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Abstract

Plant communities are affected by land-use and landscape heterogeneity and can be used as indicators of environmental change. At small-scale, species composition and species richness of plant communities are influenced by local environment and by diaspores from the surroundings. Thus they reflect the influence of both land-use type and land-use diversity. Plant community composition was studied along a gradient of agricultural disturbance in the Morvan Regional Natural Park (Burgundy, France). Six landscape units of 1 km^2 were selected along a range of increasing land-use intensity. Sixteen 0.2 m^2 sampling plots per unit were selected according to a grid-based design to estimate the percent cover of all plant species. Pattern analysis showed that local species richness increased from woodland to crop to grassland, and also increased with land-use diversity. Local plant biodiversity was maximized under intermediate disturbance intensity and minimized at low (woodland) and high (crop) disturbance levels.

Key-words: Vegetation; Biodiversity; Land-use diversity; Humus form; Land-use intensification

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1. Introduction

Plant species are good indicators of soil conditions (Dahl et al., 1967; Ellenberg et al., 1992; Lee, 1999). Natural or man-induced disturbance in soil conditions is reflected in the species composition and richness of most plant communities (Falkengren-Grerup, 1986; Pettit et al., 1995; Roem and Berendse, 2000). Some plant species are also able to modify their environment between establishment and maturity (Miles, 1985; Muys et al., 1992; Bernier, 1996) and interfere with other species through competition, biochemical control and facilitation (Facelli and Facelli, 1993; Wardle et al., 1998; Chou, 1999). Land-use history may influence soil and vegetation long after conditions for the original establishment of plant species have disappeared (Koerner et al., 1997) due to feed-back processes (Ponge, 2003), and persistence of plant organs and diaspores (Zobel and Antos, 1986; Thompson et al., 1994).

The present paper aims to discern whether local plant biodiversity expressed in terms of species richness is influenced by land-use intensification and/or landscape diversity, and whether above- and below-ground diversity follow the same trend along a gradient of land-use intensification. Land-use intensification was defined subjectively by the increasing impact of man on the landscape according to the following scale:

1. old-growth forest
2. managed forest
3. mixed landscape dominated by woodland
4. mixed landscape not dominated by a single land-use
5. mixed landscape dominated by pasture
6. mixed landscape dominated by arable crops

The choice of local plant biodiversity over regional biodiversity (Tilman, 1999; Poiani et al., 2000; Loreau et al., 2001) was due to the need to account for site factors but also for interference and facilitation processes between plant individuals and species (Hester et al., 1991a; Facelli and Facelli, 1993; Nilsson et al., 1999).

2. Material and methods

The Morvan Regional Natural Park (Burgundy, Central France) is under submontane-atlantic climate with continental influence, a mean annual rainfall of 1000 mm, an temperature of 9°C. The parent rock is granite, with moderate to strong soil acidity, and dominant humus form as mull (Perrier, 1997; Ponge et al., 2003). Forested areas (45% in the region) comprise coniferous plantations [45%, i.e. silver fir, *Abies alba* Mill., white fir, *Abies grandis* (Dougl. Ex D. Don) Lindl., Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco, spruce, *Picea abies* (L.) Karst.], and deciduous stands (55%, i.e. common beech, *Fagus sylvatica* L. and sessile oak, *Quercus petraea* (Mattusschka) Lieblein). Agricultural areas (55% in the region) consist of grassland (80%, half of which are permanent pastures and the other half temporary hay meadows) and mostly cereal crops (20%, i.e. wheat, *Triticum aestivum* L., barley, *Hordeum vulgare* L., rye, *Secale cereale* L. and Christmas trees).

Agricultural systems vary from extensive to organic farming whereas rural depopulation and forestry policies influenced the landscape over the last five decades (Plaisance, 1986). Many forests have been transformed into coniferous plantations and more recently agricultural land was afforested using national subsidies. In parallel, agriculture shifted from a short (food crop/fallow) to a long rotation system (grassland/cereal crop).

Six representative 1 km^2 landscape units were intuitively selected on the basis of regional knowledge and aerial photographs:

- Unit 1 in a 100-150 year deciduous forest landscape managed by the public sector, with natural regeneration and selection by man.

- Unit 2 in a 50 year coniferous (mainly silver fir) forest landscape managed by the public sector, with artificial regeneration (clear-cut followed by plantation). Unit 2 used to be a deciduous forest similar to Unit 1.

- Unit 3 in a landscape privately afforested 50 years ago with Douglas fir, spruce, and meadows. Remains of the old deciduous forest and some cereal crops were also present.

- Unit 4 in a mosaic of wet meadows, with some 30 years old Douglas fir and spruce.

- Unit 5 in a meadow landscape dominated by organic farming, with a rotation between meadow (6-10 years) and crop (2-4 years), with a few 20-50 year Douglas fir or spruce plantations.

- Unit 6 in an agricultural landscape dominated by conventional cereal crops with some fallow and Christmas tree.

Using aerial photographs a grid of 16 regularly spaced points (200 m mesh size) was projected on each of the six units, and retrieved using a calibrated GPS system. Each sample point was indicated by a central post used as a reference by all teams participating to the research program which involved springtails, lichens, butterflies, birds, soil macroinvertebrates, carabids, and remote sensing. The random selection of sample points was not the best method to detect vegetation patterns (Gillison and Brewer, 1985), but allowed all scientists to use the same sampling design, and comparisons between countries and taxonomic groups to be made. Vegetation was studied from July to November 2001 across a range of six nested areas (50, 25, 12.5, 5, 1 and 0.2 m^2), at fixed distance and orientation from the central post. Small-scale study of vegetation was conducted on 0.5 x 0.4 m (0.2 m^2) areas. These areas were located 10 m East from the central post. Percentage cover by the various plant species, vegetation categories (moss, lichen, herb, shrub, tree, total), stone, and litter was estimated visually to the nearest 5%.

The Humus Index was measured at each sampling plot according to Ponge et al. (2002) and Ponge et al. (2003). Waterlogging in the top 10 cm was recorded and landscape heterogeneity measured by the diversity of land-use within each unit, using Shannon (1948) formula.

Correspondence analysis (CA) was used to discern trends in the composition of plant communities (Greenacre, 1984). The principal variables were species cover, and plant categories.

Additional variables were litter and stone cover, local biodiversity, units and land-use types (Table 1), humus forms, Humus Index, and waterlogging. Discrete variables were coded as 1 or 0. To give the same weight to all parameters all variables were transformed into X = (x-m)/s + 20, x being the original value, m the mean of a given variable, s its standard deviation. The addition of a constant factor of 20 allowed all values to be positive. Following transformation, factorial coordinates of variables were interpreted directly in terms of their contribution to the factorial axes. Variables were doubled to allow for the dual nature of measurement (Greenacre, 1984).

3. Results

Mixed or herbaceous dominated landscapes (units 3 to 6) had more plant species at the local scale than forested landscapes (Table 1). The curve for local plant biodiversity followed that of land-use diversity, and increased from unit 1 to unit 4 then decreased from unit 4 to unit 6 (Fig. 1). The Spearman rank correlation coefficient between local plant biodiversity and land-use variety was significant at the 0.01 level (r_s = 0.89, d.f. = 4).

Strong differences were observed between land-uses when pooling samples (Table 1). At the local scale grassland had more plant species than arable crops, fallows being intermediate, fallows and crops having more plant species than forests. These differences were of the same order of magnitude as those observed across landscape units, but standard errors of the means were smaller. The difference between agricultural land and woodland, with a high and a low number of plant species respectively, was reduced when comparing units (Fig. 2). Species richness increased by a factor of 3 in woodland from unit 2 to 4, and decreased by a factor of 2 in agricultural land from unit 3 to 6. Species richness showed a marked decrease in arable crops along the gradient of land-use intensification, and was positively influenced by landscape heterogeneity in both woodland and agricultural land.

In the CA of plant communities[1], axis 1 was neglected because it separated only one sample with hydrophilic vegetation from all other samples. The projection of samples in the plane formed by

[1] Species list available upon request from the corresponding author

axes 2 and 3 showed three branches, i.e. woodland, grassland and arable crops, fallows being positioned according to previous land-use for the most recent or as successional stages towards woodland.

The different units were positioned in the plane of axes 2 and 3 according to the dominance of land-use types within each of them (Fig. 3). Axis 2 showed that hay meadows and pastures clearly differed from crops by a denser and richer herb vegetation. Axis 3 depicted a gradient of increasing species richness and herb cover, decreasing litter and tree cover, and decreasing Humus Index according to land-use intensification. The significance of axis 3 associated the gradient of land-use intensification from unit 1 to 6 with increasing soil biological activity, as inversely measured by the Humus Index (Ponge et al., 2002), and increasing local plant biodiversity, as expressed by species richness per 0.2 m^2. Axis 3 was significantly correlated with Humus Index ($r_s = -0.61$, $P < 10^{-4}$) and local plant biodiversity ($r_s = 0.57$, $P < 10^{-4}$).

5. Discussion

Grassland exhibited a higher level of plant biodiversity than arable crops (Fig. 2), an effect that can be explained by grazing or repeated mowing which increased nutrient cycling, created gaps, giving more chance to poorly competitive species to reach the canopy, and increased dispersion by animals or wind (Watt, 1960; Grime et al., 1987; Silverstone and Smith, 1988). Heavy grazing may, however, exert a detrimental influence on species richness (Pettit et al., 1995), whereas conventional farming may contribute to decrease plant biodiversity (Edwards, 1965). The decreasing local plant biodiversity observed in arable crops from unit 4 to 6 (Fig. 2) can be explained by a decrease in the number of landscape components, and by the absence of rotation between meadows and crops in unit 6. On the other hand, germination of dormant seeds after cultivation (Brenchley and Warington, 1930) can contribute to increase plant biodiversity when crops replaced meadows.

The land-use type did not explain all the variability observed in local plant biodiversity, since for a given land-use more heterogeneous landscapes exhibited more plant species per unit surface (Fig. 2). Strong differences in plant species composition occurred in the three habitats woodland, grassland and arable crops. Given the ability of most plant species to disperse, especially through birds and wind, the seed rain may be more diverse provided woodland, grassland and arable crops exchange diaspores at the scale of a unit. Dispersal ability (Hester et al., 1991b) and permeability of the landscape (Honnay et al., 2002) are important components of local plant biodiversity. In the Morvan region spatial heterogeneity reflects also temporal heterogeneity, through rotation between arable crops and meadows, which increased the effect of immediate dispersal (Rescia et al., 1995). In unit 4, mostly represented by small thickets and woodland contiguous to agricultural land, local plant biodiversity was high and accounted for strong landscape heterogeneity (Collinge, 1996).

Landscape diversity may have contrasting effects on soil-dwelling animal communities (Ponge et al. 2003). Above- and belowground biodiversity may reinforce each other through positive feedbacks (Perry et al., 1989; Hooper et al., 2000; Ponge, 2003). The observed decrease in springtail species richness when landscape variety increases may be related in Morvan to more rapid changes in land-use in heterogeneous than in homogeneous landscapes (Ponge et al., 2003). Plants being much more rapidly dispersed than springtails (Collembola), at least at the scale of the study unit (Hester et al., 1991b), factors which can explain changes in local biodiversity of these two taxonomic groups are not necessarily similar. However, the high nutrient status of the ecosystem could enhance biodiversity of all categories of organisms (Ponge, 2003), as was observed in unit 6. Soil fertility has been made responsive for losses of biodiversity of plants by by favouring fast-growing species (Huston, 1979; Tilman, 1982; Loreau, 1998), whereas Brandt and Rhoades (1972), Miller et al. (1977), Roem and Berendse (2000) demonstrated the contrary. We suggest that more attention should be paid to the plant toxicity of N compounds (Knight et al., 1992; Thomas et al., 1999) before claiming that nutrients are responsible for collapses in biodiversity through active competition.

Land-use type and diversity had some major effects on local plant biodiversity in the present study, although trends only were detected by CA (Benzécri, 1969; Loreau, 1998). Land-use intensification increased plant species richness by providing herbs with more light and nutrients. The highest level of disturbance (arable crops) decreased biodiversity against perennial plants and favoured annuals tolerant to agricultural practices. Compared to homogeneous ones, heterogeneous landscapes tend to include more species in the seed rain and create edge effects (Harris, 1988). As a result, the intermediate disturbance level, (hay meadows and pastures) exhibited the highest level of local biodiversity, particularly in units with high land-use diversity.

The Intermediate Disturbance Hypothesis (Connell, 1978) probably applies to vegetation (Molino and Sabatier, 2001), and to taxonomic groups with colonization rate exceeding the disturbance rate (Sheil and Burslem, 2003). The reverse is true for soil microarthropods, which benefit from a more stable environment but are vulnerable to changes in land-use (Ponge et al., 2003).

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Figure captions

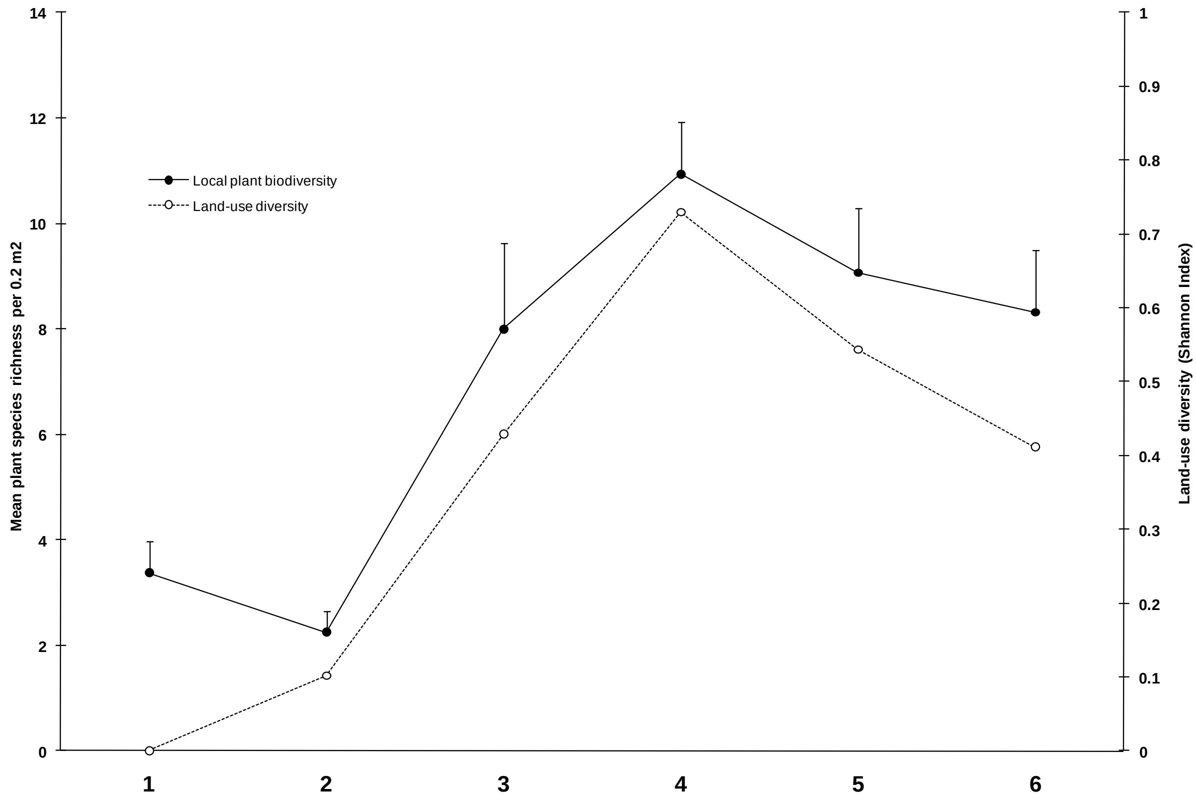
Fig. 1. Distribution of mean (± S.E.) plant species richness per 0.2 m^2 plot (local plant biodiversity) and land-use variety (Shannon Index) across six landscape units.

Fig. 2. Distribution of mean (± S.E.) plant species richness per 0.2 m^2 plot across six landscape units, in woodland, grassland and arable crops.

Fig. 3. C.A. projection of additional and some main variables along axes 2 and 3 (bold = higher; lower values).

Table 1. Land-use types and diversity indices in six landscape units (means ± standard errors S.E.)

Unit number	**1**	**2**	**3**	**4**	**5**	**6**	Plant species richness
Deciduous forest	16	1	8	0	3	0	3.57 (0.45)
Coniferous forest	0	14	2	4	2	0	3.22 (0.61)
Clearcut	0	1	0	1	0	0	
Hedgerow	0	0	0	0	1	0	
Hay meadow	0	0	4	4	4	0	13.33 (1.36)
Pasture	0	0	1	3	6	2	13.08 (0.82)
Fallow	0	0	0	1	0	5	10.33 (1.82)
Crop	0	0	1	3	0	9	7.54 (1.01)
Land-use diversity (Shannon)	0.00	0.10	0.43	0.73	0.54	0.41	
Plant species richness	3.38 (0.60)	2.25 (0.40)	8.00 (1.63)	10.94 (0.99)	9.06 (1.22)	8.31 (1.18)	


Local plant biodiversity
Land-use diversity
Mean plant species richness per 0.2 m2
Land-use diversity (Shannon Index)
0
2
4
6
8
10
12
14
0
0.1
0.2
0.3
0.4
0.5
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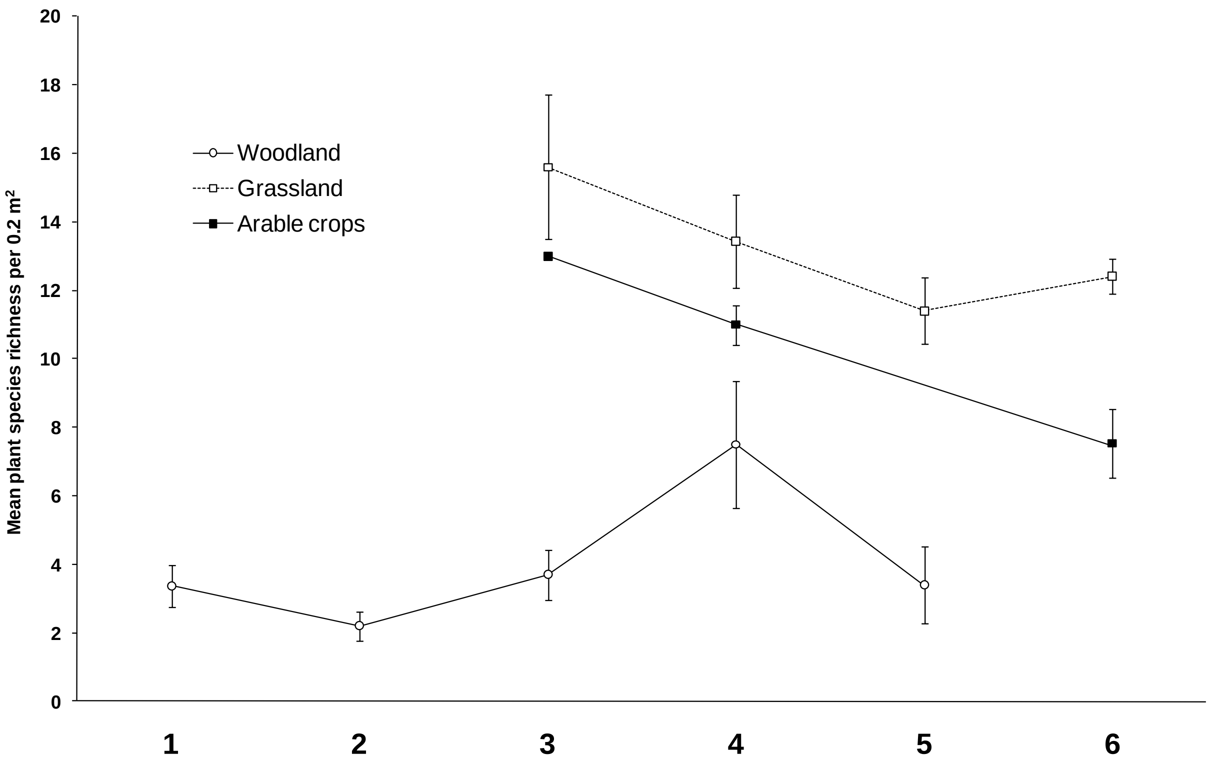
0.8
0.9
1
1
2
3
4
5
6

Fig. 1


Woodland
Grassland
Arable crops
Mean plant species richness per 0.2 m²
0
2
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6
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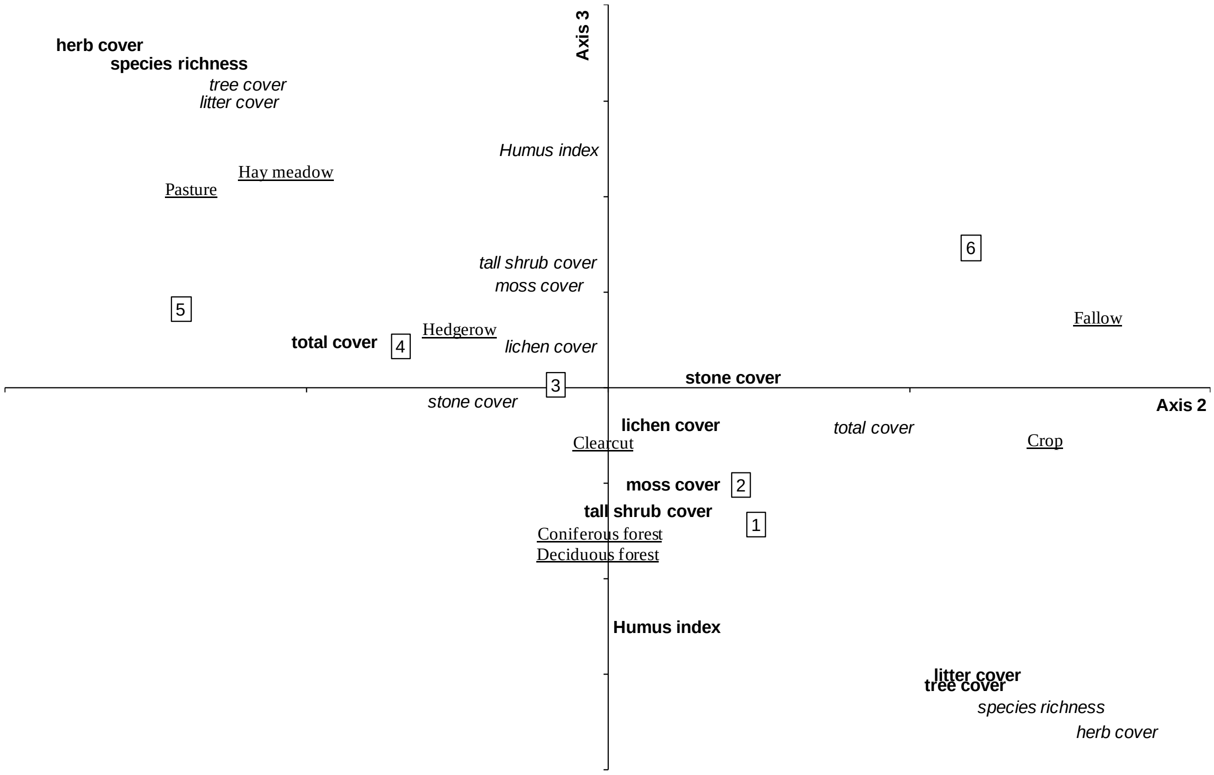
6

Fig. 2


Axis 3
herb cover
species richness
tree cover
litter cover
Humus index
Hay meadow
Pasture
6
tall shrub cover
moss cover
5
Fallow
Hedgerow
total cover
4
lichen cover
3
stone cover
stone cover
Axis 2
lichen cover
total cover
Crop
Clearcut
moss cover
2
tall shrub cover
1
Coniferous forest
Deciduous forest
Humus index
litter cover
tree cover
species richness
herb cover

1

2 Fig. 3