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Soil Macrofaunal Communities are Heterogeneous in Heathlands with Different Grazing Intensity

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ABSTRACT

Moderate grazing by cattle increases the heterogeneity of soil and vegetation. This has been suggested as an ecologically sustainable mean of managing natural environments endangered by tree encroachment, such as heathlands. Our study was performed to test the impact of grazing intensity on soil macroinvertebrate communities in heterogeneous landscapes in a private property eligible to the Natura 2000 European Network of Special Protection Areas within the Brenne Natural Regional Park (Indre, France). We sampled macroinvertebrates along a broken line crossing 5 different land-use types, from pasture to pine forest, passing through a besom heath (*Erica scoparia*) heathland at 3 levels of cattle pressure. We hypothesized that: i) litter-dwelling (mostly arthropods and mollusks) and soil-dwelling macroinvertebrates (mostly earthworms) would respond in an opposite manner to various grazing intensities, and ii) intermediate cattle pressure (pastured heath) would increase soil and community heterogeneity. The results supported the first hypothesis, which was explained by land-use impacts mediated by soil properties. However, our results supported only partly the second hypothesis since maximum dissimilarity (whether in the composition of soil macroinvertebrate communities or in soil features) was observed in only one out of the two pastured heaths where cattle pressure was intermediate.

Key Words: besom heath, cattle grazing, heterogeneity, land-use, soil macroinvertebrates

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INTRODUCTION

European heathlands occur on poor soils and are dominated by various ericaceous shrubs. They have been perpetuated by traditional management and are now protected for their patrimonial interest and biotic richness (Webb, 1998). *Erica scoparia* L., the besom heath, covers wide surfaces of more or less uniform shrubby vegetation in protected areas of south-western Europe, including France, Spain and Portugal (Bartolomé *et al.*, 2005). This monopolistic ericaceous tall shrub, known for its

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allelopathic properties (Ballester *et al.*, 1977) and tolerance to grazing (Paula and Ojeda, 2011), can accommodate more plant biodiversity under the influence of moderate cattle activity (Gachet *et al.*, 2009). Similar results have been reported for *Calluna* heath (Miles, 1981). This 'intermediate disturbance' favorableness (Denslow, 1985) is of paramount importance for the conservation or rehabilitation of heathland-dominated areas (Pakeman *et al.*, 2003).

Soil animal communities of heathland areas dominated by the besom heath (*Erica scoparia* L.) have not yet been addressed, although canopy invertebrate fauna has been studied before (Anglade and Bigot, 2001). Soil animal communities are directly impacted by vegetation through litter and roots (Ponsard *et al.*, 2000; Mitchell *et al.*, 2007; Doblas-Miranda *et al.*, 2009). However, vegetational influences on soil animal communities are also mediated by soil condition, including humus forms (Frouz *et al.*, 2008; Salmon *et al.*, 2008). We wanted to know whether soil macroinvertebrate communities were more abundant and more diversified under moderate cattle activity, as it is the case for vegetation (Gachet *et al.*, 2009). Grassy vegetation favors the abundance and species richness of soil-dwelling animals such as earthworms (Makeschin, 1997; Graefe and Beylich, 2003; Ponge *et al.*, 2013), while woody vegetation favors litter-dwelling macroarthropods (Eggerton *et al.*, 2005; Callahan Jr. *et al.*, 2006).

We hypothesized that in a heterogeneous landscape with varied cattle pressure levels, from pasture (high level) to forest (low level) and pastured heaths with intermediate level, a balance between two invertebrate groups could be observed. On the one hand, earthworms are favoured in pasture by higher pH and soil bacterial activity (Pearce, 1972; Decaëns *et al.*, 2008; Ponge *et al.*, 2013). On the other hand, most macroarthropods are favoured in forest by higher organic carbon and environmental stability (Garay and Hafidi, 1990; Nuria *et al.*, 2011). Pastured heath should, therefore, provide both higher pH and bacterial activity than forest, and greater environmental stability and thicker litter than pasture. We also hypothesized that pastured heath displayed a higher heterogeneity of macroinvertebrate communities (β -diversity) owing to soil heterogeneity induced by cattle activity (Afzal and Adams, 1992; Hirobe *et al.*, 2013).

We implemented a broken line, crossing the highest variety of land-use/soil conditions over a minimum distance, to test the impact of grazing intensity on soil macroinvertebrate communities in heterogeneous landscapes. We recorded soil macrofaunal communities along the sampling line, together with land-use and soil properties. Habitat selection can be derived from spatial segregation when dispersal limitation is absent (Ponge and Salmon, 2013). This is allowed by sampling communities of poorly mobile organisms such as soil animals (Lavelle and Spain, 2001) over a restricted area displaying a high level of heterogeneity.

MATERIALS AND METHODS

Study sites

The present study was undertaken in the Brenne Natural Regional Park, located in Indre, the Centre of France. Obviously, in this protected area heathland, forest, wetland and agricultural areas (mainly pastures) were maintained in dynamic equilibrium within a variegated landscape (Gachet *et al.*, 2009). The study was done in 2006 in a private property (Les Vigneaux, Mézières-en-Brenne, Indre, France; 46°46'07" N, 1°16'23" E), which was eligible to the Natura 2000 European Network of

Special Protection Areas, owing to its richness in threatened plant species. Moderate disturbance by cattle traffic maintained a high level of plant biodiversity, by limiting the natural encroachment of oak and the monopolistic development of heather (Gachet *et al.*, 2009). In the Grande-Brenne region traditional land management has been maintained to a large extent, displaying a variety of typical environments. ‘Buttons’ with shallow soils were covered with spontaneous scrub and forest vegetation while the surrounding land (meadows and ponds) was devoted to extensive cattle pasture and to fishing. Such practices have been widely maintained in Grande Brenne for several centuries (Trotignon and Trotignon, 2007). Five land-use types were selected along a broken line covering the range of variation from pasture to pine plantation, including grazed heath and aged heath (Fig. 1).

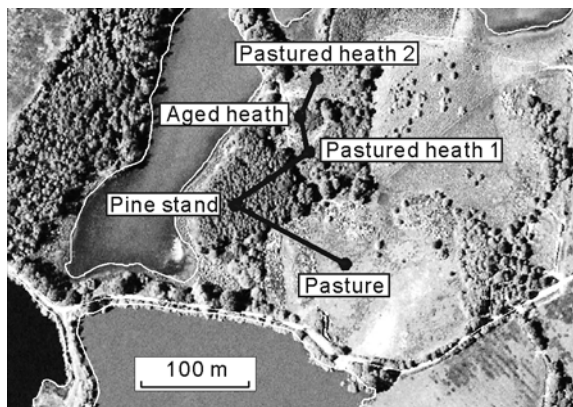


Fig. 1 Satellite map of the study site (downloaded from Google Earth[®]), indicating the broken line along which sample points were disposed in the 5 land-use types (see main text for details). The figure is oriented according to the main cardinal points. Plain grey surfaces, lined with a white contour, are water surfaces.

Fescue (*Festuca* spp.) and bent (*Agrostis* spp.) dominated the vegetation of the pasture, with an encroachment of common broom (*Cytisus scoparius* (L.) Link). The morphology of besom heath (*Erica scoparia*) allowed discerning two intensities of grazing in pastured heath. In pastured heath 1, the typical conical shape of bushes resulted from the selection of twigs by cattle. In pastured heath 2 bushes kept more or less their natural erected form. We observed a few signs of present-day cattle pressure in the aged heath, while the pine plantation was totally disused at the time of the study.

The elevation is around 120 m a.s.l., with an undulating relief due to an alternation of ‘buttons’ (on which the 5 study sites were established) and ponds. The climate is Atlantic, mild oceanic, with a mean annual temperature of 11 °C and a mean annual rainfall of 700 mm. Soils are highly heterogeneous, varying from Lithosols (top of ‘buttons’) to Gleysols (pond shores). Soil pH and C/N ratio varied from 4.4 (woodlot) to 4.9 (pasture) and from 14 (pasture) to 19 (woodlot), respectively. The humus index (Ponge *et al.*, 2002) varied to a great extent, from 1 (Eumull) in pasture and pastured heath 1 to 5.8 (Eumoder) in average in pastured heath 2.

Sampling procedure

Soil and soil macroinvertebrates were sampled on February 2006 along a broken line (Fig. 1). Five regularly spaced (6 m) sampling points were selected in each patch of the landscape mosaic, with the center of the area as the midpoint. The length sampled in each patch (24 m) was a little less than the linear extent of the smallest patch (aged heath, 30 m). By this procedure the 5 sites could be

compared on the base of similar distance effects, while avoiding edge effects. The total length of the sampling line was 262 m.

At each sampling plot a metal square (25 cm × 25 cm) was forced into the soil (litter included) down to a depth of 11 cm. Soil fauna was sampled in two steps: first by digging the soil to 5.5 cm and then to 11 cm. At each step we excavated and then sorted by hand soil and litter for visible macroinvertebrates. Soil and litter were then transported to the laboratory in plastic bags to extract the remaining invertebrates by the dry-funnel method (Macfadyen, 1961). After soil/litter collection for faunal extraction, diluted formalin (0.3%) was applied and left to infiltrate for 10 min over the sampled surface, in order to expel deeper-living earthworms. All invertebrates collected directly in the field were preserved in formalin solution diluted to 5%, while animals extracted in the laboratory were preserved in 95% ethyl alcohol.

Before applying formalin to expel earthworms, a block of soil (9.5 cm × 15 cm × 5.5 cm, length × width × height) was taken on one side of the square pit used for faunal extraction, just under the litter when present. The soil block was immediately put in a plastic box closed by a 35-μm mesh nylon net, preventing fauna from escaping while allowing free passage to gases except water vapor, and was used for the measurement of soil respiration. We estimated the humus index at each sampling plot according to the method firstly devised by Ponge *et al.* (2002). The thickness of organic horizons and the structure of horizon A were used as diagnostic features of humus forms, which were scaled from 1 (Eumull) to 7 (Dysmoder).

Laboratory analyses

Millipedes, centipedes, woodlice and earthworms were identified to species level according to keys and faunas by Bouché (1972), Sims and Gerard (1985), and Blower (1985) and Hopkin (2003). Earthworms were classified into epigeic, anecic and endogeic species according to Lavelle and Spain (2001). Macroinvertebrates were identified to order level using keys and illustrations by Perrier (1927, 1932) and Forey and Fitzsimons (1992).

Soil respiration was quantified by measuring the production of CO₂ from the 9.5 cm × 15 cm × 5.5 cm soil block. The soil block was placed in a confined box at field moisture for 4 h at 15 °C, and CO₂ production was measured using a MDC MGA3000 infrared gas analyzer. Soil respiration was expressed as the CO₂ amount per unit soil weight and C mineralization rate as the CO₂ amount per unit organic C.

After dry-funnel extraction of fauna, organic C, total N, and pH_{water} on the residual soil were measured. Soil moisture was determined by reweighing the soil after drying it at 30 °C for 15 d after faunal extraction. Organic C and total N were determined by the dry combustion method according to ISO 10694 and ISO 13878 (ISO, 1995, 1998), respectively. Soil pH_{water} was measured by potentiometry according to ISO 10390 (ISO, 2005), 3 h after adding 100 mL of deionized water to 20 mg of soil.

Data analyses

Redundancy analysis was used as a direct gradient analytical method to discern trends in the composition and diversity of soil macroinvertebrate communities (Kounda-Kiki *et al.*, 2009).

Macrofaunal composition and diversity were used as explained (dependent) variables, while land-use types and soil features (humus index and laboratory analyses) were used as explanatory variables. Some groups (earthworms, woodlice, centipedes and millipedes) were identified to species level and these data were used to calculate species richness. However, only the order level was considered for characterizing the composition of macroinvertebrate communities in redundancy analysis. All variables were standardized (mean and variance equal to 1) before analysis. A Monte-Carlo permutation test was used to test the significance of the relationships between dependent and independent variables.

Simple and partial Mantel tests (Legendre and Fortin, 1989; Cushman and Landguth, 2010) were used to prospect possible causal relationships between macroinvertebrates, land-use and soil features while discarding the effects of spatial autocorrelation. Other methods exist, such as structural equation models (Wang *et al.*, 2013). However, Mantel tests seem better adapted to the analysis of dissimilarity and spatial distances in our data, because of their spatial dependence and the non-linearity of expected relationships (Hausdorf and Hennig, 2005). Mantel tests were performed on between-sample distance matrices. Macroinvertebrate and soil distances were estimated by Spearman rank dissimilarity, $[(1 - r_s)/2]$, r_s being the Spearman rank correlation coefficient, on the base of variables studied. The distance based on land-use types was 0 when a couple of samples belonged to the same land-use type and 1 when they belonged to two different land-use types. Spatial distance between samples was the distance in meters separating two samples, using a magnification of Fig. 1 (not shown) where the position of all individual samples was reported.

The dissimilarity between the samples inside each land-use type (Spearman dissimilarity) was measured, both for soil macroinvertebrate and soil properties. The 10 values obtained (20 combinations divided by two for doubletons) were averaged for each land-use type. The dissimilarity in redundancy analysis was not used because the values could not be assigned to individual samples.

The significance of differences between the 5 land-use types was checked for macroinvertebrate community and soil features using Kruskal-Wallis non-parametric analysis followed by between-group comparisons by Dunn method with Bonferroni adjustment for multiple comparisons. XLSTAT (Addinsoft®) version 2013.4.02 was used for all calculations.

RESULTS

Redundancy analysis showed that land-use types and soil features explained a major (64%) and significant part ($P < 0.001$) of macroinvertebrate community parameters (Table I). The projection of variables in the plane of the first two canonical factors (Fig. 2) showed that the first canonical factor (40.3% of explained variance) classified land-use types with faunal affinity in the order pasture → pastured heath 1 → pastured heath 2 → aged heath → pine stand. Aged heath was much near from pastured heath 2 than it was from the pine stand. Taxonomic richness indicators (order richness for all groups, species richness for millipedes, centipedes and woodlice) increased along this gradient (Table I). There was a maximum contrast between the pine stand and the pasture for order, centipede, woodlice and millipede richness. The three heathland types exhibited intermediate values, their affinity to pasture or pine stand varying according to the group considered. The total abundance of macroinvertebrates, and that of predator and saprophagous taxa, followed the same trend as

taxonomic richness. Earthworms followed an opposite trend, whether in abundance and species richness (Table I).

TABLE I

Macrofaunal (composite data only) and soil features in 5 land-use types with different cattle grazing intensities

Code ^{a)}	Item	Parameter	Pasture	Pastured heath 1	Pastured heath 2	Aged heath	Pine stand
TA1	Soil macro-	Coleoptera (adults)	8.2 ± 1.8 ^{b)}	8.4 ± 2.5	9.4 ± 3.4	10.0 ± 1.7	15.4 ± 4.8
TA2	invertebrate	Coleoptera (larvae)	12.6 ± 3.4	11.0 ± 4.3	6.2 ± 1.1	5.4 ± 1.9	17.0 ± 3.4
TA3	variables	Coleoptera	20.8 ± 2.2	19.4 ± 3.9	15.6 ± 3.1	15.4 ± 2.8	32.4 ± 6.8
TA4		Diptera (larvae)	101.2 ± 26.8ab^{c)}	38.6 ± 7.6a	47.4 ± 22.3a	113.0 ± 53.9ab	162.6 ± 26.5b
TA5		Heteroptera	0.6 ± 0.6	2.4 ± 0.7	7.0 ± 3.4	1.8 ± 1.0	1.4 ± 0.7
TA6		Hymenoptera	2.0 ± 0.3	31.8 ± 28.1	15.4 ± 6.2	32.0 ± 14.2	14.8 ± 5.2
TA7		Insects (adults)	34.8 ± 5.0a	88.6 ± 33.9ab	79.2 ± 19.5ab	114.2 ± 14.7b	183.4 ± 49.5b
TA8		Insects (larvae)	121.0 ± 23.2ab	54.4 ± 8.5a	59.0 ± 21.8a	122.2 ± 55.5ab	184.6 ± 27.4b
TA9		Geophilomorpha	0.4 ± 0.4a	5.4 ± 1.5ab	7.4 ± 3.2ab	17.2 ± 5.0b	11.2 ± 2.1b
TA10		Lithobiomorpha	0.2 ± 0.2	0.4 ± 0.2	0.6 ± 0.6	0.4 ± 0.4	0.8 ± 0.4
TA11		Chilopoda	0.6 ± 0.4a	5.8 ± 1.7ab	8.0 ± 3.8ab	17.4 ± 5.2b	11.6 ± 2.0b
TA12		Julida	0.4 ± 0.4a	0.4 ± 0.2ab	1.6 ± 0.7ab	0.4 ± 0.2ab	3.0 ± 0.9b
TA13		Polydesmida	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	0.4 ± 0.4ab	3.0 ± 1.2b
TA14		Polyxenida	0.0 ± 0.0	0.0 ± 0.0	3.8 ± 3.1	0.8 ± 0.4	16.6 ± 10.5
TA15		Diplopoda	0.4 ± 0.4a	0.4 ± 0.2a	5.4 ± 3.3ab	1.6 ± 0.5ab	22.6 ± 10.3b
TA16		Lumbricidae	5.2 ± 1.3b	5.0 ± 1.6ab	1.0 ± 0.5a	3.2 ± 0.6ab	1.0 ± 0.6a
TA17		Anecic earthworms	2.8 ± 0.8ab	4.2 ± 1.5b	0.6 ± 0.4ab	2.0 ± 0.6ab	0.4 ± 0.4a
TA18		Endogeic earthworms	1.6 ± 1.0	0.4 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
TA19		Epigeic earthworms	0.4 ± 0.4	0.0 ± 0.0	0.2 ± 0.2	0.2 ± 0.2	0.6 ± 0.4
TA20		Stylommatophora	0.0 ± 0.0	0.6 ± 0.2	1.2 ± 0.8	0.0 ± 0.0	0.4 ± 0.2
FR1		Omnivorous	68.2 ± 11.3ab	77.6 ± 35.3ab	43.2 ± 6.9a	106.8 ± 42.7ab	111.2 ± 10.5b
FR2		Phytophagous	8.4 ± 2.7	8.2 ± 1.0	6.6 ± 2.3	3.2 ± 1.5	4.0 ± 1.3
FR3		Predator	9.8 ± 1.9a	18.2 ± 3.9ab	30.6 ± 9.9ab	31.2 ± 9.2ab	28.0 ± 4.1b
FR4		Saprophagous	73.2 ± 11.2ab	43.4 ± 6.7a	49.8 ± 21.7a	94.4 ± 21.3ab	225.6 ± 51.8b
FR5		Predator/phytophagous	0.6 ± 0.6	0.6 ± 0.4	3.8 ± 2.5	1.4 ± 0.7	0.6 ± 0.4
DE1		Abundance	155.8 ± 21.5ab	143.0 ± 41.3a	138.2 ± 21.3a	236.4 ± 48.0ab	368.0 ± 65.1b
DE2		Earthworm species richness	0.8 ± 0.4	0.0 ± 0.0	0.2 ± 0.2	0.2 ± 0.2	0.0 ± 0.0
DE3		Centipede species richness	0.4 ± 0.2a	1.4 ± 0.2ab	1.4 ± 0.4ab	1.2 ± 0.2ab	1.6 ± 0.2b
DE4		Millipede species richness	0.2 ± 0.2a	0.4 ± 0.2a	1.2 ± 0.6ab	1.2 ± 0.4ab	2.8 ± 0.4b
DE5		Woodlice species richness	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.2	0.2 ± 0.2	1.0 ± 0.4
DE6		Order richness	8.0 ± 0.5a	12.4 ± 0.5ab	12.2 ± 1.2b	10.8 ± 1.4ab	13.0 ± 0.5b

		Dissimilarity	0.058 ± 0.007 ab	0.047 ± 0.004 a	0.101 ± 0.014 b	0.068 ± 0.008 ab	0.074 ± 0.008 ab
SO1	Soil	Humus index	1.0 ± 0.0 a	1.0 ± 0.0 a	5.8 ± 0.5 b	5.0 ± 0.0 b	5.2 ± 0.2 b
SO2	variables	pH	4.89 ± 0.14 b	4.67 ± 0.08 ab	4.55 ± 0.07 ab	4.50 ± 0.13 ab	4.36 ± 0.04 a
SO3		Moisture (g kg ⁻¹)	129 ± 8 ab	136 ± 14 ab	183 ± 18 b	184 ± 42 ab	110 ± 7 a
SO4		Organic C (g kg ⁻¹)	20 ± 1 a	47 ± 6 bc	114 ± 24 c	41 ± 6 ab	55 ± 8 bc
SO5		Total N (g kg ⁻¹)	1.44 ± 0.07 a	2.69 ± 0.34 bc	5.14 ± 1.02 c	2.18 ± 0.20 ab	3.01 ± 0.49 bc
SO6		C/N	13.7 ± 0.3 a	17.0 ± 0.3 ab	21.1 ± 0.6 c	18.1 ± 0.6 bc	18.6 ± 1.4 bc
SO7		Soil respiration (μg CO ₂ g ⁻¹ soil h ⁻¹)	2.82 ± 0.28 b	2.40 ± 0.35 ab	2.96 ± 0.92 ab	1.12 ± 0.23 a	1.89 ± 0.27 ab
SO8		C mineralization rate (μg CO ₂ g ⁻¹ organic C h ⁻¹)	0.145 ± 0.020 b	0.055 ± 0.012 ab	0.028 ± 0.007 a	0.028 ± 0.006 a	0.040 ± 0.009 a
SO9		Dissimilarity	0 ± 0 a	0.007 ± 0.002 ab	0.036 ± 0.007 b	0 ± 0 a	0.007 ± 0.002 ab

^{a)}Codes are those used to draw the RDA bi-plot (Fig. 2).

^{b)}Means ± standard errors ($n = 5$), with the exception of dissimilarity ($n = 10$).

^{c)}Means in bold type within each row indicate significant variation among land-use types by Kruskal-Wallis non-parametric test and those followed by the same letter(s) within each row are not significantly different by post-hoc Dunn tests with Bonferroni adjustment for multiple comparisons.

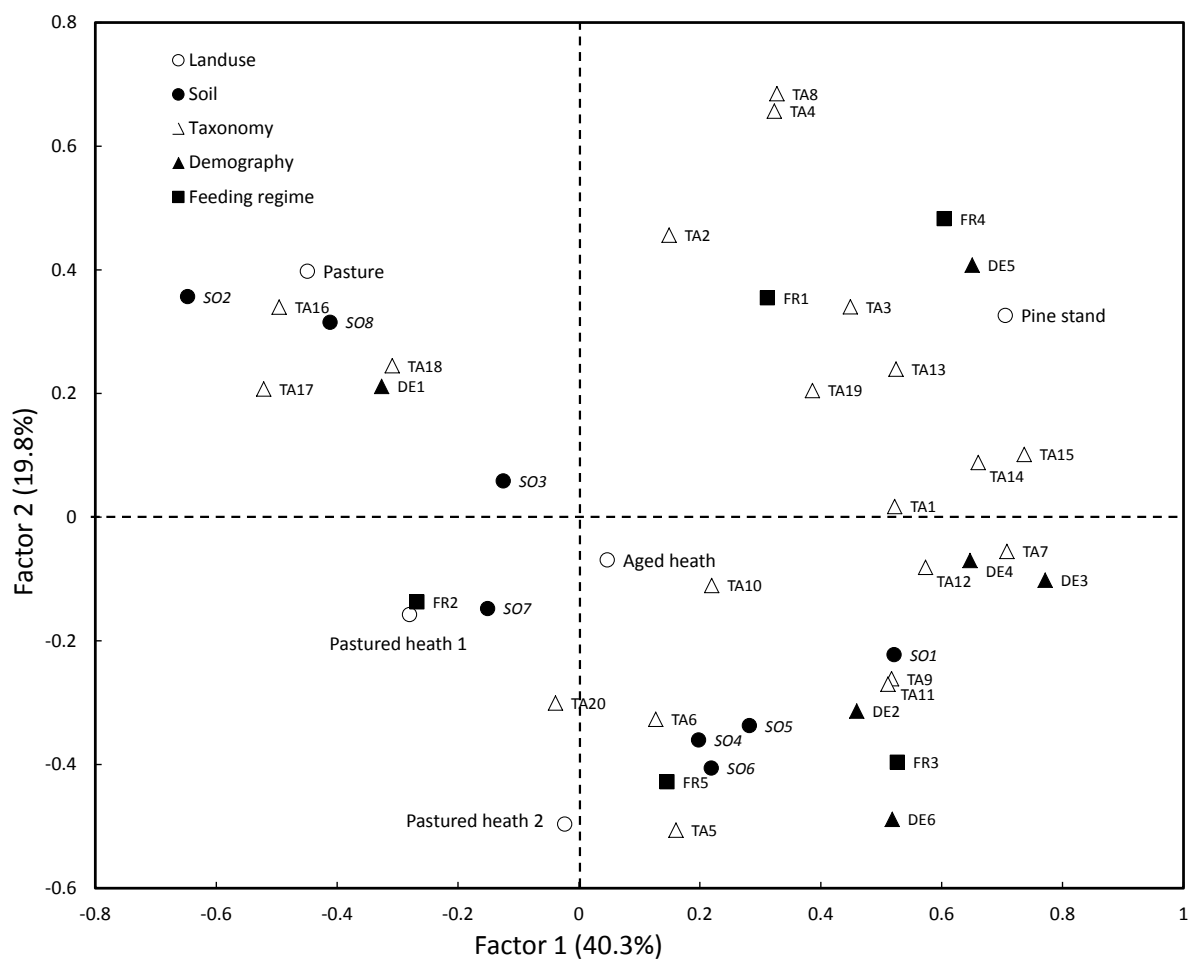


Fig. 2 Redundancy analysis: bi-plot projection of 31 macroinvertebrate community parameters as explained variables (see Table I for detailed descriptions), 5 land-use types and 8 soil features (see Table I for detailed descriptions) as explanatory variables in the plane of the first two canonical factors.

Among soil features, pH followed the gradient depicted by the first canonical factor: pH decreased from pasture to pine stand, heathland being intermediate, with a decreasing trend between pastured heath 1, pastured heath 2 and aged heath (Table I). The C mineralization rate (CO_2 produced per unit organic carbon) followed the same trend.

The second canonical factor (19.8% of explained variance) opposed pastured heath 2 to both pasture and pine stand, aged heath and pastured heath 1 being intermediate. It corresponded to an increase in taxonomic (order) richness, abundance of predator, predator/phytophagous and phytophagous animals and a decrease in saprophagous and omnivorous animals from pasture and pine stand to pastured heath 2. The between-sample dissimilarity of macroinvertebrate communities (heterogeneity or β -diversity) was the highest in pastured heath 2 (Table I). Among soil features, organic C and N and C/N were maximized in pastured heath 2, according to the trend depicted along factor 2 (Table I).

Simple and partial Mantel tests allowed discerning direct *versus* indirect relationships between land-use types, soil features and macroinvertebrates, while taking into account spatial influences (Fig. 3). The highest Mantel correlation coefficient (r_M) between distance matrices was between land-use and soil feature ($r_M = 0.46$, $P < 0.0001$). This value was poorly affected by the macroinvertebrate distance matrix taken as confounding variable ($r_M = 0.40$, $P < 0.0001$). A decrease of r_M was observed when space was taken as confounding variable, but this coefficient remained highly significant ($r_M = 0.33$, $P < 0.0001$). The correlation between soil feature and macroinvertebrate matrices was highly significant ($r_M = 0.34$, $P < 0.0001$). A decrease (more important than for the soil feature-land-use relationship) was observed when land-use was taken as confounding variable ($r_M = 0.26$, $P < 0.0001$). A similar decrease occurred when taking spatial distance as confounding variable ($r_M = 0.24$, $P < 0.0001$). Contrary to land-use-soil feature and soil feature-macroinvertebrate relationships, the relationship observed between land-use and macroinvertebrates was highly significant in the absence of confounding variables ($r_M = 0.28$, $P < 0.0001$) but decreased to a great extent when soil effects were discarded ($r_M = 0.14$, $P < 0.05$). The relationship between land-use and macroinvertebrates became nil when spatial effects were discarded ($r_M = 0.07$, $P = 0.25$). Such a decrease in the Mantel statistic when removing soil features or spatial effects indicates that a great part of the relationship between land-use and macroinvertebrate communities is indirect.

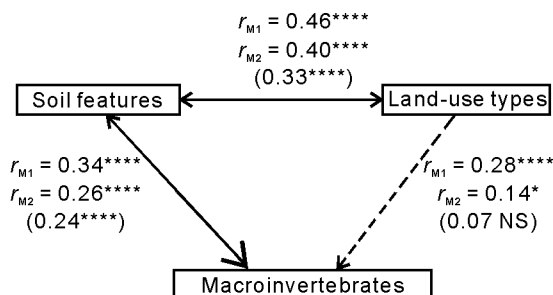


Fig. 3 Simple and partial Mantel tests between soil features, land-use types and macroinvertebrates (see text for details on the calculation of distance matrices). The first value of the Mantel correlation coefficient (r_{M1})

corresponds to simple test, the second value (r_{M2}) corresponds to partial test (discarding the effect of the third factor). Values when discarding spatial effects are indicated between brackets. Arrowed lines indicate most probable effects between soil, land-use and fauna. Two arrows of the same size at opposite sides of the same line indicate fully symmetric effects, while not fully symmetric effects are indicated by arrows of a different size. The dashed line corresponds to possible but poorly probable effects.

Partial Mantel tests showed that the relationship between soil features and fauna was still significant when the effect of land-use was discarded, meaning that within each land-use type, macroinvertebrate communities and soil features co-varied to some extent. We also observed that dissimilarities among macroinvertebrate communities and among soil features were the highest in the same land-use type, *i.e.*, pastured heath 2 (Spearman dissimilarity of 0.101 and 0.036, respectively, Table I).

DISCUSSION

Along a gradient from pasture to pine stand, passing by heathland areas at decreasing cattle pressure levels, macroinvertebrate communities shifted from a community dominated by earthworms to a community dominated by macroarthropods, thus supporting our first hypothesis. Along this gradient the abundance and taxonomic richness of macroinvertebrates per sample (*i.e.*, α -diversity) increased. Other studies showed that coniferous stands may support more diverse and abundant macroarthropod communities compared with the adjoining meadows (Eggleton *et al.*, 2005; Callahan Jr. *et al.*, 2006; Cakir and Makineci, 2013), and that coniferous litter can be consumed by a variety of macroinvertebrates (Ponge, 1991; Bernier, 1998). Our results on a land-use gradient from pasture to forest supported the studies on secondary successions in abandoned or afforested agricultural land (Scheu and Schulz, 1996; Frouz, 1997). However, at our study site Scots pine (planted) was not the spontaneous term of plant succession (oak forest) as described in Gachet *et al.* (2009). Similar results were obtained along gradients of land-use intensification (Nuria *et al.*, 2011). However, contrasting results were obtained by Decaëns *et al.* (1998), who showed that Scots pine, at the end of post-pastoral succession, exerted a detrimental influence on soil macroinvertebrate communities. Such discrepancies could be explained by the fact that Decaëns *et al.* (1998) studied a sequence of calcareous soils on chalk. In their study pine was planted in the strongly decalcified areas, thus exacerbating the acidifying influence of coniferous plantations. On the contrary, at our study sites all soils were acidic, harboring soil animal and microbial communities better adapted to acidity.

Soil pH and C mineralization rate decreased along the studied land-use gradient, while the humus index increased. These trends are indicative of increased acidity and organic matter accumulation on the ground, owing at least partly to a shift from bacterial- to fungal-dominated energy channels (Hedlund *et al.*, 2004; Frouz *et al.*, 2013). Such a shift in soil trophic networks means more habitat and resources for litter-dwelling animals such as millipedes, centipedes, woodlice and fly larvae, among other groups (Garay and Hafidi, 1990; Crowther *et al.*, 2013), and less habitat and resources for soil-dwelling animals such as anecic and endogeic earthworms (Staaf, 1987; de Vries *et al.*, 2013). The cohabitation between these two groups has been only observed and explained in forest mull (Schaefer and Schauer mann, 1990; Bonkowski *et al.*, 1998; Frouz *et al.*, 2013). Besom heath occupied an intermediate position. It seemed that this Ericaceae, which suppressed herb vegetation

through its allelopathic potential (Ballester *et al.*, 1977), did not exert any detrimental influence on macroinvertebrate abundance and taxonomic richness, even when aged (Table I).

Mantel tests showed that a consistent part of the relationship between land-use and soil macrofaunal communities is mediated by soil features (Kime and Wauthy, 1984; Branquart *et al.*, 1995; Marichal *et al.*, 2014), and probably asymmetric. The double-arrowed full lines between soil features and land-use (Fig. 3) expressed visually that these relationships were symmetric and supported by well-known mechanisms. Land-use influences soil features to a great extent, mainly through vegetational influences (Damman, 1971; Willis *et al.*, 1997; Lisboa *et al.*, 2014). In turn land-use decision-making (the choice of agricultural or forest use, for instance) is at least partly dictated by pre-existing differences in soil quality (Merrington, 2006; Caldas *et al.*, 2014). The relationship between soil features and macroinvertebrates was mostly direct but not so symmetric compared with that between land-use and soil features, hence unequal arrow sizes (Fig. 3). Soil feature influences most macroinvertebrate groups (Pearce, 1972; Branquart *et al.*, 1995; Huerta and van der Wal, 2012) and in return changes under the influence of some invertebrates, in particular earthworms, known for their ecological engineering activity (Forey *et al.*, 2011; Blouin *et al.*, 2013). In our study, ecosystem engineering was mostly performed by earthworms, mainly anecics, which decreased in abundance from pasture and highly pastured heath (pastured heath 1) to pine stand (Table I). In other terms there is more macrofaunal feedback to soil in the grass-dominated pasture than in the tree-dominated forest, as confirmed by experimental studies (Alphei *et al.*, 1996; Zangerlé *et al.*, 2011).

In the slightly undulating terrain of our study site land-use type has been selected by the owner (in interaction with the free range activity of cattle and horses) in accordance to the differences in elevation and water availability. Less pastured sites (pine stand and aged heath) were at the summit of the 'button', with slightly more acidic and drier soils, while the pasture was downslope, with richer and moister soils. Land-use and geomorphology were thus linked to a great extent, as is customary in heterogeneous landscapes (Zonneveld, 1989; Kinnaird *et al.*, 2013). In addition interactions occur between the habitats in close vicinity, in the form of nutrient input subsidies, whether mediated by non-biotic (Polis and Hurd, 1996) or biotic (Van Uytvanck *et al.*, 2010) processes. All these features express the non-independence (spatial autocorrelation) of land-use types, making difficult to elucidate the influence of spatially distributed factors on biotic communities (Heiniger *et al.*, 2014).

Spatial influences on macroinvertebrate communities were mainly mediated by the land-use types and soil features, which co-varied along the sampling line studied (Fig. 1). The clustering of macroinvertebrate species is well-known (Rossi *et al.*, 1997; Cannavacciuolo *et al.*, 1998). However, the variation observed along the studied sampling line involved a variety of invertebrate orders, suggesting that it could rather be explained by the spatial autocorrelation of soil pH, moisture and element contents (Šamonil *et al.*, 2011). Moreover, the fact that the highest dissimilarity between macroinvertebrate communities (Table I) was observed in the site with the highest dissimilarity between soil properties (pastured heath 2) suggested the existence of a relationship between soil and animal heterogeneities within each of the studied land-use types.

Whether cattle grazing may increase the heterogeneity of soil macroinvertebrate communities was only partly supported by our data. Highest heterogeneity occurred in pastured heath 2 while least and lower heterogeneity occurred in pastured heath 1 and pasture, respectively (Table I). Such a difference in the response of macroinvertebrate communities to cattle grazing may be explained by the differences in cattle pressure among the sites. The heterogeneity of soil macroinvertebrate

communities (β -diversity) was the highest at an intermediate level of grazing intensity, between scarcely or non-grazed sites (aged heath and pine stand) and highly grazed sites (pasture and pastured heath 1), supporting the intermediate disturbance hypothesis (Svensson *et al.*, 2007).

In a heterogeneous landscape land-use types and correlated soil properties explained a prominent part of the heterogeneity of macroinvertebrate abundance and diversity. Heath vegetation did not display any detrimental effect on soil macroinvertebrate communities. This protected habitat (Mobaied *et al.*, 2012) lay in an intermediate position between forest and pasture, in particular when the balance between arthropods and annelids was considered along a gradient of increasing cattle activity. The heterogeneity of soil macroinvertebrate communities (β -diversity) and of soil properties peaked at intermediate levels of cattle grazing, pointing to the interest of incorporating ungulates in the management of protected areas (Putman *et al.*, 2011).

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REFERENCES

- Afzal M, Adams W A. 1992. Heterogeneity of soil mineral nitrogen in pasture grazed by cattle. *Soil Sci Soc Am J.* **56**: 1160--1166.
- Alphei J, Bonkowski M, Scheu S. 1996. Protozoa, Nematoda and Lumbricidae in the rhizosphere of *Hordelymus europaeus* (Poaceae): faunal interactions, response of microorganisms and effects on plant growth. *Oecologia.* **106**: 111--126.
- Anglade J Y, Bigot L. 2001. First determination of arthropod assemblages associated with *Erica arborea* L. and *Erica scoparia* L. *CR Acad Sci III-Vie.* **324**: 235--243.
- Ballester A, Albo J M, Vieitez E. 1977. The allelopathic potential of *Erica scoparia* L. *Oecologia.* **30**: 55--61.
- Bartolomé J, López Z G, José Broncano M, Plaixats J. 2005. Grassland colonization by *Erica scoparia* (L.) in the Montseny Biosphere Reserve (Spain) after land-use changes. *Agr Ecosyst Environ.* **111**: 253--260.
- Bernier N. 1998. Earthworm feeding activity and development of the humus profile. *Biol Fert Soils.* **26**: 215--223.
- Blouin M, Hodson M E, Delgado E A, Baker G, Brussaard L, Butt K R, Dai J, Dendooven L, Peres G, Tondoh J E, Cluzeau D, Brun J J. 2013. A review of earthworm impact on soil function and ecosystem services. *Eur J Soil Sci.* **64**: 161--182.
- Blower J G. 1985. Millipedes: Keys and Notes for the Identification of the Species. Brill, London.

- Bonkowski M, Scheu S, Schaefer M. 1998. Interactions of earthworms (*Octolasion lacteum*), millipedes (*Glomeris marginata*) and plants (*Hordelymus europaeus*) in a beechwood on a basal hill: implications for litter decomposition and soil formation. *Appl Soil Ecol.* **9**: 161--166.
- Bouché M B. 1972. Lombriciens de France: Écologie et Systématique (in French). Institut National de la Recherche Agronomique, Paris.
- Branquart E, Kime R D, Dufrêne M, Tavernier J, Wauthy G. 1995. Macroarthropod-habitat relationships in oak forests in South Belgium. I. Environments and communities. *Pedobiologia.* **39**: 243--263.
- Cakir M, Makineci E. 2013. Humus characteristics and seasonal changes of soil arthropod communities in a natural sessile oak (*Quercus petraea* L.) stand and adjacent Austrian pine (*Pinus nigra* Arnold) plantation. *Environ Monit Assess.* **185**: 8943--8955.
- Caldas M M, Bergtold J S, Peterson J M, Graves R W, Earnhart D, Gong S, Lauer B, Brwon J C. 2014. Factors affecting farmers' willingness to grow alternative biofuel feedstocks across Kansas. *Biomass Bioenerg.* **66**: 223--231.
- Callahan Jr M A, Richter Jr D D, Coleman D C, Hofmockel M. 2006. Long-term land-use effects on soil invertebrate communities in Southern Piedmont soils, USA. *Eur J Soil Biol.* **42**: S150--S156.
- Cannavacciuolo M, Bellido A, Cluzeau D, Gascuel C, Trehen P. 1998. A geostatistical approach to the study of earthworm distribution in grassland. *Appl Soil Ecol.* **9**: 345--349.
- Crowther T W, Stanton D W G, Thomas S M, A'Bear A D, Hiscox J, Jones T H, Voříšková J, Baldrian P, Boddy L. 2013. Top-down control of soil fungal community composition by a globally distributed keystone consumer. *Ecology.* **94**: 2518--2528.
- Cushman S A, Landguth E L. 2010. Spurious correlations and inference in landscape genetics. *Mol Ecol.* **19**: 3592--3602.
- Damman A W H. 1971. Effect of vegetation changes on the fertility of a Newfoundland forest site. *Ecol Monogr.* **41**: 253--270.
- Decaëns T, Dutoit T, Alard D, Lavelle P. 1998. Factors influencing soil macrofaunal communities in post-pastoral successions of western France. *Appl Soil Ecol.* **9**: 361--367.
- Decaëns T, Margerie P, Aubert M, Hedde M, Bureau F. 2008. Assembly rules within earthworm communities in North-Western France---A regional analysis. *Appl Soil Ecol.* **39**: 321--335.
- Denslow J S. 1985. Disturbance-mediated coexistence of species. In Pickett S T A, White P S (eds.) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, San Diego. pp. 307--323.
- de Vries F T, Thébault E, Liiri M, Birkhofer K, Tsiafouli M A, Bjørnlund L, Jørgensen H B, Brady M V, Christensen S, de Ruiter P C, d'Hertefeldt T, Frouz J, Hedlund K, Hemerik L, Gera Hol W H, Hotes S, Mortimer S R, Setälä H, Sgardelis S P, Uteseny K, van der Putten W H, Wolters V, Bardgett R D. 2013. Soil food web properties explain ecosystem services across European land use systems. *P Natl Acad Sci USA.* **110**: 14296--14301.
- Doblas-Miranda E, Sánchez-Piñero F, González-Megías A. 2009. Different structuring factors but connected dynamics shape litter and belowground soil macrofaunal food webs. *Soil Biol Biochem.* **41**: 2543--2550.
- Eggleton P, Vanbergen A J, Jones D T, Lambert M C, Rockett C, Hammond P M, Beccaloni J, Marriott D, Ross E, Giusti A. 2005. Assemblages of soil macrofauna across a Scottish land-use

- intensification gradient: influences of habitat quality, heterogeneity and area. *J Appl Ecol.* **42**: 1153--1164.
- Forey E, Barot S, Decaëns T, Langlois E, Laossi K R, Margerie P, Scheu S, Eisenhauer N. 2011. Importance of earthworm-seed interactions for the composition and structure of plant communities: a review. *Acta Oecol.* **37**: 594--603.
- Forey P, Fitzsimons C. 1992. Les Insectes (in French). Librairie Gründ, Paris.
- Frouz J. 1997. Changes in communities of soil dwelling dipteran larvae during secondary succession in abandoned fields. *Eur J Soil Biol.* **33**: 57--65.
- Frouz J, Prach K, Pižl V, Háněl L, Starý J, Tajovský K, Materna J, Balík V, Kalčík J, Řehouňková K. 2008. Interactions between soil development, vegetation and soil fauna during spontaneous succession in post mining sites. *Eur J Soil Biol.* **44**: 109--121.
- Frouz J, Thébault E, Pižl V, Adl S, Cajthaml T, Baldrián P, Háněl L, Starý J, Tajovský K, Materna J, Nováková A, de Ruiter P C. 2013. Soil food web changes during spontaneous succession at post mining sites: a possible ecosystem engineering effect on food web organization? *PLoS One.* **8**: e79694.
- Gachet S, Sarthou C, Bardat J, Ponge J F. 2009. The state of change of *Erica scoparia* L. heathland through cattle grazing and oak colonisation. *Rev Ecol-Terre Vie.* **64**: 3--17.
- Garay I, Hafidi N. 1990. Study of a mixed forest litter of hornbeam (*Carpinus betulus* L.) and oak (*Quercus sessiliflora* Smith). III. Organization of the edaphic macroarthropod community as a function of litter quantity. *Acta Oecol.* **11**: 43--60.
- Graefe U, Beylich A. 2003. Critical values of soil acidification for annelid species and the decomposer community. *Newsl Enchytraeidae.* **8**: 51--55.
- Hausdorf B, Hennig C. 2005. The influence of recent geography, palaeogeography and climate on the composition of the fauna of the central Aegean Islands. *Biol J Linn Soc.* **84**: 785--795.
- Hedlund K, Griffiths B, Christensen S, Scheu S, Setälä H, Tschamntke T, Verhoef H. 2004. Trophic interactions in changing landscapes: responses of soil food webs. *Basic Appl Ecol.* **5**: 495--503.
- Heiniger C, Barot S, Ponge J F, Salmon S, Botton-Divet L, Carmignac D, Dubs F. 2014. Effect of habitat spatiotemporal structure on collembolan diversity. *Pedobiologia.* **57**: 103--117.
- Hirobe M, Kondo J, Enkhbaatar A, Amartuvshin N, Fujita N, Sakamoto K, Yoshikawa K, Kielland K. 2013. Effects of livestock grazing on the spatial heterogeneity of net soil nitrogen mineralization in three types of Mongolian grasslands. *J Soils Sediment.* **13**: 1123--1132.
- Hopkin S. 2003. The Woodlouse Name Trail: A Key to Common Woodlice. Field Studies Council, Shrewsbury.
- Huerta E, van der Wal H. 2012. Soil macroinvertebrates' abundance and diversity in home gardens in Tabasco, Mexico, vary with soil texture, organic matter and vegetation cover. *Eur J Soil Biol.* **50**: 68--75.
- ISO. 1995. ISO 10694. Soil Quality---Determination of Organic and Total Carbon after Dry Combustion (Elementary Analysis). International Organization for Standardization, Geneva.
- ISO. 1998. ISO 13878. Soil Quality---Determination of Total Nitrogen Content by Dry Combustion ("Elemental Analysis"). International Organization for Standardization, Geneva.
- ISO. 2005. ISO 10390. Soil Quality---Determination of pH. International Organization for Standardization, Geneva.

- Kime R D, Wauthy G. 1984. Aspects of relationships between millipedes, soil texture and temperature in deciduous forests. *Pedobiologia*. **26**: 387--402.
- Kinnaird T C, Dixon J E, Robertson A H F, Peltenburg E, Sanderson D C W. 2013. Insights on topography development in the Vasilikós and Dhiarizos valleys, Cyprus, from integrated OSL and landscape studies. *Mediterr Archaeol Archaeom*. **13**: 49--62.
- Kounda-Kiki C, Celini L, Ponge J F, Mora P, Sarthou C. 2009. Nested variation of soil arthropod communities in isolated patches of vegetation on a rocky outcrop. *Soil Biol Biochem*. **41**: 323--329.
- Lavelle P, Spain A V. 2001. Soil Ecology. Springer, Dordrecht.
- Legendre P, Fortin M J. 1989. Spatial pattern and ecological analysis. *Vegetatio*. **80**: 107--138.
- Lisboa F J G, Chaer G M, Fernandes M F, Berbara R L L, Madari B E. 2014. The match between microbial community structure and soil properties is modulated by land use types and sample origin within an integrated agroecosystem. *Soil Biol Biochem*. **78**: 97--108.
- Macfadyen A. 1961. Improved funnel-type extractors for soil arthropods. *J Anim Ecol*. **30**: 171--184.
- Makeschin F. 1997. Earthworms (Lumbricidae: Oligochaeta): important promoters of soil development and soil fertility. In Benckiser G (ed.) Fauna in Soil Ecosystems: Recycling Processes, Nutrient Fluxes, and Agricultural Production. Marcel Dekker, New York. pp. 173--223.
- Marichal R, Grimaldi M, Feijoo M A, Oszwald J, Praxedes C, Cobo D H R, del Pilar Hurtado M, Desjardins T, da Silva Junior M L, da Silva Costa L G, Miranda I S, Oliveira M N D, Brown G G, Tsélouiko S, Martins M B, Decaëns T, Velasquez E, Lavelle P. 2014. Soil macroinvertebrate communities and ecosystem services in deforested landscapes of Amazonia. *Appl Soil Ecol*. **83**: 177--185.
- Merrington G. 2006. Using Science to Create a Better Place: the Development and Use of Soil Quality Indicators for Assessing the Role of Soil in Environmental Interactions. Environment Agency, Bristol.
- Miles J. 1981. Problems in heathland and grassland dynamics. *Vegetatio*. **46**: 61--74.
- Mitchell R J, Campbell C D, Chapman S J, Osler G H R, Vanbergen A J, Ross L C, Cameron C M, Cole L. 2007. The cascading effects of birch on heather moorland: a test for the top-down control of an ecosystem engineer. *J Ecol*. **95**: 540--554.
- Mobaied S, Ponge J F, Salmon S, Lalanne A, Riera B. 2012. Influence of the spatial variability of soil type and tree colonization on the dynamics of *Molinia caerulea* (L.) Moench in managed heathland. *Ecol Complex*. **11**: 118--125.
- Nuria R, Jérôme M, Léonide C, Christine R, Gérard H, Etienne I, Patrick L. 2011. IBQS: a synthetic index of soil quality based on soil macro-invertebrate communities. *Soil Biol Biochem*. **43**: 2032--2045.
- Pakeman R J, Hulme P D, Torvell L, Fisher J M. 2003. Rehabilitation of degraded dry heather [*Calluna vulgaris* (L.) Hull] moorland by controlled sheep grazing. *Biol Conserv*. **114**: 389--400.
- Paula S, Ojeda F. 2011. Response to recurrent disturbance in two co-occurring resprouter heath species: the ecological consequences of withstanding herbivores. *Plant Ecol*. **212**: 2035--2045.
- Perrier R. 1927. La Faune de la France Illustrée. Tome V: Coléoptères (in French). 1ère partie. Delagrave, Paris.

- Perrier R. 1932. La Faune de la France Illustrée. Tome VI: Coléoptères (in French). 2ème partie. Delagrave, Paris.
- Pearce T G. 1972. Acid intolerant and ubiquitous Lumbricidae in selected habitats in North Wales. *J Anim Ecol.* **41**: 397--410.
- Polis G A, Hurd S D. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Am Nat.* **147**: 396--423.
- Ponge J F. 1991. Food resources and diets of soil animals in a small area of Scots pine litter. *Geoderma.* **49**: 33--62.
- Ponge J F, Chevalier R, Loussot P. 2002. Humus index: an integrated tool for the assessment of forest floor and topsoil properties. *Soil Sci Soc Am J.* **66**: 1996--2001.
- Ponge J F, Pérès G, Guernion M, Ruiz-Camacho N, Cortet J, Pernin C, Villenave C, Chaussod R, Martin-Laurent F, Bispo A, Cluzeau D. 2013. The impact of agricultural practices on soil biota: a regional study. *Soil Biol Biochem.* **67**: 271--284.
- Ponge J F, Salmon S. 2013. Spatial and taxonomic correlates of species and species trait assemblages in soil invertebrate communities. *Pedobiologia.* **56**: 129--136.
- Ponsard S, Arditì R, Jost C. 2000. Assessing top-down and bottom-up control in a litter-based soil macroinvertebrate food chain. *Oikos.* **89**: 524--540.
- Putman R, Apollinio M, Andersen R. 2011. Ungulate Management in Europe: Problems and Practices. Cambridge University Press, Cambridge.
- Rossi J P, Lavelle P, Albrecht A. 1997. Relationships between spatial pattern of the endogeic earthworm *Polypheretima elongata* and soil heterogeneity. *Soil Biol Biochem.* **29**: 485--488.
- Salmon S, Frizzera L, Camaret S. 2008. Linking forest dynamics to richness and assemblage of soil zoological groups and to soil mineralization processes. *Forest Ecol Manag.* **256**: 1612--1623.
- Šamonil P, Valtera M, Bek S, Šebková B, Vrška T, Houška J. 2011. Soil variability through spatial scales in a permanently disturbed natural spruce-fir-beech forest. *Eur J Forest Res.* **130**: 1075--1091.
- Schaefer M, Schauer mann J. 1990. The soil fauna of beech forests: comparison between a mull and a moder soil. *Pedobiologia.* **34**: 299--314.
- Scheu S, Schulz E. 1996. Secondary succession, soil formation and development of a diverse community of oribatids and saprophagous soil macro-invertebrates. *Biodivers Conserv.* **5**: 235--250.
- Sims R W, Gerard B M. 1985. Earthworms: Keys and Notes for the Identification and Study of the Species. Synopses of the British Fauna No. 31. Pitman Press, London.
- Staaf H. 1987. Foliage litter turnover and earthworm populations in three beech forests of contrasting soil and vegetation types. *Oecologia.* **72**: 58--64.
- Svensson J R, Lindegarth M, Siccha M, Lenz M, Molis M, Wahl M, Pavia H. 2007. Maximum species richness at intermediate frequencies of disturbance: consistency among levels of productivity. *Ecology.* **88**: 830--838.
- Trotignon E, Trotignon J. 2007. La Brenne: la Nature en Héritage (in French). Alan Sutton, Saint-Cyr-sur-Loire.

- Van Uytvanck J, Milotic T, Hoffmann M. 2010. Nitrogen depletion and redistribution by free-ranging cattle in the restoration process of mosaic landscapes: the role of foraging strategy and habitat proportion. *Restor Ecol.* **18**: 205--216.
- Wang I J, Glor R E, Losos J B. 2013. Quantifying the roles of ecology and geography in spatial genetic divergence. *Ecol Lett.* **16**: 175--182.
- Webb N R. 1998. The traditional management of European heathlands. *J Appl Ecol.* **35**: 987--990.
- Willis K J, Braun M, Sümegei P, Tóth A. 1997. Does soil change cause vegetation change or vice versa? A temporal perspective from Hungary. *Ecology.* **78**: 740--750.
- Zangerlé A, Pando A, Lavelle P. 2011. Do earthworms and roots cooperate to build soil macroaggregates? A microcosm experiment. *Geoderma.* **167--168**: 303--309.
- Zonneveld I S. 1989. The land unit---A fundamental concept in landscape ecology, and its applications. *Landscape Ecol.* **3**: 67--86.