Satellite derived vegetation indices as surrogate of species richness and abundance of ground beetles in temperate floodplains

5 authors, including:

Denis Lafage
LOGRAMI
44 PUBLICATIONS **282** CITATIONS

Jean Secondi
LEHNA University of Lyon 1 ; University of Angers,
110 PUBLICATIONS **2,576** CITATIONS

Anita Georges
Université de Rennes 1
7 PUBLICATIONS **172** CITATIONS

Julien Pétillon
Université de Rennes 1
135 PUBLICATIONS **1,534** CITATIONS

Some of the authors of this publication are also working on these related projects:

Project Sensory ecology of Caudata View project

Project Evolutionary ecology and conservation of amphibian invasions View project

Satellite-derived vegetation indices as surrogate of species richness and abundance of ground beetles in temperate floodplains

DENIS LAFAGE,[1,2] JEAN SECONDI,[2] ANITA GEORGES,[3] JAN-BERNARD BOUZILLÉ[3] and JULIEN PÉTILLON[1]   [1]URU 420, UMR CNRS UPMC 7204, Muséum National d'Histoire National, Université de Rennes 1, Rennes Cedex, France, [2]LUNAM, GECCO, Université d'Angers, Angers, France and [3]UMR CNRS 6553 Ecobio, Université de Rennes 1, Rennes Cedex, France

Abstract. 1. Remotely sensed data are frequently employed for monitoring vegetation and for estimating herbivore diversity. Their use for predicting predator arthropod species abundance and richness has also been investigated with success for ants and beetles in forests using normalised difference vegetation index (NDVI) and for beetles in mountain forests using light detection and ranging data.

2. We investigated whether vegetation indices, derived from multispectral SPOT imagery could predict abundance and species richness of ground active spiders and ground beetles in a new ecological context, the floodplain meadows of the Loire River in Western Europe. Using pitfall traps, we collected carabids and spiders in the field.

3. Maximum vegetation height, litter-depth and plant species richness best explained species assemblages of both groups (multivariate analyses). NDVI and enhanced vegetation index (EVI 2) were strongly related to activity-density and species richness for ground beetles only, EVI 2 being the best surrogate. Relationships between vegetation indices and spider assemblage patterns were either non-significant or weak.

4. We demonstrated that EVI 2 is a good surrogate of the abundance and richness of carabid species in a temperate floodplain, and has potential as a low cost method for mapping arthropod assemblages at large spatial scales.

5. Our approach provides a tool which contributes to biodiversity assessment at large spatial scales. It can also contribute to the prioritisation of conservation areas and early change detection, as carabids are keystone indicators.

Key words. Arthropod, floodplain, Loire River, meadow, remote sensing, surrogate taxa.

Introduction

One current challenge in conservation biology is to assess and monitor biodiversity over coarse spatial scales. Several indices derived from satellite imagery provide rela-

tively cost-efficient solutions to achieve this goal. The normalised difference vegetation index (NDVI) is one of the most used of those (reviewed in Pettorelli *et al.*, 2011). NDVI depends on the reflectance peak of vegetation in the infra-red (Tucker & Sellers, 1986). It is highly correlated with photosynthetically active radiation absorbed by the plant canopy, photosynthetic capacity, net primary production, leaf area index, fraction of absorbed photosynthetically active radiation, carbon assimilation and evapotranspiration (e.g. Buermann *et al.*, 2002; Wang

Correspondence: Denis Lafage, URU 420, UMR CNRS UPMC 7204, Muséum National d'Histoire National, Université de Rennes 1, 263 Avenue du Général Leclerc, CS 74205, 35042 Rennes Cedex, France. E-mail: lafage.denis@gmail.com

et al., 2005). It thus constitutes an informative proxy to monitor photosynthesis over time, and perform temporal and spatial vegetation surveys (Myneni *et al.*, 1997). A refined form of NDVI is now being used: the enhanced vegetation index (EVI) and its adaptation for SPOT images (EVI 2). EVI and EVI 2 were developed to optimise the vegetation signal (because they are less sensitive to saturation with high biomass and to vegetation background) and to reduce atmosphere influences (Huete *et al.*, 2002).

Furthermore, spectral vegetation indices have proved useful to predict changes in herbivore (e.g. African ungulates: Pettorelli *et al.*, 2009) and non-herbivore (e.g. brown bears: Wiegand *et al.*, 2008) vertebrate distribution, abundance and life history traits (Pettorelli *et al.*, 2011), distribution of invertebrate disease vectors (Daniel *et al.*, 1998) or pests in grasslands, forests and crops (Dreiser, 1994; Brewster *et al.*, 1999). So far, very few studies have investigated the predictive capacity of NDVI for ground-dwelling non-herbivore arthropods. Jiménez-Valverde and Lobo (2006) modelled *Macrothele calpeiana* (Araneae, Hexathelidae) distribution but found no influence of NDVI. But, two studies reported positive relationships in ants (Lassau *et al.*, 2005) and carabids (Lassau & Hochuli, 2008) in Australian forests. Investigations are now focusing on the predictive power of airborne laser scanning (light detection and ranging: LiDAR). Müller and Brandl (2009) demonstrated the high predictive power of LiDAR-derived variables for beetles' assemblages. Despite its efficiency, LiDAR technology remains expensive in comparison with multispectral imagery acquisition, thus limiting its applications for large areas. The goal of our study was to test whether NDVI and EVI 2 derived from multispectral images is a good predictor of carabid and spider abundance and diversity in a new habitat: the temperate floodplain grasslands of Western Europe.

Materials and methods

The study site is located near Angers, Western France (0°32′37.7″W, 47°30′05.6″N). It is a 600 ha island circled by two rivers that is flooded about 3 months each year. Land cover is dominated by hay meadows and to a lesser extent by poplar groves. Grasslands are cut in summer and grazed in autumn. Arthropods were sampled on five parcels, four (A, B, C, D covering, respectively, 2.9, 1.4, 1.9, 1.2 ha) of which were under an environmental scheme which delays mowing to a fixed date and one (E covering 0.4 ha) which has been left unmanaged for 20 years (Fig. 1). Sampling was performed from May to June 2011, before the first mowing took place. This period corresponds to the peak of vegetation productivity in our study system.

We set 10 pitfall traps (100 mm diam.) per parcel that were located at least 25 m from parcel edges and regularly distributed following a grid pattern (20 m apart) to avoid, respectively, edge effects and interaction between traps (Topping & Sunderland, 1992). Pitfall traps were filled with preservative solution (50% monoethylene glycol, 50% water) and emptied every 2 weeks (three times during the sampling period).

Phytosociological data were recorded in June in a 1 m² quadrat around each trap using the Braun-Blanquet (1928) method: within each plot, a cover value was attributed to each plant species following the Braun-Blanquet scale. Maximum vegetation height, height of the dominant vegetation layer and litter depth were measured to the nearest centimetre. Soil conductivity, moisture and temperature were measured in May and June using a W.E.T. sensor (5 cm deep) connected to a moisture meter HH2 (both built by Delta-T Devices Ltd., Cambridge, UK). Two measurements within each quadrat were carried out.

One SPOT 5 HRG image (©CNES 2011 and 2012; Distribution Spot Image S.A.) with three bands (green, red, near infra-red) was acquired on 24 May 2011. To respect the rule stating that pixels should be two to five times smaller than the area of objects of interest (O'Neill *et al.*, 1996), we selected a product with 2.5 m resolution. The image was obtained from a pan-sharpened image (2.5 m resolution) and a multispectral image (10 m resolution). Pre-treatment of images was carried out by the CNES (Centre National d'Études Spatiales). It includes geometrical correction, radiometric correction of distortions due to differences in sensitivity of the elementary detectors of the viewing instrument, geometric correction of systematic effects (panoramic effect, Earth curvature and rotation) and radiometric distortion geometry. Atmospheric correction of the image was not realised.

NDVI and EVI 2 were computed using Grass GIS software 6.4.1 (GRASS Development Team, 2012) applied to a SPOT image (2.5 m resolution, three bands) acquired on the 24 May 2011.

NDVI is defined as: $NDVI = (R_{NIR} - R_{red})/(R_{NIR} + R_{red})$. EVI 2 is defined as $EVI\ 2 = 2.5*(R_{NIR} - R_{red})/(R_{NIR} + 2.4*R_{red} + 1)$, where R_{NIR} and R_{red} refer to the reflectance values derived from spectral radiances measured by the near-infrared channel and the red visible channel, respectively.

NDVI and EVI2 range from −1 (deep water) to 1 (maximum vegetation greenness).

To analyse the patterns of species composition, multivariate analyses were performed on activity-densities of each species (log (*n*+1) with n being the number of individuals captured per day and per trap; referred as 'abundance' thereafter). Following Legendre and Gallagher (2001), species activity-densities were transformed to a Bray–Curtis distance matrix prior to a redundancy analysis (RDA). In the RDA the distance matrix was the response variable and the environmental variables were the predictors. A forward selection procedure was used to select the environmental variables explaining the most variance in the Bray–Curtis distance matrix. Monte Carlo tests with 999 permutations were carried out to test the significance of the selected environmental factors and RDA axes.
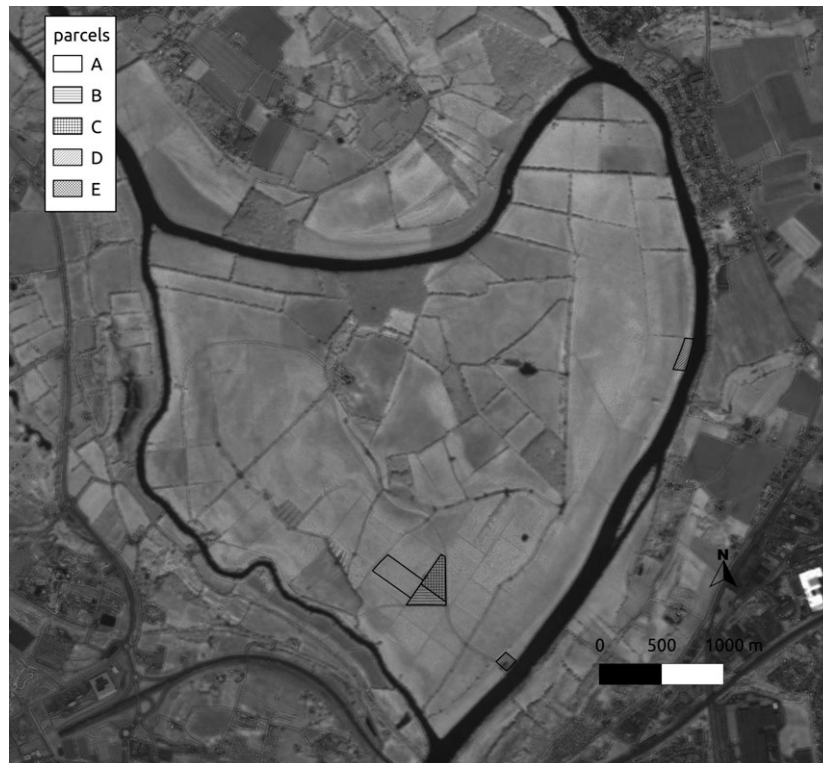
Fig. 1. Cartography of the study site with parcel sampled. Background is a greyscale SPOT image.

Phytosociological relevés were classified by Two-Way Indicator Species Analysis, TWINSPAN (Hill, 1979) under JUICE software (Tichý, 2002). Classification was carried out following the typology proposed by de Foucault (1984) to the alliance level. Each alliance corresponded to a parcel type.

To evaluate the ability of vegetation indices to predict arthropod assemblage (total activity-density and species-richness) we used analyses of covariance (ANCOVA). Species richness and activity-density were response variables, 'type of parcel' categorical fixed factor, and NDVI or EVI 2 continuous covariate (Model 1; García-Berthou, 2001). If the interaction between 'type of parcel' and NDVI or EVI 2 was not significant, a Model 2 ANCOVA assuming homogeneity of slopes was performed. If the interaction was significant, the data from both types of parcels were analysed separately with respect to their NDVI or EVI 2 (Model 3). When interaction was not significant and NDVI or EVI 2 was significant, a linear regression was performed with NDVI and EVI 2 as explanatory variable. Statistics were computed using R software 2.14.1. (R Development Core team, 2011). Models with lower Akaike information criterion (AIC) scores were selected (Akaike, 1974).

Results

A total of 5065 adult carabids and 9969 spiders (7431 adults) belonging to 63 and 42 species, respectively, were collected. Two carabid species *Poecillus cupreus* (Linnaeus, 1758) and *Harpalus ruffipes* (De Geer, 1774) accounted for more than 51% of carabids. Among spiders, Lycosidae were highly dominant (83.8% of individuals) followed by Thomisidae (5.6%). One species accounted for 54.8% of individuals: *Pardosa prativaga* (Clerk, 1757). NDVI values ranged from 0.17 to 0.255. EVI 2 values ranged from 0.27 to 0.50.

Only the first RDA axis was significant for carabids ($F_{1,42} = 17.90$, $P = 0.005$, 81.7% of total inertia explained) and for spiders ($F_{1,42} = 11.82$, $P = 0.005$, 80.1% of total inertia explained). They segregated sites according to litter depth and number of plant species for carabids (Fig. 2) and to maximum vegetation height and number of plant species for spiders (Fig. 3). Maximum vegetation height and litter depth contributed positively to axis 1, and number of plant species negatively (Figs 2 and 3).

Twinspan analysis on vegetation relevés distinguished two groups of parcels. One (A, B, C) belonged to *Oenanthion fistulosae* (de Foucault, 1984), the second [D and E (unmanaged)] to *Bromion racemosi* (Tüxen in Tüxen & Preising, 1951).

Best AIC scores were obtained with EVI 2 for all models (Table 1) so we present only results for this index. For carabid beetles, we detected no significant interaction between EVI 2 and parcel type ($F_{2,46} = 0.24$, $P = 0.626$) (Table 2), a significant effect of parcel type ($F_{1,47} = 5.52$, $P = 0.023$) and a positive relationship between EVI 2 and activity-density ($F_{1,47} = 85.54$, $P < 0.001$). Linear regression
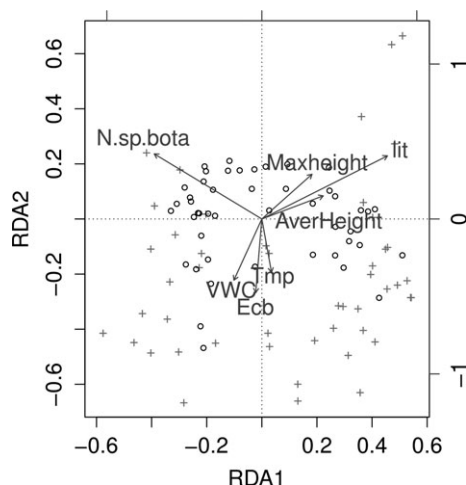
Fig. 2. Redundancy analysis (RDA) on carabid beetle species Bray-curtis distances. Sites are represented by crosses and species by circles. N.sp. bota, vegetation species richness; Maxheight, maximum height of vegetation; AverHeight, height of dominant vegetation layer; lit, litter depth; Tmp, soil temperature; VWC, soil humidity; ECb, soil conductivity.
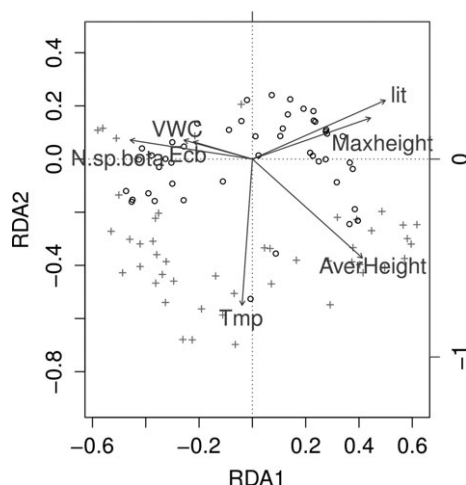

Fig. 3. Redundancy analysis (RDA) on spider species Bray-curtis distances. Sites are represented by crosses and species by circles. N.sp. bota, vegetation species richness; Maxheight, maximum height of vegetation; AverHeight, Height of dominant vegetation layer; lit, litter depth; Tmp, soil temperature; VWC, soil humidity; ECb, soil conductivity.

demonstrated a strong positive association between EVI 2 and carabid beetle activity-density (Fig. 4) ($P < 0.001$, $R^2_{adj.} = 0.61$).

A slightly different result was found for species richness (Table 2). We found no significant interaction between EVI 2 and parcel type ($F_{2,46} = 1.152$, $P = 0.289$), no effect of parcel type ($F_{1,47} = 0.13$, $P = 0.72$) and a positive relationship with EVI 2 ($F_{1,47} = 37.15$, $P<0.001$). Linear regression demonstrated a lower, but still significant, posi-

Table 1. Akaike information criterion (AIC) scores of models.

Dependant variables	Explicative variables	AIC
A carabids	NDVI	−83.25
	NDVI + parcel type	−92.46
	EVI 2	−88.9
	EVI 2 + parcel type	−94.23
S carabids	NDVI	248.7
	EVI 2	242.5
A spiders	NDVI	−35.9
	EVI 2	−36.12
S spiders	NDVI	228.8
	EVI 2	229.9

NDVI, normalised difference vegetation index; EVI, enhanced vegetation index.

tive association between EVI 2 and species richness ($P < 0.001$, $R^2_{adj.} = 0.42$) (Fig. 5).

For spider activity-density, we detected no significant interaction between EVI 2 and parcel type ($F_{2,46} = 3.74$, $P = 0.289$), no effect of parcel type ($F_{1,47} = 0.65$, $P = 0.426$) and a significant relationship with EVI 2 ($F_{1,47} = 5.16$, $P = 0.028$) (Table 2). For spider species richness, we found no interaction between parcel type and EVI 2 ($F_{2,46} = 0.08$, $P = 0.784$), no effect of parcel type ($F_{1,47} = 0.00$, $P = 0.996$) and a significant relationship with EVI 2 ($F_{1,47} = 5.48$, $P = 0.024$). Linear regressions showed significant, but weak associations between EVI 2 and activity-density and species richness for spiders ($P = 0.07$, $R^2_{adj.} = 0.07$ and $P = 0.08$, $R^2_{adj.} = 0.08$, respectively).

Discussion

We found a strong positive association between vegetation indices and carabid activity-density and species richness as Lassau and Hochuli (2008) did on forest carabids with NDVI. Best results were obtained with EVI 2 probably because this index is less sensitive to atmospheric perturbations. This positive association contradicts the well documented assumption that catches of Carabidae are greater in sparse than in dense grassland stands (e.g. Honek, 1988). This relationship could be explained by the 'bottom-up control of animal diversity' hypothesis (Siemann, 1998). The theory states that an increase in plant productivity may induce an increase in herbivore diversity by (i) increasing the activity-density of rare resources ('resource rarity hypothesis'), (ii) increasing herbivore activity-density and local persistence ('consumer rarity hypothesis') or (iii) increasing intra-specific density dependence ('density dependence hypothesis') (Siemann, 1998). Increasing the diversity of herbivores can finally increase the diversity of predators (Siemann, 1998). The positive but very weak associations between EVI 2 and spider species richness and activity-density ($r^2 < 0.10$) prevent us from considering EVI 2 as a surrogate of spider diversity. These results,

Table 2. ANCOVA and linear regressions on spider and carabid abundance (A) and species richness S. In ANCOVA F, P and R^2 values for parcel type and EVI 2 are given for model 2 (standard ANCOVA) as the interaction between EVI 2 and parcel type was not significant.

Dependant variables	Interaction EVI 2/parcel type	ANCOVA Independent variables Parcel type	EVI 2	Linear regression with NDVI Test	Model
A carabids	$F_{2,46} = 0.24$, $P = 0.626$	$F_{1,47} = 5.52$, $P = 0.023$	$F_{1,47} = 85.54$, $P < 0.001$	$P < 0.001$, $R^2_{adj.} = 0.61$	1.49*EVI 2 − 0.09
S carabids	$F_{2,46} = 1.15$, $P = 0.289$	$F_{1,47} = 0.13$, $P = 0.722$	$F_{1,47} = 37.15$, $P<0.001$	$P < 0.001$, $R^2_{adj.} = 0.42$	28.81*EVI 2 − 0.40
A spiders	$F_{2,46} = 3.74$, $P = 0.060$	$F_{1,47} = 0.65$, $P = 0.426$	$F_{1,47} = 5.16$, $P = 0.028$	$P = 0.028$, $R^2_{adj.} = 0.07$	0.67*EVI 2 + 0.48
S spiders	$F_{2,46} = 0.08$, $P = 0.784$	$F_{1,47} = 0.00$, $P = 0.996$	$F_{1,47} = 5.48$, $P = 0.024$	$P = 0.023$, $R^2_{adj.} = 0.08$	9.76*EVI 2 + 7.13

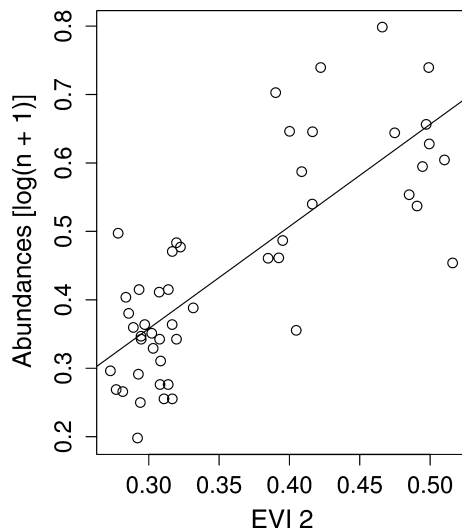NDVI, normalised difference vegetation index; EVI, enhanced vegetation index.

Fig. 4. Relationship between abundance (A) and EVI 2 in carabid beetles. Line corresponds to the linear regression model.
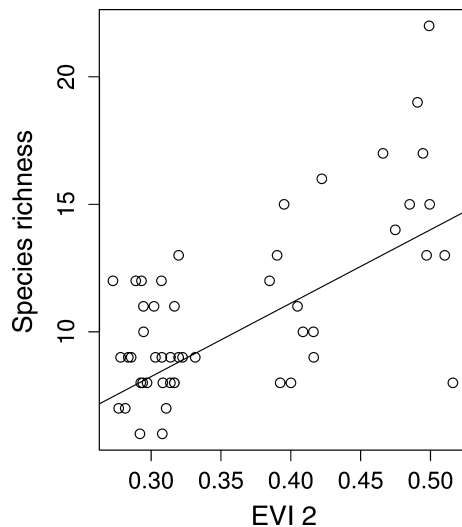

Fig. 5. Relationship between species richness (S) and EVI 2 in carabid beetles. Line corresponds to the linear regression model.

in accordance with Jiménez-Valverde and Lobo (2006), may be explained by the higher trophic level in spiders than in carabids (Girard *et al.*, 2011).

Litter depth and number of plant species best explained carabid species composition and maximum vegetation height and number of plant species best explained spiders species composition in our study area. Carabids are usually considered dependent on several abiotic and biotic factors, including: (i) temperature or humidity, (ii) food conditions, (iii) presence and distribution of competitors, and (iv) life history and season, including migration between hibernation and reproduction habitats (Lövei & Sunderland, 1996). In our study, assemblages of species were not related to temperature or humidity because of the small size of the study area, but this link may be difficult to demonstrate for all the population, as seasonal dynamics vary between species (Honek, 1997). Also, soil temperature was measured only twice during our study (to evaluate synchronic differences in assemblages among traps, and not with temporal changes), which was probably not sufficient to accurately assess the influence of this parameter on spiders and ground beetles.

It has been hypothesised that taxonomic diversity of plant species is directly correlated with the diversity of herbivores (the 'taxonomic diversity hypothesis') because to each additional plant species corresponds specialised consumers (e.g. Siemann, 1998). These effects might cascade up from plant diversity via herbivore diversity to predator diversity (Hunter & Price, 1992). In our case, plant species-richness was highly negatively correlated with EVI 2 and thus to species richness of carabid beetles. This could be explained by the presence of competitive plant species. In grasslands plant communities, highly competitive species (in our case *Elytrigia repens* and *Agrostis stolonifera*) reduce diversity and increase biomass (i.e. an increase in EVI 2) (Amiaud *et al.*, 2008). The 'Taxonomic diversity' (e.g. Siemann, 1998) and 'bottom-up control of animal diversity' (Siemann, 1998) hypotheses seem to reject each other in the floodplain grasslands studied.

Habitat variables that usually affect ground dwelling spider assemblages are litter depth (e.g. Lawrence & Wise 2004), vegetation structure (e.g. Downie *et al.*, 1995),

plant species composition (Dennis *et al.*, 2001) and soil moisture content (Ter Braak, 1986). Plant species-richness and the maximum height of vegetation are the two explanatory variables here. The positive association between EVI 2 and activity-density and species richness of spiders is significant but very weak. These results are in opposition with the assumption that catches of Lycosidae (the highly dominant family in our study) are greater on sparsely rather than densely vegetated ground (Honek, 1988).

Many studies have investigated relationships between arthropods and the abiotic environment (e.g. Sinclair *et al.*, 2006; Lessard *et al.*, 2011) but few studies specifically compared spiders' and carabids' responses to abiotic factors. Pétillon *et al.* (2008) demonstrated a similar positive response to soil moisture in both groups. In contrast, carabids showed no response to vegetation variables and litter depth, whereas spiders did. Our results are partly in opposition with those of Pétillon *et al.* (2008) as we did not find any effect of soil moisture on carabids and spiders. Both groups were sensitive to vegetation structure (maximum vegetation height for spider and litter-depth for carabids). Biases in capture efficiency of traps are reported in the literature. Indeed, high-density vegetation reduces the mobility of ground-dwelling arthropods (Thomas *et al.*, 2006) and might thus decrease the efficiency of the pitfall traps in densely vegetated habitats. In our case, catches were more numerous in high densely vegetated plots despite this possible bias. So, the bias in sampling efficiency caused by indirect effects of management (spatial variations of vegetation density) seems negligible or absent and specimens were really more numerous in densely vegetated plots.

In conclusion, EVI 2 can be used to estimate activity-density and species richness of carabids in floodplains. Considering the relatively low cost and increasing availability of multispectral images, EVI 2 seems to be a useful proxy of carabid populations over large areas. Remotely sensed imagery also allows plant diversity assessment (Rocchini *et al.*, 2007). Thus, EVI 2 could contribute to multitaxa biodiversity assessment and monitoring over large areas which meet the current demands of managers. It could also be used in prioritising conservation areas and early change detection, as carabids are considered as keystone indicators [group of species affecting its environment and therefore other species disproportionately strongly relative to its abundance (Mills *et al.*, 1993)].

Acknowledgements

References

Akaike, H. (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, **19**, 716–723.

Amiaud, B., Touzard, B., Bonis, A. & Bouzillé, J.-B. (2008) After grazing exclusion, is there any modification of strategy for two guerrilla species: *Elymus repens* (L.) Gould and *Agrostis stolonifera* (L.)? *Plant Ecology*, **197**, 107–117.

Braun-Blanquet, J. (1928) *Pflanzensoziologie. Grundzüge der Vegetationskunde*. Springer, Wien, AT.

Brewster, C.C., Allen, J.C. & Kopp, D.D. (1999) IPM from space: using satellite imagery to construct regional crop maps for studying crop-insects interaction. *American Entomologist*, **45**, 105–117.

Buermann, W., Dong, J., Zhou, L. & Myneni, R.B. (2002) Analysis of a multi-year global vegetation leaf area index data set. *Journal of Geophysical Research Atmospheres*, **107**, ACL 14-1–ACL 14-16.

Daniel, M., Kolar, J., Zeman, P., Pavelka, K. & Sadlo, J. (1998) Predictive ap of *Ixodes ricinus* high-incidence habitats and tick-borne encephalitis risk assessment using satellite data. *Experimental and Applied Acarology*, **22**, 417–433.

De Foucault, B. (1984) *Systémique, structure et synsystématique des prairies hygrophiles des plaines atlantiques françaises*. Tome I. Rouen Haute Normandie.

Dennis, P., Young, M.R. & Bentley, C. (2001) The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of Nardus stricta grassland in upland Scotland. *Agriculture, Ecosystems & Environment*, **86**, 39–57.

Downie, I.S., Butterfield, J.E.L. & Coulson, J.C. (1995) Habitat preferences of sub-montane spiders in northern England. *Ecography*, **18**, 51–61.

Dreiser, U. (1994) Mapping of desert locust habitats in Africa using landsat thematic mapper data. *GeoJournal*, **32**, 55–60.

García-Berthou, E. (2001) On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. *Journal of Animal Ecology*, **70**, 708–711.

Girard, J., Baril, A., Mineau, P. & Fahrig, L. (2011) Carbon and nitrogen stable isotope ratios differ among invertebrates from field crops, forage crops, and non-cropped land uses. *Ecoscience*, **18**, 98–109.

GRASS Development Team (2012) Geographic resources analysis support system (GRASS) software.

Hill, M.O. (1979) *TWINSPAN – A FORTRAN Program for Arranging Multivariate Data in An Ordered Two-Way Table by Classification of Individuals and Attributes*. Cornell University, New York, New York.

Honek, A. (1988) The effect of crop density and microclimate on pitfall trap catches of Carabidae, Staphylinidae (Coleoptera), and Lycosidae (Araneae) in cereal fields. *Pedobiologia*, **32**, 233–242.

Honek, A. (1997) The effect of temperature on the activity of Carabidae (Coleoptera) in fallow field. *European Journal of Entomology*, **94**, 97–104.

Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X. & Ferreira, L.G. (2002) Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, **83**, 195–213.

Hunter, M.D. & Price, P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, **73**, 724–732.

Jiménez-Valverde, A. & Lobo, J.M. (2006) Distribution determinants of endangered Iberian spider *Macrothele calpeiana* (Araneae, Hexathelidae). *Environmental Entomology*, **35**, 1491–1499.

Lassau, S.A., Cassis, G., Flemons, P.K.J., Wilkie, L. & Hochuli, D.F. (2005) Using high-resolution multi-spectral imagery to estimate habitat complexity in open-canopy forests: can we predict ant community patterns? *Ecography*, **28**, 495–504.

Lassau, S.A. & Hochuli, D.F. (2008) Testing predictions of beetle community patterns derived empirically using remote sensing. *Diversity and Distributions*, **14**, 138–147.

Lawrence, K.L. & Wise, D.H. (2004) Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia*, **48**, 149–157.

Legendre, P. & Gallagher, E. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.

Lessard, J.-P., Sackett, T.E., Reynolds, W.N., Fowler, D.A. & Sanders, N.J. (2011) Determinants of the detrital arthropod community structure: the effects of temperature and resources along an environmental gradient. *Oikos*, **120**, 333–343.

Lövei, G.L. & Sunderland, K.D. (1996) Ecology and behaviour of ground beetles (Coleoptera: Carabidae). *Annual review of entomology*, **41**, 231–256.

Mills, L.S., Soulé, M.E. & Doak, D.F. (1993) The keystone-species concept in ecology and conservation. *BioScience*, **43**, 219–284.

Müller, J. & Brandl, R. (2009) Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. *Journal of Applied Ecology*, **46**, 897–905.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asar, G. & Nemani, R.R. (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.

O'Neill, R.V., Hunsaker, C.T., Timmins, S.P., Jackson, B.L. & Jones, K.B. (1996) Scale problems in reporting landscape pattern at the regional scale. *Landscape Ecology*, **11**, 169–180.

Pétillon, J., Georges, A., Canard, A., Lefeuvre, J.-C., Bakker, J.P. & Ysnel, F. (2008) Influence of abiotic factors on spider and ground beetle communities in different salt-marsh systems. *Basic and Applied Ecology*, **9**, 743–751.

Pettorelli, N., Bro-Jørgensen, J., Durant, S.M., Blackburn, T. & Carbone, C. (2009) Energy availability and density estimates in African ungulates. *The American Naturalist*, **173**, 698–704.

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M. & Kausrud, K. (2011) The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Climate Research*, **46**, 15–27.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*.

Rocchini, D., Ricotta, C. & Chiarucci, A. (2007) Using satellite imagery to assess plant species richness: the role of multispectral systems. *Applied Vegetation Science*, **10**, 325–331.

Siemann, E. (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, **79**, 2057–2070.

Sinclair, B.J., Scott, M.B., Klok, C.J., Terblanche, J.S., Marshall, D.J., Reyers, B. & Chown, S.L. (2006) Determinants of terrestrial arthropod community composition at Cape Hallett, Antarctica. *Antarctic Science*, **18**, 303–312.

Ter Braak, C.J.F. (1986) Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167–1179.

Thomas, C.F.G., Brown, N.J. & Kendall, D.A. (2006) Carabid movement and vegetation density: Implications for interpreting pitfall trap data from split-field trials. *Agriculture, Ecosystems & Environment*, **113**, 51–61.

Tichý, L. (2002) JUICE, software for vegetation classification. *Journal of Vegetation Science*, **13**, 451–453.

Topping, C. & Sunderland, K.D. (1992) Limitations to the pitfall traps in ecological-studies exemplified by a study of spiders in a field of winter-wheat. *Journal of Applied Ecology*, **29**, 485–491.

Tucker, C.J. & Sellers, P.J. (1986) Satellite remote sensing of primary production. *International Journal of Remote Sensing*, **7**, 1395–1416.

Tüxen, R. & Preising, E. (1951) *Erfahrungsgrundlagen fuer die pflanzensoziologische Kartierung des westdeutschen Gruendlandes*. Stolzenau, Weser, Germany.

Wang, Q., Adiku, S., Tenhunen, J. & Granier, A. (2005) On the relationship of NDVI with leaf area index in a deciduous forest site. *Remote Sensing of Environment*, **94**, 244–255.

Wiegand, T., Naves, J., Garbulsky, M.F. & Fernandez, N. (2008) Animal habitat quality and ecosystem functioning: exploring seasonal patterns using NDVI. *Ecological Monographs*, **78**, 87–103.