44 | 0.72 | 0.72 | 0.75 | 0.91 | 0.78 | 0.78 | LUU6 | 2.69 | 3.41 | 6.35 | 6.07 | 4.77 | 2.80 | 2.09 | 4.34 |
| Log alfa | | | | | | | | | Simpson (1/D) | | | | | | | | |
| LUU1 | 6.31 | 8.28 | 8.04 | 9.58 | 4.37 | 1.86 | 5.16 | 4.52 | LUU1 | 7.14 | 4.73 | 5.84 | 7.23 | 8.83 | 1.61 | 8.69 | 5.06 |
| LUU2 | 1.84 | 4.16 | 7.44 | 9.10 | 6.82 | 2.40 | 4.20 | 3.93 | LUU2 | 1.49 | 2.52 | 8.88 | 6.67 | 7.50 | 1.49 | 4.11 | 5.99 |
| LUU3 | 6.02 | 6.40 | 9.46 | 7.84 | 4.75 | 6.19 | 4.48 | 5.20 | LUU3 | 7.05 | 5.66 | 10.25 | 8.59 | 4.97 | 4.49 | 5.07 | 7.50 |
| LUU4 | 5.04 | 4.31 | 9.38 | 9.56 | 4.08 | 11.80 | 2.15 | 5.22 | LUU4 | 5.21 | 3.52 | 11.27 | 7.84 | 4.82 | 9.67 | 1.39 | 6.14 |
| LUU5 | 6.54 | 3.43 | 8.05 | 8.08 | 6.65 | 5.28 | 5.33 | 5.11 | LUU5 | 8.16 | 1.63 | 10.31 | 10.49 | 11.89 | 6.16 | 5.67 | 8.58 |
| LUU6 | 2.89 | 3.55 | 9.37 | 8.24 | 6.41 | 6.18 | 2.60 | 5.56 | LUU6 | 3.45 | 2.25 | 11.60 | 8.24 | 9.29 | 9.09 | 4.84 | 8.80 |
| Jack Knife | | | | | | | | | Beta diversity (Whittaker) | | | | | | | | |
| LUU1 | 36 | 57 | 51 | 55 | 23 | 11 | 29 | 27 | LUU1 | 2.92 | 3.13 | 2.09 | 3.13 | 4.97 | 4.33 | 3.19 | 1.68 |
| LUU2 | 11 | 34 | 50 | 54 | 33 | 15 | 25 | 24 | LUU2 | 4.50 | 2.91 | 2.28 | 2.35 | 4.08 | 3.71 | 4.06 | 2.07 |
| LUU3 | 26 | 39 | 59 | 44 | 27 | 25 | 25 | 31 | LUU3 | 4.19 | 4.24 | 3.53 | 3.12 | 3.65 | 6.11 | 3.65 | 2.40 |
| LUU4 | 28 | 23 | 54 | 56 | 21 | 26 | 14 | 30 | LUU4 | 3.82 | 4.94 | 3.92 | 4.57 | 6.15 | 8.48 | 5.12 | 2.71 |
| LUU5 | 31 | 22 | 53 | 47 | 35 | 18 | 24 | 28 | LUU5 | 4.22 | 4.77 | 3.00 | 3.11 | 4.39 | 6.33 | 4.75 | 2.66 |
| LUU6 | 22 | 21 | 58 | 47 | 35 | 14 | 9 | 25 | LUU6 | 3.54 | 7.38 | 3.00 | 2.89 | 4.83 | 9.67 | 5.86 | 3.17 |

Country codes: Portugal—PT; Spain—SP; France—FR; Switzerland—CH; Hungary—HU; United Kingdom—UK; Ireland—IR; Finland—FIN.

Table 2. Partial correlations (using country as co-variable) between biodiversity descriptors and land-use metrics

| | No species | Margalef | Log α | Jack-Knife | Shannon | Pielou | Simpson | β -diversity | Abundance |
|----------|------------|----------|--------------|------------|---------|--------|---------|--------------------|-----------|
| For_NP | 0.37* | 0.37* | 0.38** | 0.39** | 0.35* | 0.17 | 0.31* | -0.36* | 0.16 |
| For_%NP | -0.02 | -0.09 | -0.10 | -0.02 | -0.10 | -0.17 | -0.08 | -0.41** | 0.07 |
| For_Area | -0.03 | -0.09 | -0.14 | -0.05 | -0.10 | -0.18 | -0.22 | -0.44** | 0.08 |
| For_AMN | -0.29* | -0.32* | -0.39** | -0.33* | -0.32* | -0.26 | -0.36* | -0.10 | -0.16 |
| GPS_NP | 0.21 | 0.27 | 0.30* | 0.16 | 0.21 | 0.17 | 0.12 | 0.25 | 0.07 |
| GPS_%NP | -0.08 | 0.00 | -0.01 | -0.14 | 0.02 | 0.10 | -0.11 | 0.38** | -0.10 |
| GPS_Area | 0.27 | 0.34* | 0.35* | 0.31* | 0.28 | 0.19 | 0.35* | 0.19 | 0.01 |
| GPS_AMN | 0.14 | 0.17 | 0.17 | 0.21 | 0.13 | 0.05 | 0.23 | 0.03 | -0.03 |
| Agr NP | 0.02 | 0.05 | 0.11 | 0.04 | 0.11 | 0.12 | 0.28 | 0.14 | -0.05 |
| Agr_%NP | -0.05 | -0.01 | -0.05 | -0.00 | 0.01 | 0.06 | 0.18 | 0.25 | -0.10 |
| Agr_Area | -0.35* | -0.34* | -0.26 | -0.35* | -0.22 | 0.03 | -0.11 | 0.47** | -0.19 |
| Agr_AMN | -0.35* | -0.32* | -0.24 | -0.36* | -0.16 | 0.16 | -0.07 | 0.54*** | -0.23 |
| PR | 0.40** | 0.48** | 0.55*** | 0.40** | 0.46** | 0.37* | 0.37* | -0.06 | 0.11 |

*P<0:05; **P<0:01; ***P<0:001.

For_forest cover; GPS_grassland+pasture+shrub cover; Agr_agricultural cover. NP_no of patches; %NP_percentage of NP; Area_% of area covered; AMN_average patch area; PR_patch richness (see text for codes).

Table 3. Partial correlations (using country as co-variable) between the average number of species and average abundance with the percentage cover of the main land-use types at each LUU

| | No. species on forest points | Abundance on forest points | No. species on open land-use points | Abundance on open land-use points |
|----------|------------------------------|----------------------------|-------------------------------------|-----------------------------------|
| For_Area | 0.40** | 0.25 | -0.58*** | -0.67*** |
| GPS_Area | -0.17 | -0.12 | 0.58*** | 0.56*** |
| Agr_Area | -0.39** | -0.33* | 0.07 | 0.26 |

*P<0:05; **P<0:01; ***P<0:001.

Codes as in [Table 2](#).

Table 4. Summary of the GLM analysis for each biodiversity descriptor: significance and optimum values (plus standard error)

| | F ratio | <i>P</i> -value | Optimum value (SE) |
|--------------------|---------|-----------------|--------------------|
| No. species | 9.63 | <0.0001 | -0.48 (0.17) |
| Margalef | 21.66 | <0.0001 | -0.98 (0.32) |
| Log α | 22.32 | <0.0001 | -2.4 (0.68) |
| Jack-Knife | 7.91 | <0.01 | -0.64 (0.21) |
| Shannon | 79.64 | <0.0001 | -1.14 (0.18) |
| Pielou | 58.75 | <0.0001 | -1.92 (0.43) |
| Simpson | 43.75 | <0.0001 | -1.64 (0.26) |
| β -diversity | 4.01 | <0.05 | Not estimated |

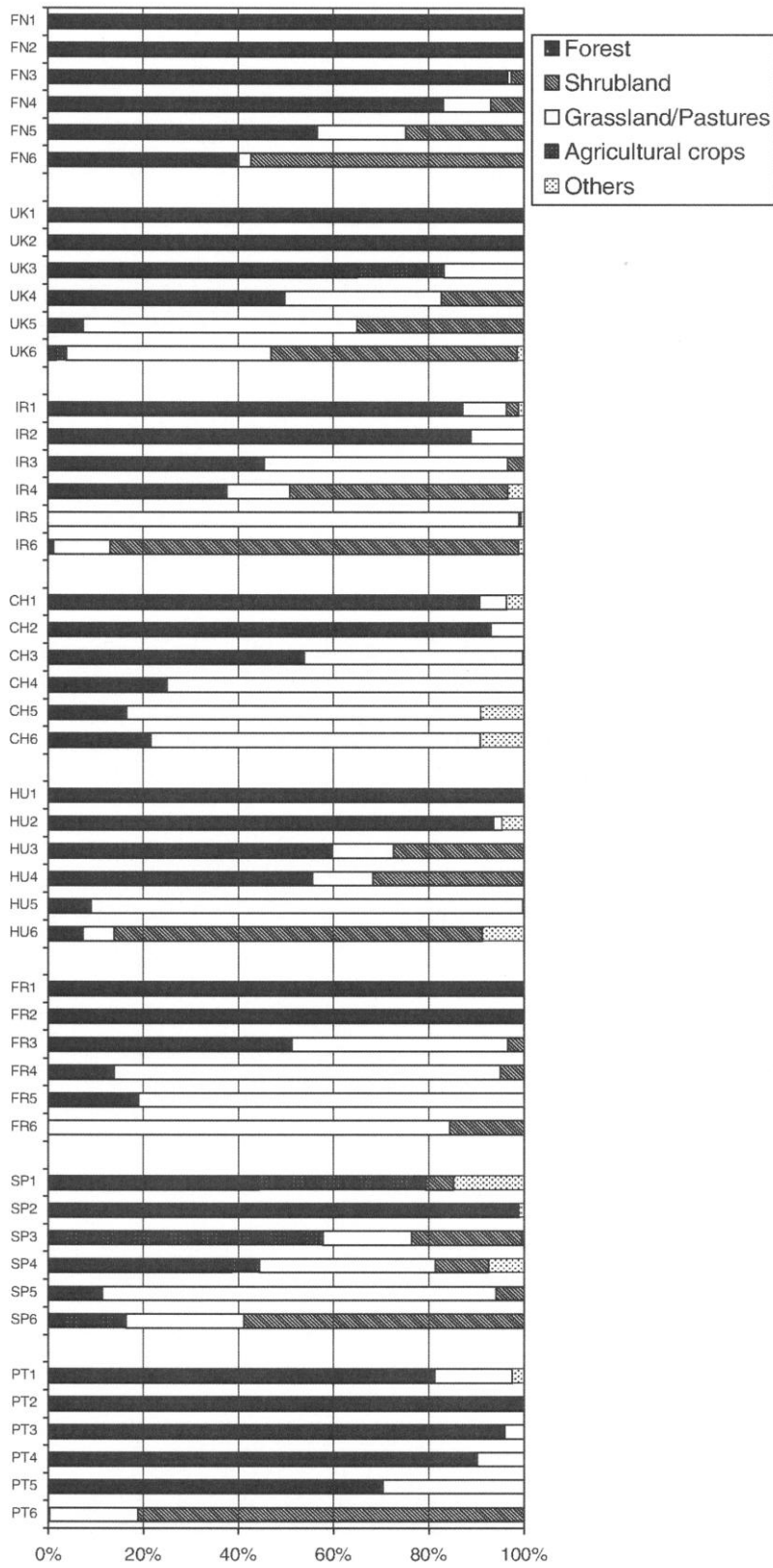


Fig. 1

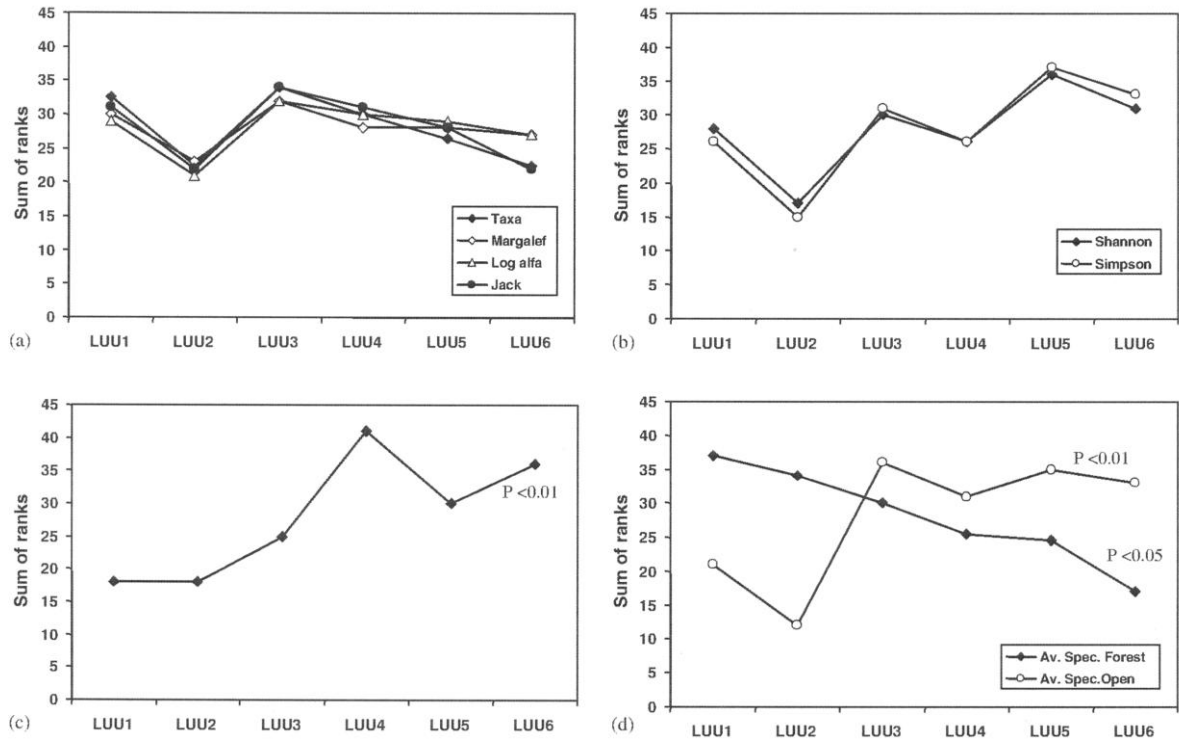


Fig. 2

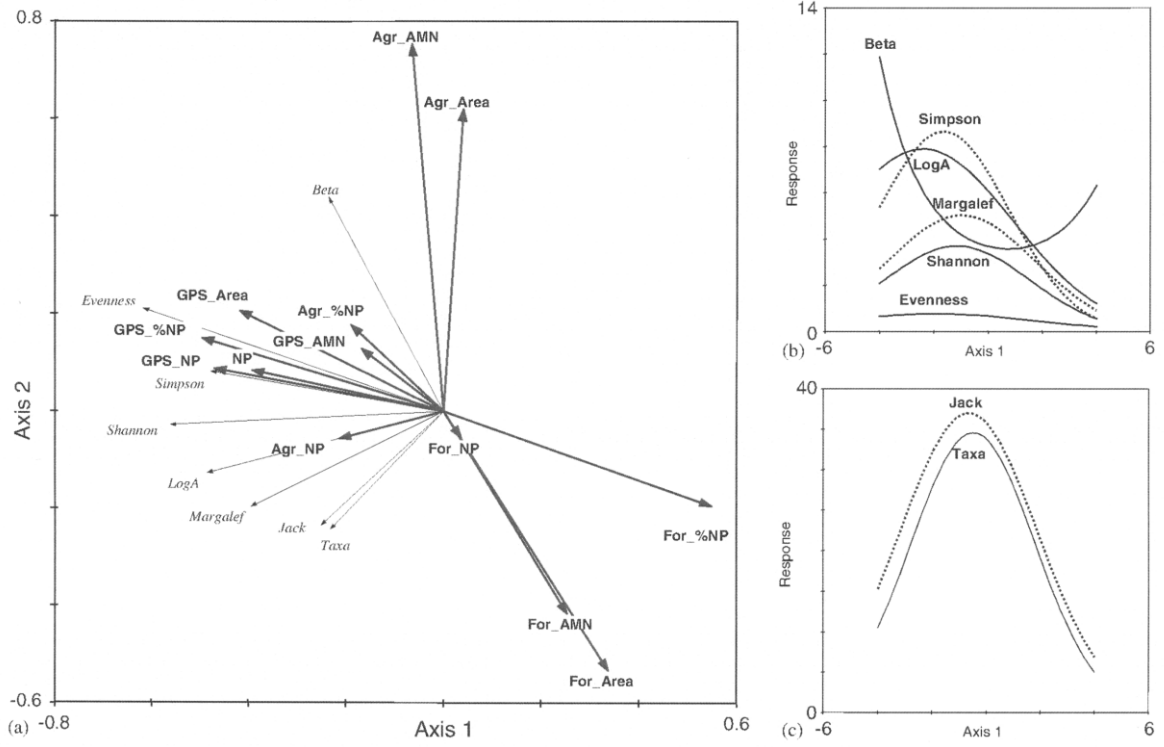


Fig. 3