Landscape Ecology (2006) 21:281–295
DOI 10.1007/s10980-005-0144-7
© Springer 2006

Research article

Spatial and seasonal patterns of cattle habitat use in a mountain wooded pasture

Florian Kohler[1,2], François Gillet[1,2,3,*], Stéphanie Reust[1], Helene H. Wagner[4], Fawziah Gadallah[1], Jean-Michel Gobat[1] and Alexandre Buttler[2,3]
*[1]Laboratory of Plant Ecology, University of Neuchâtel, 2007 Neuchâtel, Switzerland; [2]WSL, Swiss Federal Research Institute, Antenne romande, 1015 Lausanne, Switzerland; [3]EPFL, Swiss Federal Institute of Technology, Laboratory of Ecological Systems, 1015 Lausanne, Switzerland; [4]WSL, Swiss Federal Research Institute, 8903 Birmensdorf, Switzerland; *Author for correspondence. Present address: EPFL-ENAC-ISTE-ECOS, Ecublens Station 2, CH-1015 Lausanne, Switzerland (e-mail: francois.gillet@epfl.ch)*

Received 7 June 2004; accepted in revised form 23 June 2005

Key words: Autocorrelation, Dung deposition, Herbage removal, Jura mountains, Principal coordinates of neighbour matrices, Redundancy analysis, Silvopastoral landscape, Switzerland, Trampling, Variance partitioning

Abstract

Management-oriented models of cattle habitat use often treat grazing pressure as a single variable summarizing all cattle activities. This paper addresses the following questions: How does the spatial pattern of cattle effects vary between cattle activities in a highly heterogeneous landscape? Do these patterns change over the grazing season as forage availability decreases? What are the respective roles of natural and management-introduced structures? We estimated the intensity of herbage removal, dung deposition and trampling after each of three grazing periods on a grid of 25 m $\times$25 m cells covering an entire paddock in the Swiss Jura Mountains. We found no significant positive correlations between cattle effects. Spatial patterns weakened through the season for grazing and trampling, whereas dunging patterns changed little between grazing periods. Redundancy analysis showed that different cattle effects were correlated with different environmental variables and that the importance of management-introduced variables was highest for herbage removal. Autocorrelograms and partial redundancy analyses using principal coordinates of neighbour matrices suggested that dunging patterns were more coarse-grained than the others. Systematic differences in the spatial and seasonal patterns of cattle effects may result in complex interactions with vegetation involving feedback effects through nutrient shift, with strong implications for ecosystem management. In heterogeneous environments, such as pasture-woodland landscapes, spatially explicit models of vegetation dynamics need to model cattle effects separately.

Introduction

Landscape ecology deals with the interaction between pattern and process (Turner 1989; Turner et al. 2001). The relationship between organisms and their spatially structured environment is often treated as a unidirectional behavioural response (e.g. habitat selection) to landscape pattern. However, the interaction may be more complicated, for two reasons. First, organism response to

the environment is often complex, as it is highly scale-dependent (Wiens 1989), and this scale-dependence may not only depend on the organism under study, but also on which activity is considered (Thompson and McGarigal 2002). Second, organism behaviour may have positive feedback effects on the ecosystem, reinforcing or mitigating the intensity of the resource pattern. For example, a change in the dominant herbivore after the foundation of the Swiss National Park resulted in a shift in the spatial pattern and directional change of vegetation (Schutz et al. 2003). Cattle, present before the establishment of the Park, grazed in wide areas but rested in limited areas around stables and shelter. Over centuries, this grazing pattern resulted in a considerable nutrient enrichment of the resting sites. Red deer, now the major herbivore, preferentially graze at night on the nutrient-rich former cattle resting places, but are widely dispersed during the day, effectively reversing the nutrient transfer. The grazing pattern of cattle thus created a positive feedback leading to pasture degradation, whereas the grazing pattern of red deer results in a negative feedback stabilizing the system. The understanding of such dynamics requires an understanding of the patterns of organism response.

While ecological flows in landscape mosaics, non-linear dynamics and landscape complexity, and landscape sustainability have been identified as top research priorities in landscape ecology (Wu and Hobbs 2002), we would add that understanding how non-linear dynamics and complex interactions affect ecological flows in landscapes may be crucial for effective sustainable management. For instance, the sustainable management of heterogeneous semi-natural systems such as wooded pastures may be greatly facilitated by the development of spatially explicit models of landscape dynamics which take into account the hierarchical organisation of complex ecological systems (Wu and David 2002). In order to develop such models, we need to investigate the mutual relationships between landscape structure, livestock activities and vegetation dynamics.

Silvopastoral ecosystems consist of a grazed mosaic of woodland and grassland with a complex spatial structure (Etienne 1996). These systems are widespread, yet the causes and consequences of spatial heterogeneity in their structure and function are poorly understood. Here, we take as a case study a cattle-grazed wooded pasture in the Swiss Jura mountains.

In large pastures, the overall stocking rate influences cattle habitat use and may induce more or less heterogeneous grazing patterns. At low stocking rates, cattle will preferentially graze the most easily accessible areas with the most available high-quality forage, while other areas may be under-utilised. At higher stocking rates, the depletion of the preferred grazing areas forces the animals to graze the pasture more evenly. Hence, the patchiness of a pasture depends not only on the natural resource variability and the overall stocking rate, but also on the patterns of livestock activity in space and time (Verweij 1995). Many management schemes use a rotational system with multiple small paddocks in order to achieve a more homogeneous use of resources. Within each paddock, a seasonal change from selective to more uniform grazing is to be expected. The installation of fences, salt and watering points introduces additional landscape elements that may affect livestock activity.

Patterns of cattle habitat use

Livestock activity is an important factor for structuring vegetation in silvopastoral ecosystems (Olff and Ritchie 1998). At fine resolution (bite and feeding station *sensu* Bailey et al. 1996), cattle may influence vegetation through three ways: (1) herbage removal, (2) dung and urine deposition, and (3) trampling. These three activities have different impacts on the vegetation, creating fine-grained mosaics in the herb layer (Kohler et al. 2004). However, most models of rangeland vegetation dynamics are implemented at a landscape level and ignore fine-grained pattern (Weber et al. 1998; Hahn et al. 1999; Van Oene et al. 1999; Gillet et al. 2002; Cousins et al. 2003). Generally 'grazing pressure' is used as an overall index of livestock effects and is assessed through mapping either foraging or dung deposition. This is a convenient simplification, but there is evidence that the spatial patterns of grazing, dunging and trampling are not congruent.

(1) The spatial pattern of foraging is the best studied attribute of cattle activity (Senft et al. 1987; Coughenour 1991; Bailey et al. 1996). The selection of grazing locations by cattle depends on

herbage quality and quantity, water availability, relief, slope, elevation, aspect, natural and artificial barriers, herd social interactions, prior experience, and climate (Rice et al. 1983). Cattle preferentially graze plant communities of high nutritive value (Osuji 1974; Anderson and Kothmann 1980; Roath and Krueger 1982) and this preference seems to partially control the distribution of cattle in a paddock (Van Rees and Hutson 1983; Senft et al. 1985; Putman et al. 1987). Pinchak et al. (1991) concluded that the distance to water and physiographic complexity were the primary controls on cattle distribution, but that forage quality was an important predictor of cattle habitat use at finer grains.

(2) The spatial distribution of faeces and urine from cattle is not uniform and their concentration is often higher in areas of special attraction, such as near water sources, gates or fences, and in shade and shelter belts (Petersen et al. 1956, Marsh and Campling 1970; Peterson and Gerrish 1996; White et al. 2001). In mountainous regions, cattle faeces are significantly associated with slope, aspect, topographic position and season (Tate et al. 2003). For instance, daily faecal load is higher in flat areas and during the dry season (Costa et al. 1990). Observations from dairy cows in an intensively grazed, rotationally stocked pasture showed that the number of defecations and urinations were highly correlated with the time cows spent in those areas (White et al. 2001); manure concentration was higher around the water tank, especially during warm-weather periods.

(3) The distribution of trampling effects depends not only on the number and pressure of foot steps in an area, but also on the sensitivity of the vegetation to trampling (Roovers et al. 2004), which is likely to be affected by slope, soil texture and water content. On steep ground grazed by sheep and red deer, Hester and Baillie (1998) showed that at low densities, vegetation was more affected by trampling than by herbage removal.

Problems in assessing grazing patterns

The relationships between these different livestock effects are poorly understood. Many studies have included a 'grazing treatment' with little or no consideration for the spatial and temporal patterns of the multiple grazing effects. Such patterns are difficult to study because each pasture or paddock is a functional unit whose parts are directly linked by activity patterns. Consequently, patterns can only be meaningfully described over an entire paddock. Such exhaustive coverage is labour-intensive and puts important constraints on data collection. As the observations are inherently dependent in space and time, autocorrelation must be taken into account during the statistical analysis for three reasons. First, autocorrelation renders unadjusted statistical tests too liberal. Second, autocorrelation may result from a spatially structured confounding factor. Hence, spatially structured multivariate responses to environmental factors are often assessed after partialling out the spatial component of variation using constrained ordination (Borcard et al. 1992). This provides an assessment of the variation explained by environmental variables alone (ecological dependence), spatial variables alone ('strict' spatial autocorrelation) and the shared variation due to spatially dependent environmental descriptors (spatial dependence) (Legendre 1993). Finally, spatial autocorrelation may result from a spatial process, which is of interest in itself. Further analysis of the spatial component can be used to assess the characteristic spatial grain of such a process (Borcard and Legendre 2002).

Questions and hypotheses

For management purposes, it is important to distinguish between cattle responses to environmental characteristics of natural origin (topography, soil, vegetation, microclimate), which are primarily site-dependent, and those introduced by management (fences, gates, salt or water sources), which are more easily controlled and may be adapted for optimal range management.

Our purpose was to provide an exhaustive description of spatial and seasonal patterns of grazing, dunging and trampling for an entire paddock within a wooded pasture, and to relate the observed patterns to natural and management-introduced (hereafter, introduced) environmental structures, while accounting for spatial autocorrelation.

This paper addresses the following questions: How do the spatial patterns of each cattle effect differ in a mountainous wooded pasture? Do these patterns change during the grazing season? What

are the relationships between cattle effects and local site conditions? What are the respective roles of natural and introduced structures in explaining the patterns of cattle effects? What is the characteristic spatial scale of the pattern of each cattle effect?

We focused on three working hypotheses: (1) Inside the paddock, the spatial pattern of cattle effects depends on the type of activity: in particular, grazing and dunging are expected to occur in different locations. (2) The intensity of the pattern and thus the strength of spatial autocorrelation of each cattle effect weakens over the course of the season. (3) Each cattle effect is affected by different environmental structures.

We thus assess whether the assumption of 'grazing pressure' as an overall index of cattle effects is a valid simplification for modelling the interactions between cattle and vegetation at a landscape level.

Methods

Study site

The study was conducted in the Jura Mountains of northwestern Switzerland at Orvin, Métairie d'Evilard (47°09′ N 7°10′ W). The climate is predominantly oceanic, with a mean annual precipitation of about 1600 mm (with more than 400 mm as snow) and a mean annual temperature of 7 °C. The ground is covered with snow from November to April.

We chose a paddock of 23.2 ha which provided a typical example of an extensively managed wooded pasture in the Jura Mountains (see Perrenoud et al. (2003) for a detailed site description). Elevation varies from about 1170 m a.s.l. in the south of the paddock to 1250 m in the north. Overall aspect is south-east, with flat or sloping ground and a heterogeneous soil mosaic (Calcisols, Cambisols, Leptosols and Luvisols, Deckers et al. (1998)). The heterogeneity of soils is mainly due to geomorphology and linked to the variable thickness of a superficial stratum of allochtonous siliceous loess covering the Jurassic limestone substratum (Havlicek and Gobat 1996). Outcrops of bedrock appear along erosion rifts.

Phytocoenoses include open pastures, closed forests and wooded pastures with scattered or clumped trees. Trees tend to occur around rock outcrops. Ungrazed, the climax vegetation is a beech-fir forest, but currently the dominant tree species are *Fagus sylvatica, Acer pseudoplatanus* and *Picea abies*. The herb layer is a mosaic of grazed meadow (dominated by *Festuca nigrescens* and *Alchemilla monticola*), short-grass (*Carex montana, Alchemilla conjuncta*), tall-grass (*Dactylis glomerata, Hypericum maculatum*) and understorey (*Poa chaixii, Luzula sylvatica*) communities. This landscape is the result of centuries of mixed land use combining cattle grazing and forestry.

Management is extensive with a rotational grazing system during the summer period only. In 2001, our study period, 120 heifers (49.2 Adult Bovine Units) stayed three times in the paddock (three 'rotations'): 13 days in June, 10 days in July and 19 days in August and September. The stocking rate was equivalent to 2.12 cows ha^{-1} throughout the grazing period. The herd was a mix of Holstein and Swiss Brown breeds belonging to various owners. The paddock is delimited by a rectilinear stone wall on its west side and by a wire fence elsewhere. Two watering points are installed in the north-east (Figure 1).

Sampling design

Our data correspond to the geostatistical data model of a random field, where the observations represent a systematic sample of the surface of the study area. Such data, however, invariably suffer from the 'modifiable areal unit problem' (Jelinski and Wu 1996; Dungan et al. 2002): the arbitrarily defined size and shape of the sampling unit may have a strong influence on the statistical results. The relevant pattern is revealed only when the scale of analysis approaches the operational scale of the phenomenon under study (Wiens 1989; Wu 2004). Habitat selection may be a hierarchical process where organisms respond to environmental factors differently at different scales (e.g., Thompson and McGarigal 2002). In this paper, we specifically focus on cattle response at the level of the feeding station (*sensu* Bailey et al. 1996) and over an extent corresponding to the whole area of the pastoral management unit – the paddock – in which cattle graze freely. The grain was chosen to correspond both to the size of a feeding station

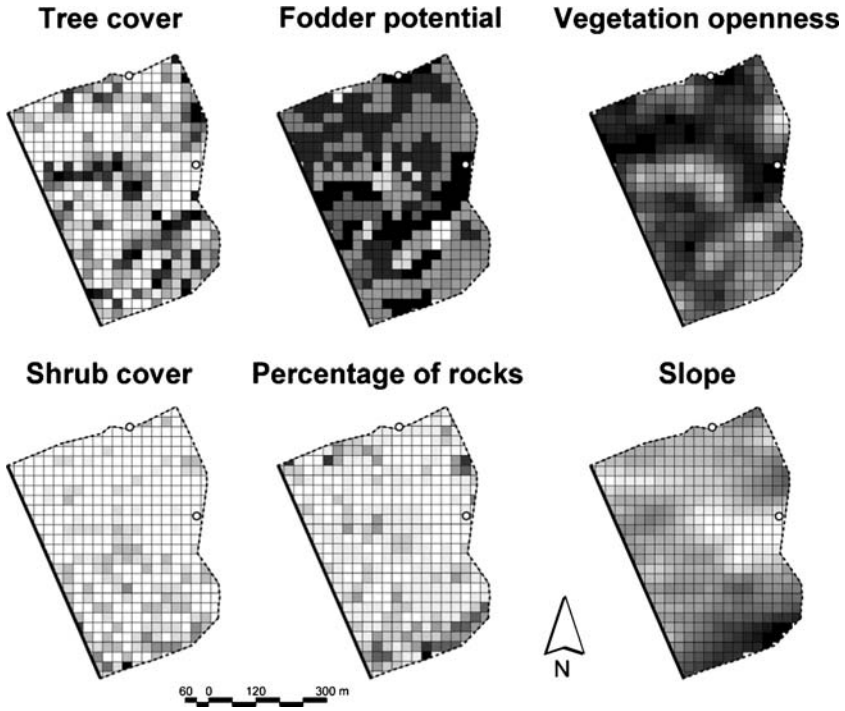

Figure 1. Maps of six natural environmental variables in relation to management-introduced structures. The paddock is subdivided into 393 cells. Darker shading corresponds to higher values of each variable. Circles indicate the two watering points. The dashed line represents the wire fence and the solid thick line the stone wall.

and to the minimum size of a phytocoenosis *sensu* Gillet and Gallandat (1996).

We subdivided the paddock into a grid of square cells of 25 m, the nodes of this grid being superposed to a digital elevation model with 25 m resolution (DHM25©, 1994, Swiss Federal Office of Topography). Stakes were placed at the corners of each cell to ensure correct positioning. Edge cells covering less than 100 m^2 of paddock area were excluded from the analysis (remaining $n = 393$). Using the terminology of Dungan et al. (2002), the observation extent was 23.2 ha (maximum length 695 m), grain was between 100 and 625 m^2 (maximum length 25 m) and lag was 0 (contiguous cells). Cattle effects were observed over a temporal extent of one season, a temporal grain of about 5 days and a temporal lag of about 1 month.

Cattle effects

Immediately after every grazing period, one observer estimated the effects of three cattle activities within each cell. The large number of observations required ($n = 393$) meant that data had to be collected extremely rapidly. While based on visual estimations by the same observer, the accuracy of the grazing and trampling descriptors was tested at the beginning of the study to ensure consistency in space and time.

(1) For herbage removal, we estimated foraging intensity of the herb layer in each cell using a three-level variable (0.05: 0–10% of shoot biomass removed; 0.30: 10–50% removed; 0.75: > 50% removed). Field estimation of the biomass removed was based on vegetation height and direct traces of grazing. This three-level grazing descriptor is a compromise between precision and efficiency.

(2) We counted the number of dung pats in each cell and used dung density (number of faeces per 100 m^2) as a quantitative descriptor of dunging.

(3) The most visible effects of trampling on the herb layer were the presence of bare soil and flattened vegetation. The percentage of the cell showing trampling effects was visually estimated to the nearest 10%, with additional intervals at 5 and 95%.

Note that the three descriptors reflect to some degree cumulative effects between rotations. It was impossible to observe only the fresh impact after

each grazing period. On the other hand, herbage removal was not purely cumulative due to regrowth of shoots, and a considerable proportion of dung pats disappeared between rotations, probably due to rain.

Environmental descriptors

To assess the effect of introduced structures (three continuous variables), we computed the distance from the centre of each cell to the nearest watering point, to the nearest stone wall and to the nearest wire fence using ArcGIS 8.3. (ESRI Corp.).

For each cell, we collected six environmental descriptors of natural structures, mapped in Figure 1. Tree cover, shrub cover and percentage of rock outcrops were visually estimated in the field using intervals of 10%. The annual fodder potential of the herb layer (i.e. the estimated quantity of forage produced in an average year, in units of biomass per area per year) was calculated from the pastoral value of vegetation units (see Gillet and Gallandat 1996 for details), using the vegetation map drawn by Perrenoud et al. (2003). The average slope for each cell was calculated from the digital elevation model with 25-m resolution using ArcView 3.3 (ESRI Corp.).

Vegetation openness (VO) was calculated from the average tree cover ($Tcov$) in a 3×3 moving window centred on the focal cell:

$$\mathrm{VO} = 1 - \frac{\sum_{i=1}^{9} Tcov_i}{900}$$

VO ranges from 0 to 1. To avoid edge effects, tree cover for cells falling at or outside the paddock boundary was estimated using an aerial photograph.

Statistical analysis

Cattle effects after each rotation were mapped with ArcView 3.3 (ESRI Corp.) and the mean and coefficient of variation (CV) were calculated.

To assess the degree of spatial autocorrelation, we calculated correlograms for each effect after each rotation, using R 1.9.1 (R Development Core Team 2004, 'ncf' library available at http://onb.ent.psu.edu) and Moran's I with 10 equidistant distance classes (class width 25 m). Because, in general, spatial statistics are calculated to a distance no more than one-half to one-third of the extent of the study domain (Dungan et al. 2002), we limited the range to 250 m, which also ensured that we obtained enough pairs for stable statistical estimates (minimum number = 38).

Correlations between all variables were estimated using Spearman's rank coefficient in order to gauge the strength and the direction of the bivariate relationships. We corrected the significance tests for spatial autocorrelation using the procedure of Dutilleul (1993) as implemented in the Mod_t_test program (Legendre 2001). No corrections were made for multiple tests, as we are searching for general patterns rather than making specific tests of hypotheses.

To analyse the variation of cattle effects in relation to local environmental conditions, redundancy analysis (RDA) was performed using R ('vegan' library) and CANOCO 4.5 (ter Braak and Smilauer 2002). Cattle effects for all three rotations were included as response variables ($3\times3 = 9$ response variables, $n = 393$ cells). These nine variables were square-root transformed and a range standardisation applied. For the range standardisation, each seasonal value was divided by the maximum value observed for the same cattle effect over the three rotations. This response matrix was constrained by the nine quantitative explanatory variables describing introduced and natural landscape structures.

In addition, partial RDAs were performed to describe and explain the spatial pattern of each cattle effect. A spatial explanatory matrix was constructed with the principal coordinates of neighbour matrices (PCNM analysis) (Borcard and Legendre 2002; Borcard et al. 2004). This method uses the eigenvectors of the principal coordinate analysis (PCoA) of a truncated matrix of geographic distance among cells as spatial descriptors and permits the detection of patterns at a wide range of distances. Geographic distances were calculated from the x and y coordinates of the cell centroids. Eigenvectors (PCNMs) were computed with the Spacemaker program (Borcard and Legendre 2001). To truncate the distance matrix, the highest value retained for geographic distance was 36 m, including the eight nearest neighbours of each cell; any value higher than 36 m was replaced by 144 m (4×36). 223 PCNMs were calculated. To avoid overfitting in the regression

model due to the large number of explanatory variables, we performed a Monte Carlo test for each cattle effect and retained only significant PCNMs ($p < 0.01$). If the geographic coordinates x and y appeared as significant explanatory variables, we included them first as covariables in the model to detrend the data, as recommended by Borcard and Legendre (2002). Following Brind'Amour et al. (2005), we grouped the selected PCNMs into three sets based on wavelength to define fine-scale (0–50 m period), medium-scale (50–150 m) and large-scale structures (150–700 m). We then performed a series of partial redundancy analyses (Legendre and Legendre 1998) with each set of variables (as well as x and y coordinates) to assess the importance of each spatial scale in explaining the cattle effects. As PCNM extracts independent axes, there is no shared variation between the three sets of spatial variables.

For each cattle effect, we assessed the relative importance of introduced and natural landscape structures and determined the amount of spatial structure that was unexplained by partialling out selected environmental factors using partial RDA and variance partitioning. For this analysis, we used three sets of explanatory variables: (1) introduced structures (three variables), (2) natural structures (six variables) and (3) spatial structure (12–24 significant PCNMs together with x and y coordinates). The variation in the response dataset was partitioned into that explained by each dataset and that shared by the datasets (see Borcard et al. 1992 and Økland and Eilertsen 1994 for details). Partial RDAs and permutation tests were computed with R and 'vegan' library.

Results

Spatial patterns of grazing, dunging and trampling

Cattle effects varied in space and time (Figure 2), and effects accumulated over the season. Cattle initially grazed near fences, avoiding the stone wall and the centre of the paddock, but by the end of the season, cattle had intensively grazed almost the whole area. However, the paddock was completely visited at each rotation, with all cells showing at least one cattle effect.

For all cattle effects, we observed positive spatial autocorrelation at shorter distances (Figure 3). For herbage removal after the first rotation, there was a significant positive autocorrelation from 0 to 150 m. After the second rotation, the structure was weaker, and after the third rotation it was replaced by a relatively homogenous pattern with significant positive autocorrelation only from 0 to 50 m. The CV decreased dramatically from the first to the last rotation (Table 1).

For the dunging pattern after the first and second rotations, we found significant positive autocorrelation from 0 to 250 m. For the third rotation, positive autocorrelation occurred at shorter distances (0 to 200 m) but the correlogram was similar (Figure 3). Dung density increased during the season, but principally in places where it was already high, so that the coefficient of variation decreased only slightly (Table 1). The structure of the trampling pattern did not change through the season, with significant positive autocorrelation at short distances (0–75 m or 100 m) (Figures 2 and 3). In contrast to grazing and dunging, the CV of trampling increased slightly between the first and the second rotation before decreasing after the third rotation (Table 1).

Correlations among cattle effects

The different cattle effects were not generally correlated and the only two correlations that were significant after accounting for spatial autocorrelation were negative (Table 2): after the second rotation between dunging and grazing, and after the third rotation between dunging and trampling.

Correlations between cattle effects and environmental variables

The relationship between cattle effects and environmental variables varied with effect and over time.

Herbage removal was most strongly correlated to the distance to the wire fence after the first rotation, but was not otherwise correlated with introduced structures (Table 3). Correlations to natural structures were weaker and detectable only after the third rotation.

In contrast, dunging and trampling tended to be correlated to natural structures. Dunging was

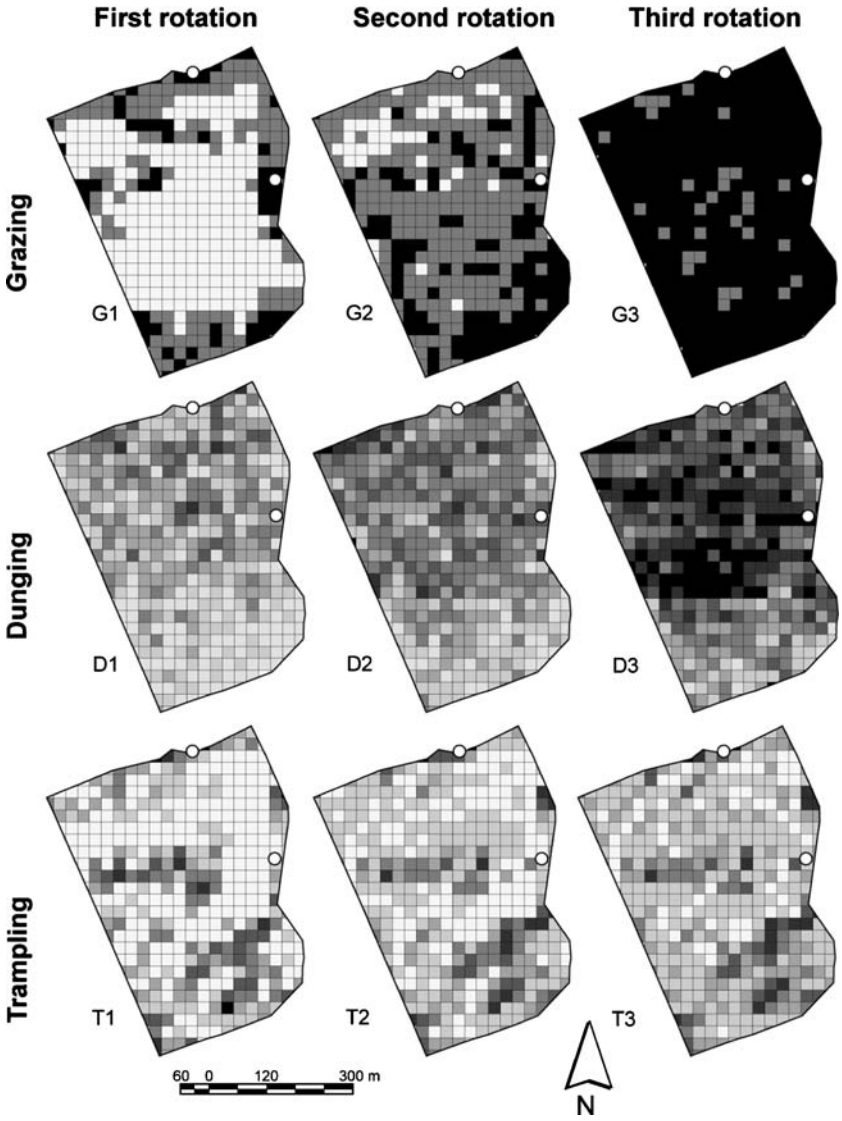

Figure 2. Maps of three types of cattle effects after each of three rotations. The paddock is subdivided into 393 cells. Darker shading corresponds to higher values of the variable for each activity in all rotations. Circles indicate the two watering points.

correlated most strongly with slope, but also with rockiness and VO, with little seasonal change. Trampling was correlated with all natural structures except slope, and correlations weakened over time.

RDA with environmental variables

The RDA biplot shows a clear separation of the three sets of response variables on the first two axes (Figure 4). Axis 1 was closely related to VO and axis 2 to distance to the wire fence. Monte Carlo permutation tests were significant for both the first and second axes and for the overall model ($p = 0.001$ all tests). A repeated analysis for each rotation separately produced similar results (data not shown).

Seasonal changes were larger for herbage removal than for other effects. The relatively homogeneous distribution of herbage removal after the third rotation resulted in the variable G3 lying close to the origin of the ordination biplot. The distance to the wire fence was important in

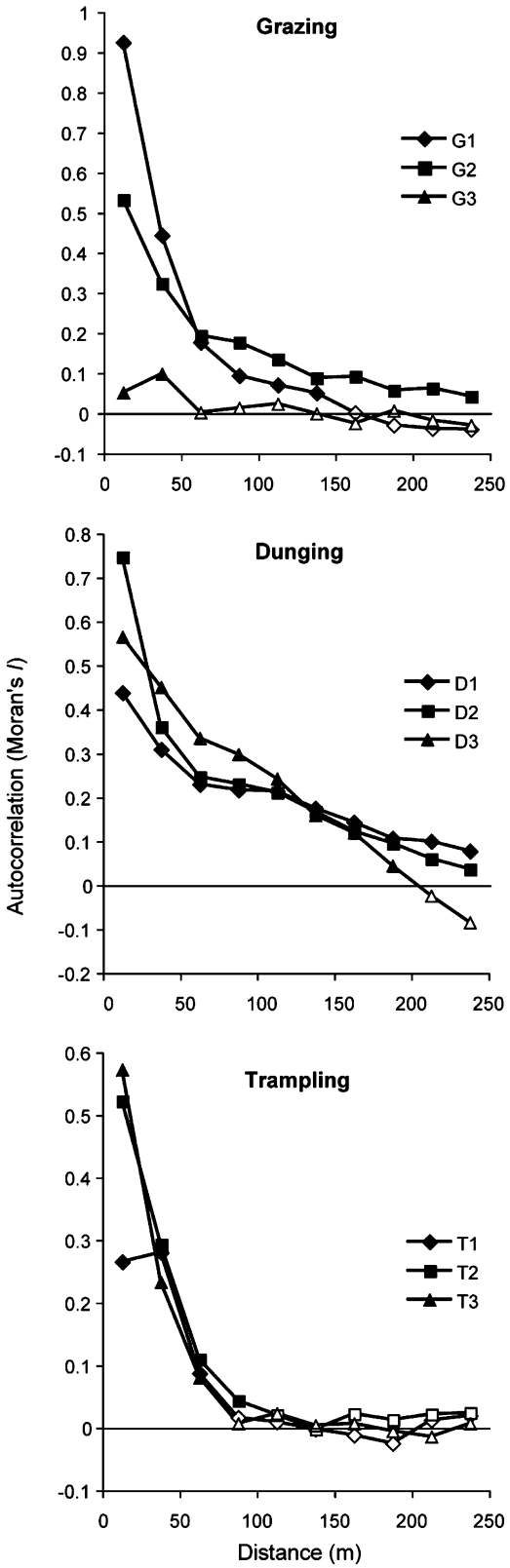

Figure 3. Moran's *I* correlograms of the three cattle effects at each rotation. Solid black symbols indicate significant correlations after a progressive Bonferroni correction (Legendre and Legendre 1998, p. 671). Diamonds: first rotation; squares: second rotation; triangles: third rotation. G: herbage removal; D: dung density; T: trampling effect; 1, 2, 3: rotation. Points are placed in the middle of each class.

explaining grazing patterns, although its influence decreased over time, in parallel to the removal of forage over the season.

By contrast, the pattern of dung deposition was rather constant over the season, as indicated by the similar position of the three seasonal dunging variables in the biplot, and the pattern shows a mild tendency to strengthen over time, as shown by the increasing length of the vectors. They were mainly negatively correlated with slope and rock outcrops.

Trampling patterns were also rather constant over the season and mainly influenced by natural structures. As for dung density, the three seasonal trampling variables had similar positions in the biplot, but tended to weaken slightly over time. They were positively correlated with tree cover and negatively correlated with VO and fodder potential.

Partial RDA using spatial variables

For herbage removal, x and y coordinates as well as 24 PCNMs were incorporated in the spatial model. Four variables were retained for large-scale, 16 for medium-scale and four for fine-scale structures. Examples of spatial structure for these three scales are presented in Figure 5. The spatial model explained 48.7% of the variation of the

Table 1. Mean and CV of each cattle effect measured after each rotation (n = 393 cells).

Attribute	Rotation 1	Rotation 2	Rotation 3
Herbage removal (percent)			
Mean	22.2	40.8	71.6
CV	1.083	0.579	0.167
Dunging (dung pats per 100 m^2)			
Mean	2.24	3.52	6.51
CV	0.688	0.563	0.551
Trampling (percent)			
Mean	13.1	13.1	16.2
CV	0.935	0.961	0.745

Table 2. Correlations between cattle effects for each rotation (n = 393 cells). The p-value of the Spearman's rank correlation coefficient (r_s) was corrected for spatial autocorrelation by Dutilleul's procedure (*$p < 0.05$, **$p < 0.01$ and *** $p < 0.001$). G: herbage removal; D: dung density; T: trampling effect; 1, 2, 3: rotation.

Rotation 1	r_s	Rotation 2	r_s	Rotation 3	r_s
D1 vs. T1	0.012	D2 vs. T2	−0.166	D3 vs. T3	− 0.201*
D1 vs. G1	−0.165	D2 vs. G2	−0.347*	D3 vs. G3	−0.100
T1 vs. G1	0.099	T2 vs. G2	0.012	T3 vs. G3	−0.028

Table 3. Correlations between cattle effects and environmental variables (n = 393 cells). The p-value of the Spearman's rank correlation coefficient (r_s) was corrected for spatial autocorrelation by Dutilleul's procedure (*$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$). VO: vegetation openness; Tcov: tree cover; Scov: shrub cover; Fpot: fodder potential; Rock: percentage of rock outcrops; DWater: distance to the nearest watering point; DWall: distance to the nearest wall; DWF: distance to the nearest wire fence; G: herbage removal; D: dung density; T: trampling effect; 1, 2, 3: rotation.

	Natural structures						Management-introduced structures		
	VO	Tcov	Scov	Fpot	Rock	Slope	DWater	DWall	DWF
G1	−0.066	0.006	0.032	−0.051	0.213	0.192	−0.032	0.111	−0.548**
G2	−0.212	0.035	0.154	−0.002	0.196	0.365	0.201	0.059	−0.115
G3	0.141*	−0.149**	0.001	0.110*	−0.071	0.095	0.021	0.041	−0.121
D1	0.303*	−0.067	−0.229	0.152*	−0.265*	−0.476*	−0.382	0.127	0.113
D2	0.390**	−0.156	−0.208	0.232**	−0.277**	−0.537*	−0.317	0.036	0.148
D3	0.324**	−0.202**	−0.220*	0.244***	−0.366**	−0.498*	−0.260	0.019	0.340
T1	−0.499***	0.636***	0.290***	−0.462***	0.475***	0.191	0.152	−0.106	−0.052
T2	−0.455***	0.499***	0.273**	−0.380***	0.370**	0.247	0.181	−0.102	−0.017
T3	−0.425***	0.465**	0.219**	−0.351***	0.366**	0.213	0.119	−0.030	−0.045

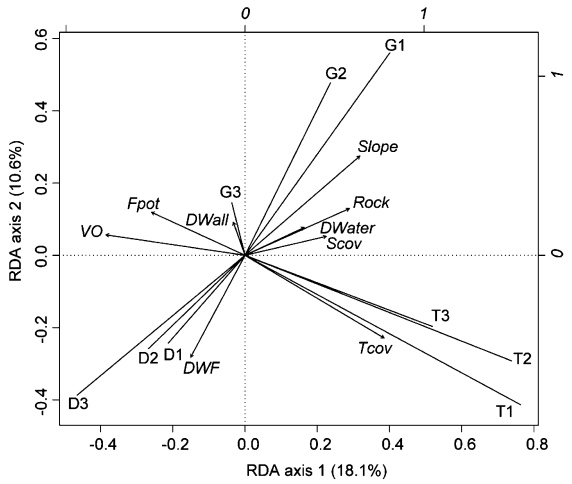

Figure 4. Biplot of axes 1 and 2 of RDA on the three variables describing cattle effects after each rotation, constrained by nine environmental variables (labels and scale). *Fpot*: fodder potential; *Tcov*: tree cover; *Scov*: shrub cover; *Rock*: percentage of rock outcrops; *VO*: vegetation openness; *DWater*: distance to the nearest watering point; *DWall*: distance to the nearest wall; *DWF*: distance to the nearest wire fence; G: herbage removal; D: dung density; T: trampling effect; 1, 2, 3: rotation.

grazing dataset (Figure 6) with medium-scale structures most important.

For dunging, x, y and 12 PCNMs were incorporated in the model. Two variables were retained for large-scale, eight for medium-scale and two for fine-scale structures. Spatial structure explained 48.3% of the variation (Figure 6) and the geographic coordinates were most important, indicating a topographical gradient.

For trampling, only the y coordinate and 14 PCNMs were incorporated in the model. Two variables were retained for large-scale, 10 for medium-scale and two for fine-scale structures. The model explained 33.8% of the variation (Figure 6), with the medium-scale structures most important.

Variance partitioning using partial RDA with spatial and environmental variables

Variance partitioning allows the division of variance into non-exclusive parts to assess the relative

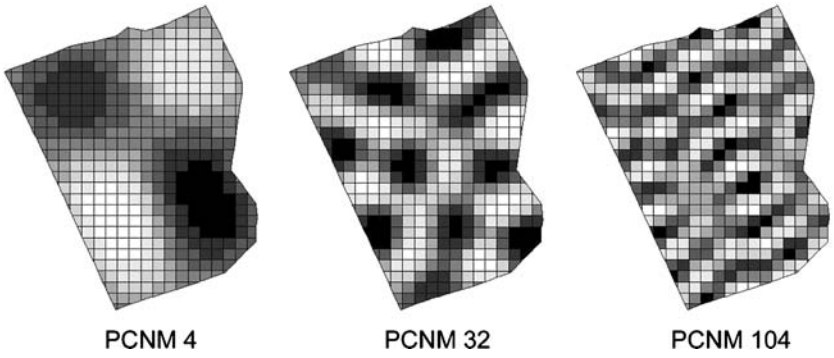

Figure 5. Examples of spatial structures used as explanatory variables in the RDAs based on principal coordinates of neighbour matrices: PCNM 4 (large scale), PCNM 32 (medium scale) and PCNM 104 (fine scale).

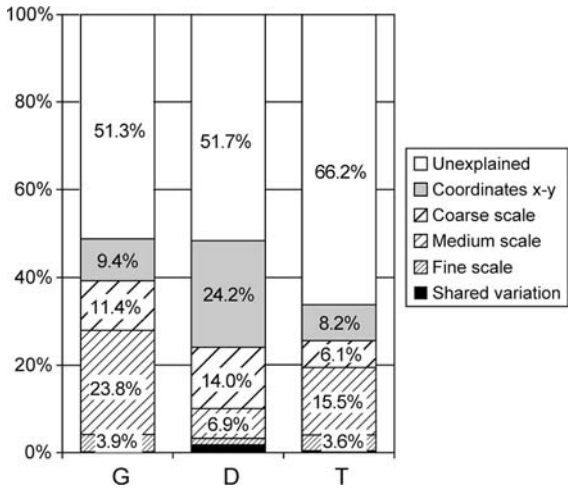

Figure 6. Spatial variation partitioning with partial RDA for each cattle effect (three rotations) constrained by geographic coordinates and significant PCNMs grouped into three scale classes (spatial variables only). Partitions smaller than 2% are drawn but not labelled. G: herbage removal; D: dung density; T: trampling effect.

contribution of environmental and spatial variables. Variation explained by spatial structure but not shared by other explanatory variables may reflect some contagious biological process (such as cattle herding behaviour), which is independent from environmental components included in the analysis (spatial autocorrelation *sensu* Legendre 1993). Alternatively, it may be due to a spatially structured, unmeasured factor.

For herbage removal, introduced structures were somewhat more important (22.3%) than natural structures (12.7%). The shared variation (spatial dependence *sensu* Legendre 1993) between spatial variables and the two other sets was high (Figure 7). The variables used here to describe introduced structures are geographic distances and thus are inherently spatial, so that the large overlap between introduced structures and spatial variables is not surprising. The variables have different underlying spatial models however, and the 1.3% variation explained by introduced structure variables alone reflects the difference between these models. The largest single partition in the model was 26.5%, explained by spatial structure alone.

For dung density, the most important set was the spatial structure (48.3%), while natural and introduced structures explained similar amounts (30.7 and 33.0% respectively). Most of the explained variation in the model was shared by the three sets of variables (25.9%) (Figure 7).

The effect of trampling was principally influenced by natural structures, which explained 39.1% of the variation, of which about half (20.5%) was shared with spatial structure. Introduced structures explained only 3.6% of the variation. With 33.8% of explained variation, spatial effects were less important than natural structures (Figure 7).

Discussion

Our first hypothesis, that the spatial pattern of cattle effects differs strongly between cattle activities, was strongly supported by the data. Areas with high dung-pat density did not correspond to the most or least grazed areas. This is consistent with the findings by Cook (1966), comparing the number of dung pats and the forage use by cattle.

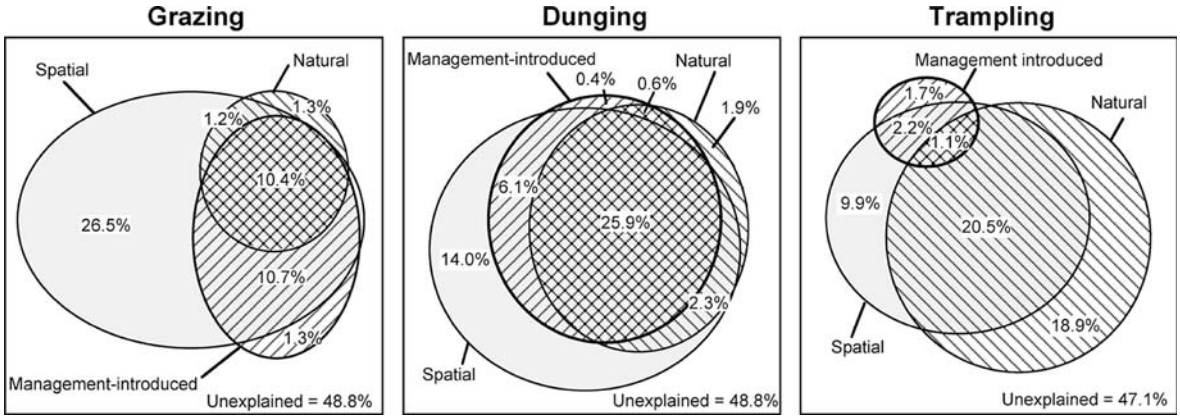

Figure 7. Variation partitioning with partial RDA for each cattle effect (three rotations) constrained by spatial, introduced and natural environmental variables. G: herbage removal; D: dung density; T: trampling effect.

Trampling effects were not strongest in high grazing or high dunging areas.

Second, we expected the spatial pattern of each cattle effect to weaken through the season. As forage is depleted, the cattle are forced to use less-preferred areas of the paddock, resulting in a more homogeneous pattern. This was true principally for foraging, but less so for trampling, perhaps due to resistance of some areas to trampling effects. The observable trampling effect is not reducible to trampling intensity but is strongly influenced by the sensitivity of the soil-vegetation complex (Roovers et al. 2004). The pattern of dunging was stable but intensified over the season. Changes within each cattle effect across time were smaller than differences between effects.

Results of correlation and ordination analyses supported our third hypothesis that the three cattle effects are influenced by different environmental conditions. In particular, the relative importance of introduced and natural landscape features for explaining patterns was very different between cattle effects.

Results for herbage removal suggest that at the beginning of the season, when resources were abundant everywhere, heifers grazed preferentially near the wire fence, and later chose places with high fodder potential. Owens et al. (1991) also documented the importance of introduced structures on the utilisation patterns of a paddock. Forage quality, measured as fodder potential and negatively correlated with tree cover (Miller and Krueger 1976), seemed to play a role only by the third rotation, when almost all the paddock area was grazed. In contrast to many authors (e.g., Roath and Krueger 1982; Pinchak et al. 1991), we found that distance to water was not a strong predictor, possibly because it was never large. Hart et al. (1993) showed that herbage removal was more uniform in small pastures than in larger areas because the travel distance to water was shorter.

In contrast, dung deposition occurred mostly in flat, open areas without rock outcrops and with low tree and shrub covers near the centre of the paddock. Costa et al. (1990) has also shown slope to be the main factor. Flat areas are chosen by cattle as resting places (Peterson and Woolfolk 1955; Senft et al. 1985; Jewell 2002; Gander et al. 2003) and dung drop occurs mainly at the end of the rest. Low tree cover, few rock outcrops and high fodder potential are also linked to resting places. Trampling effects tended to occur in wooded areas and in rocky areas with poor forage quality. There was a clear influence of natural structure but no evidence for a direct influence of introduced structure. Areas with high tree cover serve as refuge places during rain or hot periods (Mitlohner et al. 2001), but their understorey vegetation is also naturally sparse and the trampling effect is thus more important and visible. A high percentage of rock outcrops corresponds generally to a low soil thickness, which is more easily affected by trampling. Thus, the observed trampling pattern is influenced by both site conditions and cattle behaviour.

Spatial analysis showed significant autocorrelation and systematic differences in the patterns of

the three cattle effects. All distributions were significantly autocorrelated for short distances, suggesting a contagious process, which is not unexpected for gregarian animals (Shiyomi and Tsuiki 1999). Social links are strong and heifers are rarely observed in groups of less than 10 individuals, generally all engaged in the same activity (Roath and Krueger 1982; Pratt et al. 1986). Shiyomi and Tsuiki (1999) showed that the strength of aggregation varied with activity: lower during resting than for feeding and highest while moving. This is consistent with the degree of autocorrelation of each cattle effect we measured. Patterns did not seem to be at the same scale for the three effects: the two partial RDA analyses suggested that the dunging pattern was more coarse-grained than the others.

Spatial autocorrelation that is not explained by environmental factors may be a result of cattle behaviour or a response to hidden environmental variables. The degree of autocorrelation was different between cattle effects and leads to new hypotheses about possible mechanisms. In particular, a large amount of spatial structure in herbage removal remained unexplained. Little is known about cattle behaviour in highly heterogeneous ecosystems and further observations, taking into account differences among breeds (hill climbers and bottom dwellers), age and nursing status (Bailey et al. 2001), as well as management practices, are needed.

If, as we expect, the observed patterns of habitat use are consistent over many years, differences in spatial distribution of cattle effects at the landscape level may have important ecosystem implications (Jewell 2002; Gander at al. 2003). In particular, the spatial segregation of feeding and excretion should lead to a transfer of nutrients from feeding places to resting places, with trampling effects concentrated in intermediate situations, i.e. moving places. The summer of 2001 was a normal season with respect to climatic and management conditions. However, patterns might vary in warm and dry conditions, as suggested by results from intensive pasture systems, where the heterogeneity of the spatial distribution of faeces and urine was increased (White et al. 2001). A more precise assessment of nutrient transfer and its implication on grass growth and nutrient leaching requires a modelling approach (McGechan and Topp 2004).

Conclusion

We have shown that the patterns of grazing, dunging and trampling systematically differed in a heterogeneous wooded pasture. These overlapping patterns will lead to variable and changing local combinations of biotic constraints and disturbances, affecting vegetation dynamics. Cattle maintain complex interactions with vegetation and thus contribute to its variability and heterogeneity in the landscape. Cattle activity, which is influenced by landscape structure, maintains and reinforces this heterogeneous structure, particularly through a positive feedback loop involving shrub cover, tree cover and fodder potential (Gillet et al. 2002). Dynamic, spatially explicit models calibrated with experimental data are needed to specify optimal stocking rates taking into account the spatial heterogeneity of grazing pressure and to predict effects of management-introduced structures. By considering natural structures when paddock limits and watering points are defined, the efficiency of introduced structures as tools for managing cattle habitat use may be increased.

Our results show that it is necessary to distinguish the three components of cattle effect in spatially explicit dynamic models of silvopastoral ecosystems. Research in grazing ecology clearly needs to consider spatial patterns and how results may be affected by the choice of sampling locations. By emphasizing the role of spatial heterogeneity in grazing systems, this study bridges rangeland management with landscape ecology and opens new perspectives in the spatial modelling of livestock–vegetation interactions at the landscape level.

Acknowledgments

We acknowledge support from the Swiss National Science Foundation (grant number 31- 64116.00 and NCCR Plant Survival). We are also grateful to Daniel Borcard, Jianguo Wu and two anonymous reviewers for their useful comments.

References

Anderson D.M. and Kothmann M.M. 1980. Relationship of distance traveled with diet and weather for hereford heifers. J. Range Manage. 33: 217–220.

Bailey D.W., Gross J.E., Laca E.A., Rittenhouse L.R., Coughenour M.B., Swift D.M. and Sims P.L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. J. Range Manage. 49: 386–400.

Bailey D.W., Kress D.D., Anderson D.C., Boss D.L. and Miller E.T. 2001. Relationships between terrain use and performance of beef cows grazing foothill rangeland. J. Animal Sci. 79: 1883–1891.

Borcard D., Legendre P. and Drapeau P. 1992. Partialling out the spatial components of ecological variation. Ecology 73: 1045–1055.

Borcard D. and Legendre P. 2001. SpaceMaker Program. Département de sciences biologiques, Université de Montréal, URL http://www.fas.umontreal.ca/BIOL/legendre/.

Borcard D. and Legendre P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecol. Model. 153: 51–68.

Borcard D., Legendre P., Avois-Jacquet C. and Tuomisto H. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85: 1826–1832.

Brind'Amour A., Boisclair D., Legendre P. and Borcard D. 2005. Multiscale spatial distribution of a littoral fish community in relation to environmental variables. Limnol. Oceanogr. 50: 465–479.

Cook C.W. 1966. Factors affecting utilization of mountain slopes by cattle. J. Range Manage. 19: 200–204.

Costa G., Mosimann E. and Zagni C. 1990. Effet de la présence nocturne au pâturage sur les performances d'un troupeau laitier et sur ses restitutions à l'alpage. Fourrages 123: 305–311.

Coughenour M.B. 1991. Spatial components of plant–herbivore interactions in pastoral, ranching, and native ungulate ecosystems. J. Range Manage. 44: 530–542.

Cousins S.A.O., Lavorel S. and Davies I. 2003. Modelling the effects of landscape pattern and grazing regimes on the persistence of plant species with high conservation value in grasslands in south-eastern Sweden. Landscape Ecol. 18: 315–332.

Deckers J.A., Nachtergaele F.O. and Spaargaren O.C. (ed.)1998. World Reference Base for Soil Resources: Introduction. Publishing Company Acco, Leuven, The Netherlands.

Dungan J.L., Perry J.N., Dale M.R.T., Legendre P., Citron-Pousty S., Fortin M.J., Jakomulska A., Miriti M. and Rosenberg M.S. 2002. A balanced view of scale in spatial statistical analysis. Ecography 25: 626–640.

Dutilleul P. 1993. Modifying the t test for assessing the correlation between two spatial processes. Biometrics 49: 305–314.

Etienne M. 1996. Western European Silvopastoral SystemsINRA Editions, Paris, France.

Gander A., Rockmann A., Strehler C. and Güsewell S. 2003. Habitat use by Scottish Highland cattle in a lakeshore wetland. Bull. Geobot. Inst. ETH 69: 3–13.

Gillet F., Besson O. and Gobat J.M. 2002. PATUMOD: a compartment model of vegetation dynamics in wooded pastures. Ecol. Model. 187: 267–290.

Gillet F. and Gallandat J.D. 1996. Integrated synusial phytosociology: some notes on a new, multiscalar approach to vegetation analysis. J. Veg. Sci. 7: 13–18.

Hahn B.D., Richardson F.D. and Starfield A.M. 1999. Frame-based modelling as a method of simulating rangeland production systems in the long term. Agricult. Syst. 62: 29–49.

Hart R.H., Bissio J., Samuel M.J. and Waggoner J.W. 1993. Grazing systems, pasture size, and cattle grazing behavior, distribution and gains. J. Range Manage. 46: 81–87.

Havlicek E. and Gobat J.M. 1996. Les apports éoliens dans les sols du Jura: état des connaissances et nouvelles données en pâturages boisés. Etude et Gestion des Sols 3: 167–178.

Hester A.J. and Baillie G.J. 1998. Spatial and temporal patterns of heather use by sheep and red deer within natural heather/grass mosaics. J. Appl. Ecol. 35: 772–784.

Jelinski D.E. and Wu J. 1996. The modifiable areal unit problem and implications for landscape ecology. Landscape Ecol. 11: 129–140.

Jewell P. 2002. Impact of cattle grazing upon vegetation of an Alpine pasture. Ph.D. Thesis. ETHZ, Zurich, Switzerland, 304 pp.

Kohler F., Gillet F., Gobat J.-M. and Buttler A. 2004. Seasonal vegetation changes in mountain pastures due to simulated effects of cattle activity. J. Veg. Sci. 15: 143–150.

Legendre P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74: 1659–1673.

Legendre P. 2001. Program Mod_t_test. Département de sciences biologiques, Université de Montréal.URL http://www.fas.umontreal.ca/BIOL/legendre/.

Legendre P. and Legendre L. 1998. Numerical Ecology, 2nd English edition. Elsevier Science BV, Amsterdam, The Netherlands.

Marsh R. and Campling R.C. 1970. Fouling of pastures by dung. Herbage Abstracts 40: 123–130.

McGechan M.B. and Topp C.F.E. 2004. Modelling environmental impacts of deposition of excreted nitrogen by grazing dairy cows. Agricult. Ecosyst. Environ. 103: 149–164.

Miller R.F. and Krueger W.C. 1976. Cattle use on summer foothill rangelands in Northeastern Oregon. J. Range. Manage. 29: 367–371.

Mitlohner F.M., Morrow J.L., Dailey J.W., Wilson S.C., Galyean M.L., Miller M.F. and McGlone J.J. 2001. Shade and water misting effects on behavior, physiology, performance, and carcass traits of heat-stressed feedlot cattle. J. Animal Sci. 79: 2327–2335.

Økland R.H. and Eilertsen O. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. J. Veg. Sci. 5: 117–126.

Olff H. and Ritchie M.E. 1998. Effects of herbivores on grassland plant diversity. Trends Ecol. Evol. 13: 261–265.

Osuji P.O. 1974. The physiology of eating and the energy expenditure of the ruminant at pasture. J. Range Manage. 27: 437–443.

Owens M.K., Launchbaugh K.L. and Holloway J.W. 1991. Pasture characteristics affecting spatial-distribution of utilization by cattle in mixed brush communities. J. Range Manage. 44: 118–123.

Perrenoud A., Känzig-Schoch U., Schneider O. and Wettstein O. 2003. Exploitation durable des pâturages boisés. Un exemple appliqué du Jura suisse. Nachhaltige Bewirtschaftung von Wytweiden. Ein Fallbeispiel aus dem Schweizer Jura. Editions Haupt, Zürich, Switzerland.

Petersen R.G., Lucas H.L. and Woodhouse W.W. 1956. The distribution of excreta by freely grazing cattle and its effect on pasture fertility. I. Excretal distribution. Agron. J. 48: 440–444.

Peterson P.R. and Gerrish J.R. 1996. Grazing systems and spatial distribution of nutrients in pastures: livestock management considerations. In: Joost R.E. and Roberts C.A. (eds), Nutrient Cycling in Forage Systems. Potash and Phosphate Institute and the Foundation for Agronomy Research, Manhattan, Kansas, USA, pp. 203–212.

Peterson R.A. and Woolfolk E.J. 1955. Behavior of hereford cows and calves on short grass range. J. Range Manage. 8: 51–57.

Pinchak W.E., Smith M.A., Hart R.H. and Waggoner J.W. 1991. Beef-cattle distribution patterns on foothill range. J. Range Manage. 44: 267–275.

Pratt R.M., Putman R.J., Ekins J.R. and Edwards P.J. 1986. Use of habitat by free-ranging cattle and ponies in the New Forest, Southern England. J. Appl. Ecol. 23: 539–557.

Putman R.J., Pratt R.M., Ekins J.R. and Edwards P.J. 1987. Food and feeding-behavior of cattle and ponies in the New Forest, Hampshire. J. Appl. Ecol. 24: 369–380.

R Development Core Team. 2004. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org.

Rice R.W., MacNeil M.D., Jenkins T.G. and Koong L.J. 1983. Simulation of the herbage/animal interface of grazioso land. In: Lauenroth W.K., Skogerboe G.V. and Flug M. (eds), Analysis of Ecological Systems: State-of-the-Art in Ecological Modeling. Developments in Ecological Modelling 5.. Elsevier, Amsterdam, The Netherlands, pp. 475–488.

Roath L.R. and Krueger W.C. 1982. Cattle grazing and behavior on a forested range. J. Range Manage. 35: 332–338.

Roovers P., Verheyen K., Hermy M. and Gulink H. 2004. Experimental trampling and vegetation recovery in some forest and heathland communities. Appl. Veg. Sci. 7: 111–118.

Schutz M., Risch A.C., Leuzinger E., Krusi B.O. and Achermann G. 2003. Impact of herbivory by red deer (*Cervus elaphus* L.) on patterns and processes in subalpine grasslands in the Swiss National Park. Forest Ecol. Manage. 181: 177–188.

Senft R.L., Coughenour M.B., Bailey D.W., Rittenhouse L.R., Sala O.E. and Swift D.M. 1987. Large herbivore foraging and ecological hierarchies. BioScience 37: 789–797.

Senft R.L., Rittenhouse L.R. and Woodmansee R.G. 1985. Factors influencing patterns of cattle grazing behavior on shortgrass steppe. J. Range Manage. 38: 82–87.

Shiyomi M. and Tsuiki M. 1999. Model for the spatial pattern formed by a small herd in grazing cattle. Ecol. Model. 119: 231–238.

Tate K.W., Atwill E.R., McDougald N.K. and George M.R. 2003. Spatial and temporal patterns of cattle feces deposition on rangeland. J. Range Manage. 56: 432–438.

ter Braak C.J.F. and Smilauer P. 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, New York, USA.

Thompson C.M. and McGarigal K. 2002. The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). Landscape Ecol. 17: 569–586.

Turner M.G. 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. System. 20: 171–197.

Turner M.G., Gardner R.H. and O'Neill R.V. 2001. Landscape Ecology in Theory and Practice: Pattern and Process. Springer-Verlag, New York, NY, USA.

Van Oene H., Van Deursen E.J.M. and Berendse F. 1999. Plant–herbivores interaction and its consequences for succession in wetland ecosystems: a modelling approach. Ecosystems 2: 122–138.

Van Rees H. and Hutson G.D. 1983. The behavior of free-ranging cattle on an alpine range in Australia. J. Range Manage. 36: 740–743.

Verweij P.A. 1995. Spatial and temporal modelling of vegetation patterns. Burning and grazing in the paramo of Los Nevados National Park, Colombia. Ph.D. Thesis. International Institute for Geo-Information Science and Earth Observation: Enschede, The Netherlands, 234 pp.

Weber G.E., Jeltsch F., Van Rooyen N. and Milton S.J. 1998. Simulated long-term vegetation response to grazing heterogeneity in semi-arid rangelands. J. Appl. Ecol. 35: 687–699.

White S.L., Sheffield R.E., Washburn S.P., King L.D. and Green J.T. 2001. Spatial and time distribution of dairy cattle excreta in an intensive pasture system. J. Environ. Qual. 30: 2180–2187.

Wiens J.A. 1989. Spatial scaling in ecology. Funct. Ecol. 3: 385–397.

Wu J. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. Landscape Ecol. 19: 125–138.

Wu J. and David J.L. 2002. A spatially explicit hierarchical approach to modelling complex ecological systems: theory and applications. Ecol. Model. 153: 7–26.

Wu J. and Hobbs R. 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landscape Ecol. 17: 355–365.