



Can we predict butterfly diversity along an elevation gradient from space?

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An important challenge in ecology is to predict patterns of biodiversity across eco-geographical gradients. This is particularly relevant in areas that are inaccessible, but are of high research and conservation value, such as mountains. Potentially, remotely-sensed vegetation indices derived from satellite images can help in predicting species diversity in vast and remote areas via their relationship with two of the major factors that are known to affect biodiversity: productivity and spatial heterogeneity in productivity. Here, we examined whether the Normalized Difference Vegetation Index (NDVI) can be used effectively to predict changes in butterfly richness, range size rarity and beta diversity along an elevation gradient. We examined the relationship between butterfly diversity and both the mean NDVI within elevation belts (a surrogate of productivity) and the variability in NDVI within and among elevation belts (surrogates for spatial heterogeneity in productivity). We calculated NDVI at three spatial extents, using a high spatial resolution QuickBird satellite image. We obtained data on butterfly richness, rarity and beta diversity by field sampling 100 m quadrats and transects between 500 and 2200 m in Mt Hermon, Israel. We found that the variability in NDVI, as measured both within and among adjacent elevation belts, was strongly and significantly correlated with butterfly richness. Butterfly range size rarity was strongly correlated with the mean and the standard deviation of NDVI within belts. In our system it appears that it is spatial heterogeneity in productivity rather than productivity per se that explained butterfly richness. These results suggest that remotely-sensed data can provide a useful tool for assessing spatial patterns of butterfly richness in inaccessible areas. The results further indicate the importance of considering spatial heterogeneity in productivity along elevation gradients, which has no lesser importance than productivity in shaping richness and rarity, especially at the local scale.

Elevation gradients and species diversity

Ecologists have a long lasting interest in diversity patterns across spatial gradients (Rosenzweig 1995, Lomolino 2001). Many earlier studies have examined changes in biodiversity along elevation gradients, yet no single spatial pattern has been identified thus far (Shmida and Wilson 1985, Rahbek 1995, 2005, Lomolino 2001, Grytnes and McCain 2007, Nogués-Bravo et al. 2008). Therefore, despite the interest in predicting patterns along climatic gradients, such predictions remain challenging. This is especially true in remote areas that are difficult to access and to sample in the field, such as mountains (Levin et al. 2007). The current availability of satellite imagery at detailed spatial resolutions (Kark et al. 2008) has created an opportunity to study and gain information about remote areas (Levin et al. 2007). Several studies (Bawa et al. 2002, Oindo 2002, Kerr and Ostrovsky 2003, Foody and Cutler 2006, Levin et al. 2007, Gillespie et al. 2008) have suggested that plant species richness can be

effectively predicted using simple indices derived from remotely-sensed images, such as the Normalized Difference Vegetation Index (NDVI; Tucker 1979, Tucker and Sellers 1986). This predictive ability is likely related to the fact that both primary productivity and habitat heterogeneity, two of the major factors shaping biodiversity patterns, can be relatively easily estimated by calculating satellite-derived vegetation indices (Kerr and Ostrovsky 2003, Gillespie et al. 2008, Rocchini et al. 2010, for reviews on the use of satellite images in ecology and biodiversity research).

While predicting animal diversity using vegetation indices is more challenging, because NDVI is based on vegetation-related variables, Kerr et al. (2001) have shown that remote sensing tools can accurately predict butterfly richness at a semi-continental scale using low spatial resolution satellite imagery (1 and 8 km) and biodiversity data at a coarse scale (2.5° grid cells). They found that satellite-derived heterogeneity measures of land cover were strongly correlated with butterfly richness when examined

across Canada. However, the potential of remotely-sensed estimates of spatial heterogeneity in productivity to predict animal diversity at smaller scales (covering a small area using high spatial resolution satellite imagery and high spatial resolution biodiversity data) is less well understood.

Our study focuses on butterflies, which are often considered to be good surrogates of biodiversity, being tightly dependant on a range of plants. They are known to respond to various environmental factors, to vegetation changes (reviewed in Pe'er and Settele 2008a) and to climate changes (Parmesan et al. 1999, Thomas et al. 2004). Butterflies are relatively easy to sample in the field (Nowicki et al. 2008, Pe'er and Settele 2008b), and have been successfully used in studies of ecological gradients (Blair 1999, Fleishman et al. 2000) and in conservation and global change research (Samways 1989, Kremen 1992, Kim 1993, Parmesan et al. 1999, Thomas et al. 2004, Pin Koh and Sodhi 2005, Thomas 2005, Parmesan 2006). However, fewer studies have tested the productivity–richness relationship in butterflies using remotely sensed indices of vegetation (but see Kerr et al. 2001, Bailey et al. 2004, Seto et al. 2004). The relationship between spatial heterogeneity in productivity (as estimated using remotely sensed vegetation indices) and species richness along local gradients has especially remained under-explored (Bailey et al. 2004). This is surprising, since spatial environmental heterogeneity is hypothesized to be an important factor shaping ecological communities and is related with species richness (Rosenzweig 1995, Atauri and de Lucio 2001, Rocchini et al. 2010). Furthermore, spatial heterogeneity in productivity has received much attention in studies at large scales (Kerr and Packer 1997, Jetz and Rahbek 2002).

Here, we aim to examine whether butterfly richness, rarity, and beta diversity along an elevation gradient (hereby termed diversity estimates, see Methods) can be accurately predicted using satellite-derived vegetation indices. We asked whether the mean NDVI and estimates of spatial variation in NDVI can successfully predict: 1) butterfly richness within elevation belts along the elevation gradient, 2) changes in species composition among elevation belts, and 3) changes in range size rarity along the elevation gradient. We predicted that the mean values of NDVI and the spatial heterogeneity in NDVI, both within and among 100 m elevation belts, will be useful predictors for butterfly richness, beta diversity and rarity along the elevation gradient.

While we did not aim to examine the effect of all potential environmental variables affecting species diversity along the altitudinal gradient, we did examine the effect of two major factors that can potentially confound the NDVI–richness relationship along the elevation gradient, namely area and the mid-domain effect (Grytnes and McCain 2007). A mid-domain effect (a peak in richness at mid-elevations, or mid landmass, due to spatial geometric constraints), is predicted where landmass boundaries, such as mountain tops, restrict species ranges and the overlap of variously sized ranges creates a peak in species richness at mid-elevations (Colwell and Lees 2000, Colwell et al. 2004, Grytnes and McCain 2007).

Methods

Study area

Located in north-eastern Israel along the border with Lebanon and Syria, Mt Hermon (33.25°N, 35.48°E), is part of the Anti-Lebanon Mountains, which are isolated from the main mountain ranges of the Middle East, Asia and Europe (Shmida 1977). The parent material is homogeneous, hard Jurassic limestone and dolomite, forming Terra Rossa soils (Shmida 1977). The terrain is characterized by steep rocky limestone Karst slopes (Auerbach and Shmida 1993). Mt Hermon is an elongated anticline that extends NE-SW over 35 km and rises from 300 to 2814 m over a 13-km distance on its SW side in Israel, where our study area is located (the highest point is 2224 m). The climate is Mediterranean, with rainy or snowy winters, and hot dry summers. Precipitation ranges from 600 to 1500 mm yr⁻¹ along the mountain, and above an elevation of 1500 m consists mostly of snow. As in other mountains, temperature decreases, while solar radiation and precipitation increase with elevation. Snow usually begins to cover the slopes of Mt Hermon in the first half of January and lasts until April. Snow patches usually remain until June above 1900 m, mainly on SE facing slopes and in the valleys (Shmida 1980).

Three main vegetation belts have been defined in earlier studies of Mt Hermon (Shmida 1977, 1980). These include: 1) evergreen Mediterranean maquis (300–1200 m); 2) the xero-montane open forest (1200–1900 m) and 3) the subalpine Tragacanthic belt (1900–2814 m) (Fig. 1). The part of the Hermon in Israel ranges approximately 7300 ha, most of which is a nature reserve since 1972 (Levin et al. 2007).

Selection of study sites and sampling design

Most studies of butterfly richness, as well as systematic monitoring schemes, rely on line transect sampling (van Swaay et al. 1997, Kühn et al. 2008, Nowicki et al. 2008), as described by Pollard (1977) and standardized by Pollard and Yates (1993). Quadrat sampling is less often used for butterfly sampling (but see Su et al. 2004, Grill et al. 2005). However, quadrat sampling enables one to concentrate higher sampling effort in given locations and provides comparative ability with sampling methodologies used for other taxa, such as quadrat sampling for plants or point-counts for birds. To examine changes in diversity both among and within elevation belts, we conducted both line transect and quadrat sampling.

We divided the elevation range of our study area (500–2200 m) into elevation classes 100 m high, thus obtaining 17 elevation belts. The area of the elevation belts ranged between a minimum of 5.8 ha (2100–2200 m) to 117 ha (1300–1400 m). To reduce variability resulting from different surface aspects, all quadrats and transects were located on SW facing slopes (following Levin et al. 2007), which are the most common slopes in the study area, corresponding with the shape of the Mt Hermon anticline that extends from SW to NE (see Levin et al. 2007 for

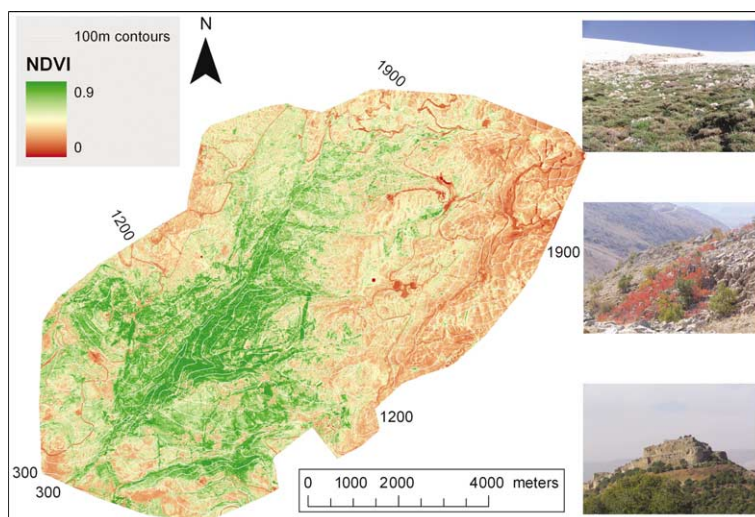


Figure 1. Map showing NDVI values in the study area on Mt Hermon. The photos on the right show the three major vegetation belts, from top to bottom: subalpine Tragacanthic belt (above 1900), xero-montane open forest (1200–1900 m) and evergreen Mediterranean maquis (300–1200 m). Photos by S.K.

further details). We marked two grid squares of 50×20 m (1000 m^2) within each 100 m elevation belt, totalling 34 quadrats. This enabled us to examine changes along the elevation gradient and to obtain repetition within elevation belts. The grid squares were pre-selected using remote sensing tools, being those with NDVI values close to the median NDVI of the whole elevation belt in the SW slope of the study area, so as to assure that they indeed represent vegetation of their respective elevation belt. The same quadrats were used for plant sampling in an earlier study (Levin et al. 2007).

Butterfly sampling

We sampled the butterflies along the elevation gradient between 500 and 2200 m. Butterfly sampling was conducted during two years in the peak activity season of most Hermon butterflies (February–September 2005, and March–August 2006; sensu Benyamini 2002), with each of the vegetation belts visited on average over 15 separate dates. Butterfly sampling was conducted by two Lepidoptera experts capable of recognizing all species in the field (O.L. and G.P.). A butterfly expert and a note-taker walked along parallel lines inside each sampling quadrat for 20 min. The sampling duration of 20 min in the quadrats was determined based on species-accumulation curves generated in preliminary work, using EstimateS ver. 8.0 (Colwell 2006). These indicated that accumulation is reached, on average, after 12 ± 3 min of sampling (sampling $\geq 95\%$ of the species). The transect lines began from the corner of each quadrat and led to the next quadrat (i.e. they were located outside the quadrats). Each line transect was 300 m long (the length was determined based again on species-accumulation curves (Colwell 2006), indicating the accumulation of at least 95% of the species within 250 ± 50 m of sampling). The transect line was divided into sections 50 m long (Pollard and Yates 1993) in order to allow the calculation of species-accumulation curves with distance. The line transects were marked by metal rods

(0.5 m high) in order to ensure accurate repetition of transects during all sampling visits. Butterfly species recognition in both quadrats and transect lines was performed visually. All individuals first seen within a distance of 5 m from the observers were recorded. When needed, in order to verify identification, we captured the butterfly with a sweeping net and then immediately released it at same location. Line transect sampling and quadrat sampling were performed sequentially.

All sampling was performed between 9:00 am (10:00 am in elevations >1500 m) and 15:00, when ambient temperatures were $>20^\circ\text{C}$, cloud cover was $<50\%$, and wind speed was $<4 \text{ km h}^{-1}$. Weather conditions were recorded using a hand-held Kestrel 4000 weather station. Repeated sampling visits to each 100 m elevation belt were organized so that there were different starting times for each belt in order to reduce potential biases that are related to the timing of sampling.

Diversity estimates

In order to increase statistical power, we pooled the data from the two quadrats and transects within each 100 m elevation belt. This was done after a preliminary analysis, which showed that the butterfly diversity estimates were rather similar for quadrats and for transects when analysed separately and since our goal in this paper was not to compare the different methodologies. We calculated values of richness, beta diversity and range size rarity as sampled in each 100 m elevation belt. Species richness (alpha diversity) was calculated by summing up all the species that were observed in the two quadrats and transects within each 100 m elevation belt. Following McCain (2004), species were assumed to be present at an elevation if they were detected at both higher and lower elevations adjacent to a given belt. In cases where larger elevation-belt gaps in appearance were found (over 100 m), we only “filled in” the occurrence of a species in a given elevation belt if the data was consistent with the known range of distribution of

the species in Mt Hermon based on the literature (Benyamini 1993, 2002). Filling in was done for 25 of the 83 butterfly species sampled in this study. For 15 of these 25 species only a single elevation belt was filled-in. Results were very similar when analysis was repeated without filling in.

Various estimators for beta diversity have been suggested in the literature, as reviewed by Koleff et al. (2003). We adopted the β_{sim} (beta sim) estimator, which was considered by Lennon et al. (2001) and Koleff et al. (2003) as a reliable estimate. Preliminary results indicated that it produced very similar results to the estimator β_t used by Wilson and Shmida (1984) in their earlier study of plants in Mt Hermon. Beta sim (β_{sim}) was calculated as follows:

$$\beta_{sim} = \frac{\min(b, c)}{\min(b, c) + a} \quad (1)$$

where for each two neighbouring 100 m elevation belts (X and Y): a = the number of species observed in both X and Y, b = the number of species in Y that are not observed in X, c = the number of species in X that are not observed in Y. High values of β_{sim} indicate that there were few species shared between two adjacent elevation belts (i.e. a high turnover rate).

Rarity has been defined and estimated in the literature using many different approaches (Gaston 1994, Izco 1998). Because we were interested in the relative range size rarity within the mountain area, rather than in rarity over the whole distribution range, we used an estimate that quantifies the confinement of species to a small number of elevation belts in the mountain range. This approach has been used in many recent spatial ecology and large-scale conservation studies (Myers et al. 2000), and in Mt Hermon in a study by Levin et al. (2007). Range size rarity (RSR) was calculated for each elevation belt as the sum of the inverse of the range sizes of all the species occurring in it (Williams et al. 1996, Williams 2000):

$$RSR = \sum (1/C_i) \quad (2)$$

where C_i is the number of elevation belts occupied by species i . We estimated range size as the number of elevation belts in which the species occurred (of the seventeen 100 m altitude belts sampled).

Remote sensing analyses

We used a high spatial resolution QuickBird satellite image of the study area that was acquired during mid-spring (26 May 2004), when vegetation flowering is at its peak (Shmida 1977, 1980, Levin et al. 2007). The image has a spatial resolution of 2.4 m in its four spectral bands that cover the visible and near infrared spectral regions. We corrected the satellite image for atmospheric scattering and absorption and for topographic effects of shading using the atmospheric/topographic correction of multispectral sensors for rugged terrain as applied in ATCOR 3 ver. 7.1 (Richter 1998), which is considered a reliable model for atmospheric corrections (Ben-Dor et al. 2005). We used a Digital Elevation Model (DEM) obtained from the Survey of Israel at a spatial resolution of 25 m (Hall et al. 1999) for calculating the slope, aspect and the sky view factor (i.e. the

visible area of the sky as dependent upon the surrounding topography).

We then calculated normalized difference vegetation index (NDVI), one of the earliest remotely sensed vegetation indices applied in the literature (Rouse et al. 1973, Tucker 1979). Its relationship with vegetation productivity is well established, and it is one of the most commonly used vegetation indices (Kerr and Ostrovsky 2003, Pettorelli et al. 2005, Levin et al. 2007), especially in biodiversity studies (Gillespie et al. 2008). NDVI was calculated as follows:

$$NDVI = (NIR - R) / (NIR + R) \quad (3)$$

where NIR = reflectance in the near infrared band of an image pixel, R = reflectance in the red band of an image pixel.

Because NDVI is a ratio index shading effects have only a minor effect on it (Lillesand and Kiefer 1994). We also compared the results with three other remotely sensed vegetation indices designed for overcoming issues of variability in the soil background, atmospheric haze, and saturation of the NDVI in cases of dense vegetation, including the Soil Adjusted Vegetation Index (Huete 1988), the Enhanced Vegetation Index (Huete et al. 2002) and the percentage of tree cover (as in Levin et al. 2007). Because results were generally similar for the four satellite-derived vegetation indices and because correlations with diversity estimates were strongest for NDVI, we report here only the results for NDVI (detailed results for the three other indices are available from the authors upon request).

In addition to calculating the mean and standard deviation (SD) of NDVI within the elevation belts, we quantified the change in NDVI among elevation belts along the elevation gradient. When examining changes in the values of NDVI along a gradient, multiple statistics can be used, such as the difference in NDVI among elevation belts and the ratio between adjacent belts (compare with Walker et al. 2003). Here, we initially calculated four different estimates for the change in NDVI along the elevation gradient. These include:

rate of change in NDVI between each two neighbouring elevation belts (RC1):

$$RC1_x = NDVI_x / NDVI_{x+1} \quad (4)$$

degree of change in NDVI between each two neighbouring elevation belts (DC1):

$$DC1_x = NDVI_x - NDVI_{x+1} \quad (5)$$

rate of change in NDVI between the elevation belt above and below the belt in focus (RC2):

$$RC2_x = NDVI_{x-1} / NDVI_{x+1} \quad (6)$$

degree of change in NDVI between the elevation belt above and below the belt in focus (DC2):

$$DC2_x = NDVI_{x-1} - NDVI_{x+1} \quad (7)$$

where subscript x represents elevation belt x , subscript $x+1$ stands for the elevation belt adjacent to and above elevation belt x , and subscript $x-1$ stands for the elevation belt adjacent to and below elevation belt x .

RC2 and DC2 were used to examine elevation gradients at a somewhat larger vertical distance, one that is still relevant for butterflies (200 vs 100 m). Negative values of

DC indicate that NDVI values increase with elevation. We deliberately avoided using absolute values of DC, as the sign provided also an index for the directionality of changes (i.e. upwards or downwards) along the elevation gradient. This is especially important for butterflies, since some species perform directional hilltopping behaviour in which they ascend to mountain summits for the purpose of mating (Shields 1967, Alcock 1987, Ehrlich and Wheye 1988, Pe'er et al. 2004).

Because butterflies are usually not limited in their activity to a single quadrat, in order to calculate NDVI statistics comparing the different 100 m belts, we used three spatial extents (coverage areas) in the mountain. These included: 1) the total area within each of the 0.1 ha quadrats and a buffer zone of 5 m on both sides of the transects, within each of the 100 m elevation belts; 2) the total area of the SW facing aspect of each 100 m elevation belt in our study region. This was the aspect in which our sampling quadrats and transects were located; 3) the total area of the 100 m elevation belt in our study region (all aspects).

At each of these spatial extents, we examined the relationship between the different butterfly diversity estimates and the mean NDVI, SD, RC1, RC2, DC1 and DC2. This enabled us to examine which spatial scale of NDVI best predicts changes in local butterfly diversity within and among elevation belts.

Data analysis

To examine the mid-domain effect, we ran 1000 Monte Carlo simulations without replacement. This was done in order to compare the observed species richness with the predictions of a null model simulating species richness based on empirical range sizes for each belt between 500 and 2200 m. The empirical range sizes were derived from the field data. We compared our results with 95% confidence intervals generated by the simulations. This was done based on analytical stochastic models (Colwell and Hurr 1994) using the Mid-Domain-Null program, which takes into account the lower and upper elevations of the species ranges (McCain 2004).

We calculated the linear regressions with the mean and SD of NDVI (within vegetation belts) or between adjacent belts (DC1, DC2, RC1 and RC2 among vegetation belts) as the independent variable (at the three spatial scales of our analysis) and each of the butterfly diversity estimates, including richness, β_{sim} and range size rarity as the dependent variables. Variables were log-transformed when needed. To account for autocorrelation along the elevation gradient, we used the method developed by Dutilleul (1993), as applied in PASSAGE 1.1 (<www.passagesoftware.net/>). To account for the potential effect of area of the different vegetation belts along the elevation gradient on the relationships and to examine whether the area of the elevation belts had a confounding effect on the observed relationships between NDVI and diversity estimates, we performed a partial correlation analysis, as well as a multiple regression analysis (using JMP 7.0 SAS Inst.). We examined whether statistical significance is maintained after calculating the relationship between each of the NDVI estimates

(mean and SD of NDVI per belt, DC1, DC2, RC1, RC2) and the residuals from the relationship between area and butterfly diversity, which was used as the dependent variable. This was calculated for the total area (log transformed) at each of the three spatial extents considered in this study.

Results

Butterfly diversity along the elevation gradient

Overall, in a total of 120 km of line transect sampling and 116 h of quadrat sampling, we recorded 10 513 individual butterflies belonging to 83 species and six butterfly families. Butterfly species richness showed a bimodal pattern with elevation, peaking between 1300 and 1500 m (48 species within each of the two 100 m belts) and between 1800 and 1900 m (46 species; Fig. 2a). Range size rarity showed local maxima at two intermediate elevation ranges (900–1000 and 1300–1400 m) and then increased sharply towards the highest elevation belts (Fig. 2b). Beta sim (β_{sim}) diversity showed multiple peaks along the gradient, the largest of which was at the elevation range between 1900 and

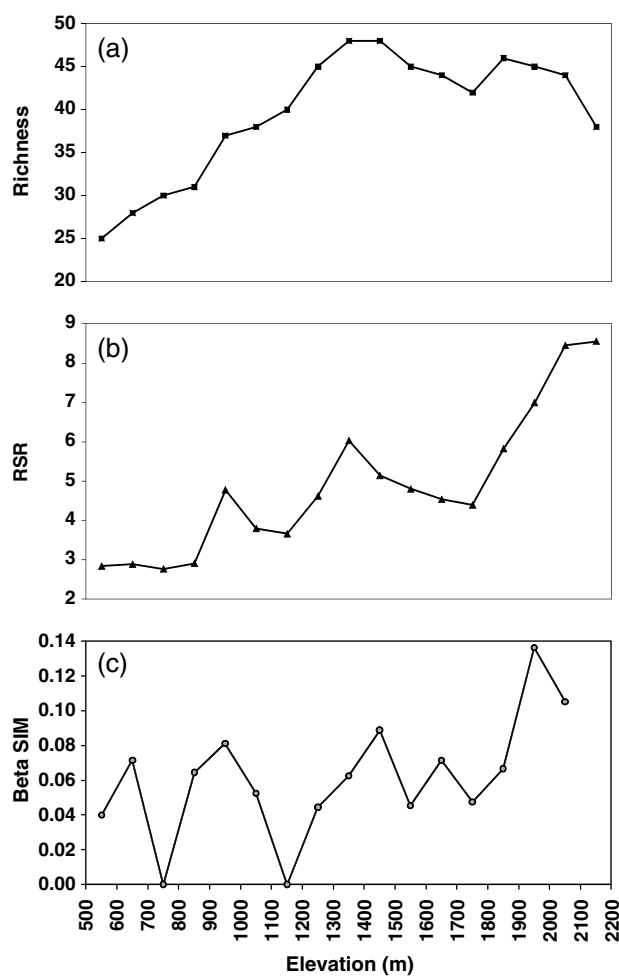


Figure 2. Changes in butterfly diversity along the elevation gradient in Mt Hermon showing: (a) species richness, (b) range size rarity (RSR) and (c) beta diversity (β_{sim}).

2000 m (Fig. 2c). Range size rarity showed a significant positive relationship with β_{sim} ($R^2=0.47$, $p<0.01$, $n=16$), and a significant (weaker) positive relationship with species richness ($R^2=0.36$, $p<0.02$, $n=17$).

Changes in vegetation indices along the elevation gradient

Mean NDVI showed a hump-shaped pattern along the elevation gradient, peaking between 900 and 1200 m and gradually declined to its minimum value at the highest elevation belts (Fig. 3). The SD of NDVI remained relatively constant up to 1200 m, above which it gradually declined with increasing elevation (Fig. 3). The values of DC1, DC2, RC1 and RC2, however, increased with elevation up to 1200 m and 1300 m, respectively, after which they declined (with a minor peak around 1850 m; Fig. 3; the changes in RC1 and RC2 with elevation are similar to those of DC1 and DC2, and are therefore not shown).

Relationship between butterfly diversity and NDVI

Richness was strongly correlated with all variables estimating spatial heterogeneity in productivity, including DC1, DC2, RC1 and RC2 (Table 1, Fig. 4). However, the relationship between butterfly richness and mean and standard deviation (SD) of NDVI was weak and was not significant (Table 1). The relationship between richness and the rates of change in NDVI between elevation belts was strong, and remained significant after correcting for autocorrelation effects (Table 1). Unlike richness, range size rarity was significantly correlated with mean NDVI as well as with all the variables expressing the spatial heterogeneity in NDVI: SD, DC1, DC2, RC1, RC2 (Table 1, Fig. 5). Of the diversity estimates tested (richness, β_{sim} and range size rarity), beta diversity (β_{sim}) was in most cases the least strongly correlated with NDVI variables.

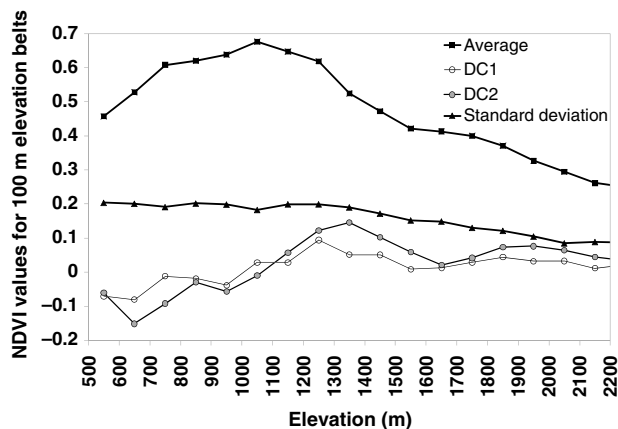


Figure 3. NDVI values (mean, standard deviation, DC1 and DC2) per 100 m elevation belt. DC1 stands for the difference between the mean of a given elevation belt and the elevation belt above it, while DC2 stands for the difference between the mean values of the elevation belts below and above each elevation belt in Mt Hermon.

When comparing NDVI estimates deriving from the three spatial extents examined (quadrats and transects, SW slope, and the area of the whole elevation belt within the study area), NDVI estimates deriving from the largest spatial extent (the entire elevation belt), were in most cases more strongly correlated with all butterfly diversity measures than those deriving from the quadrats and transects alone (Table 1).

The area of the vegetation belts was not significantly correlated with butterfly richness at any spatial extent (Table 2). Butterfly rarity (RSR) was, however, significantly correlated with area (after log transformation) at the spatial scale of the SW aspect of the elevation belt (Table 2). However, in most cases, the correlations between NDVI and both richness and range size rarity remained statistically significant after taking into account the effect of the (log transformed) area of the elevation belts using a residual analysis (Table 3), as well as when performing a multiple regression analysis (Table 4). In most cases area was non-significant in the multiple regression analysis (Table 4). No mid-domain effect was detected. Species richness did not fall within the 95% prediction curves of the model based on the 1000 simulations of the Mid-Domain Null model (Fig. 6). When we included the effect of autocorrelation on the significance of the correlations, the significance of the regression model declined, as expected (Table 1). However, in some of the cases, the correlation remained significant between richness and spatial heterogeneity between the elevation belts (DC1, DC2, and RC1), also when spatial autocorrelation was taken into account.

Discussion

We found that the NDVI was a strong predictor of butterfly richness along the elevation gradient in Mt Hermon, explaining up to 80% of the total variation in butterfly richness (Fig. 4). However, it was not the mean NDVI, but rather its variability among elevation belts, that best predicted butterfly richness within the elevation belts. Mean NDVI is considered a good surrogate for net primary productivity (Gillespie et al. 2008). Butterfly richness along the elevation gradient appears to be more strongly shaped by spatial heterogeneity in productivity than by productivity per se at the local spatial scale examined here. This suggests that the most commonly used remotely-sensed vegetation statistic, namely the mean NDVI is in some cases not the most efficient estimate if one aims to predict richness and diversity patterns along spatial gradients (e.g. elevation). In such cases, it may be more useful to study the spatial heterogeneity in NDVI.

Here we show the importance of spatial heterogeneity in productivity at the small regional scale. The importance of heterogeneity in studies using remote sensing indices has been shown at much larger (e.g. continental) scales. For example, in their work on mammals, Kerr and Packer (1997) found that in the higher energy regions of North America, the best predictor of mammal richness was topographic heterogeneity and local variation in energy availability. At a regional scale, Aauri and de Lucio (2001) examined the relationships between landscape structure, land use and richness of birds, amphibians, reptiles and

Table 1. Pearson correlation coefficients between NDVI statistics calculated at three spatial extents and butterfly diversity estimates, including richness, range size rarity (RSR) and beta sim (β_{sim}). The number sign (#) marks significance at the 0.05 level when taking into account the effect of autocorrelation.

Correlation coefficients between each NDVI statistic and butterfly diversity estimates		Spatial extent		
NDVI statistic	Butterfly diversity	Entire 100 m elevation belt	SW aspect of the 100 m elevation belt	Quadrats + transects within the 100 m elevation belt
Average	Richness	-0.33	-0.07	-0.08
Log (average)	RSR	-0.79***	-0.68**	-0.66**
Average	Beta sim	-0.55*	-0.55*	-0.41
Standard deviation	Richness	-0.46	-0.17	-0.25
Log (standard deviation)	RSR	-0.86***	-0.76***	-0.63**
Standard deviation	Beta sim	-0.67**	-0.64**	-0.16
DC1	Richness	0.85*** #	0.78***	0.33
	Log RSR	0.55*	0.56*	0.43
	Beta sim	-0.04	-0.01	0.25
DC2	Richness	0.90*** #	0.81***	0.44
	Log RSR	0.68**	0.70**	0.47
	Beta sim	0.03	0.14	0.15
RC1	Richness	0.88*** #	0.81***	0.51*
	Log RSR	0.68**	0.68**	0.28
	Beta sim	0.07	0.11	0.05
RC2	Richness	0.90***	0.79***	0.59*
	Log RSR	0.81***	0.82***	0.37
	Beta sim	0.18	0.27	0.00

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

butterflies in a Mediterranean landscape (Madrid, Spain). They found that the response of species richness to land use heterogeneity varied depending on the group of species considered. The most important factor affecting bird and butterfly richness in their study was landscape heterogeneity, while other factors, such as the specific composition of land use, played a secondary role (Atauri and de Lucio 2001).

In the montane ecosystem examined here, spatial heterogeneity in productivity between elevation belts explains butterfly richness better than mean productivity. What biological factors may lead to these results? One possibility is that the spatial heterogeneity in productivity estimated here represents the variety of habitat types available to the butterflies at local spatial scales and within relatively short distances (dozens of meters to kilometres). Such heterogeneity is particularly beneficial for adult

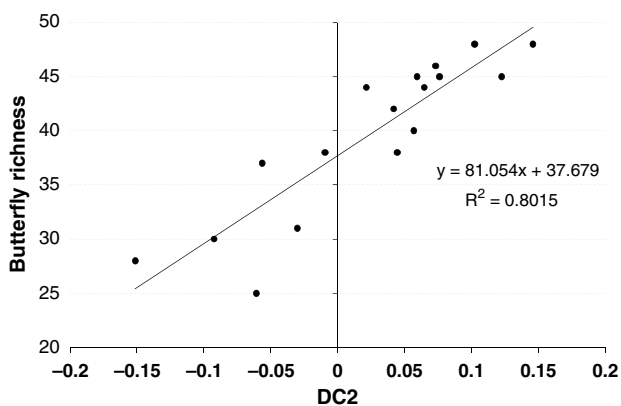


Figure 4. The relationship between DC2 (defined in eq. 7) and butterfly species richness in Mt Hermon.

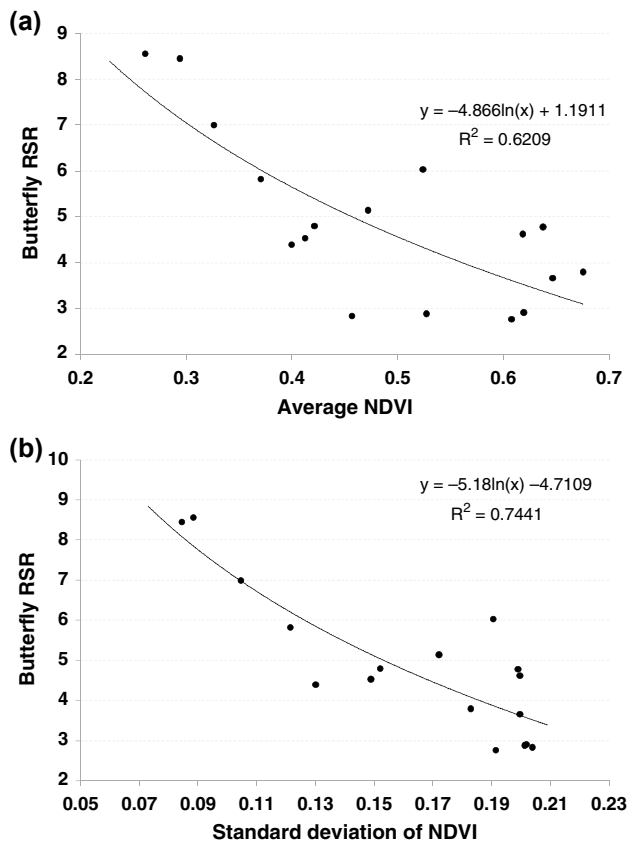


Figure 5. (a) The relationship between average NDVI values within each 100 m elevation belt and butterfly range size rarity (RSR) in Mt Hermon; (b) the relationship between the standard deviation of NDVI within each 100 m elevation belt and butterfly range size rarity (RSR).

Table 2. Pearson correlation coefficients between the area of the three spatial extents examined in the study and butterfly diversity estimates, including richness, range size rarity (RSR) and beta sim (β_{sim}).

Correlation coefficients between area and butterfly diversity estimates		Spatial extent		
Area	Butterfly diversity	Entire 100 m elevation belt	SW aspect of the 100 m elevation belt	Quadrats+transects within the 100 m elevation belt
Area	Richness	0.39	-0.01	0.16
Log (area)	Richness	0.23	-0.01	0.10
Area	RSR	-0.32	-0.68**	0.15
Log (area)	RSR	-0.55*	-0.74***	0.07
Area	Beta sim	-0.30	-0.52	0.39
Log (area)	Beta sim	-0.40	-0.55*	0.34

*p < 0.05, **p < 0.01, ***p < 0.001.

butterflies, allowing them to utilize a variety of resources. While being highly dependent on particular host plants during larval development, adult butterflies often have different habitat requirements than those of the larvae (Benyamini 2002, Settele et al. 2009). Our results may also be partly shaped by the specific habitat and host plants of the butterflies' larvae, but information about larval spatial distribution along the elevation gradient is not sufficient for analyzing such potential effect.

Another explanation may be that the high spatial heterogeneity in productivity represents high turnover of habitats and changes in conditions, which allow more species to co-occur in transitional areas (Shmida and Wilson 1985). This supports findings from earlier studies, which suggest that areas of sharp environmental transition (ecotones) are especially rich both in species richness and

in rare species because they serve as meeting areas between different communities and/or due to the unique environmental conditions found in ecotonal environments (reviewed in Kark and van Rensburg 2006). We found two peaks in beta diversity in the transition areas between Mt Hermon's three vegetation belts. A peak in the beta-diversity of plants was also found between 1200 and 1300 m on Mt Hermon, corresponding to the transition between a maquis and montane flora (Wilson and Shmida 1984). This supports the hypothesis that transition areas are zones of high turnover, where spatial heterogeneity is high (Shmida and Wilson 1985, Kark and Van Rensburg 2006). Our findings here also support the prediction and recent findings at continental and regional scales that areas with high turnover tend to show higher levels of rarity and local endemism (Kark et al. 2007, van Rensburg et al. 2009).

Thus far, relatively few studies have examined the relationship between butterfly richness and satellite-derived vegetation indices that estimate productivity (but see Kerr et al. 2001). Some studies found relatively weak positive relationships, while others showed none (see Bailey et al. 2004, Seto et al. 2004 and references therein). Few studies have examined the relationship between butterfly richness, rarity and NDVI heterogeneity in space at local scales. Bailey et al. (2004) studied butterfly and bird richness and its correlation with NDVI heterogeneity using Simpson's diversity index. While heterogeneity in NDVI predicted the total species richness of birds ($R^2 = 0.75$), no association occurred between NDVI heterogeneity and species richness of butterflies in any of the vagility classes tested in their work (Bailey et al. 2004). These included low vagility (an individual is likely to move on the order of dozens of meters in its lifetime); intermediate (an individual may move hundreds of meters); and high (an individual may move more than a kilometer) (Bailey et al. 2004). The authors suggested that for butterflies, NDVI may not be the best measure of environmental heterogeneity and that other measures (e.g. elevation) may be more appropriate (Bailey et al. 2004). However, the lack of relationship between spatial heterogeneity in productivity and butterfly richness may partly result from the estimates used to measure heterogeneity in NDVI, rather than from the lack of suitability of NDVI in predicting environmental heterogeneity. We propose that future studies should calculate spatial heterogeneity in productivity along the elevation gradient, quantifying changes in productivity between altitudinal gradients. This approach is more equivalent

Table 3. Partial correlations: Pearson correlation coefficients between NDVI statistics calculated at the spatial extent of the entire elevation belt and residuals of the butterfly diversity estimates (after predicting their values with area as the independent variable), including richness, range size rarity (RSR) and beta sim (β_{sim}).

Correlation coefficients between each NDVI statistic and residuals of butterfly diversity estimates		Spatial extent
NDVI statistic	Butterfly diversity estimate	Entire 100 m elevation belt
Average	Richness	-0.60*
	RSR	0.30
	Beta sim	-0.59*
Standard deviation	Richness	-0.75***
	RSR	-0.41
	Beta sim	-0.76***
DC1	Richness	0.75***
	RSR	0.71**
	Beta sim	0.14
DC2	Richness	0.81***
	RSR	0.79***
	Beta sim	0.16
RC1	Richness	0.84***
	RSR	0.78***
	Beta sim	0.25
RC2	Richness	0.88***
	RSR	0.84***
	Beta sim	0.31

*p < 0.05, **p < 0.01, ***p < 0.001.

Table 4. Multiple regression coefficients and the adjusted R^2 between the area and NDVI variables as the independent variables and butterfly diversity (richness, RSR or β_{sim}) at the spatial extent of the entire elevation belt.

	NDVI variable	Richness	RSR	Beta-sim
R^2		0.77 ***	0.71 ***	0.15
Coefficient of area	RC1	1.355	-1.54 ***	-0.02
Coefficient of NDVI variable		69.28 ***	13.32 ***	0.12
R^2		0.85 ***	0.71 ***	0.43 **
Coefficient of area	Standard deviation of NDVI within an elevation belt	0.24 ***	0.01	0.0002
Coefficient of NDVI		-177.8 ***	-42.14 ***	-0.67 **

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

to beta diversity estimates used for estimating turnover of species in space, focusing on changes between neighbouring cells.

The relatively weak correlations found here between productivity (mean NDVI) and butterfly richness may result from the fact that in some cases butterfly species are constrained by the identity of the plant species available, and particularly by the presence of specific host plants, rather than by total plant richness or vegetation cover (Kelly and Debinski 1998, Pe'er and Settele 2008b). In such cases, productivity would not be a good predictor of butterfly richness, compared with, for instance, larger or more generalistic taxa that depend more directly on productivity (see Shochat 1999 for birds). Whereas plant richness above 2000 m amounted to <40% of the peak plant richness (found at about 1000 m; Levin et al. 2007), butterfly richness above 2000 m reached almost 80% of the peak butterfly richness (found at about 1400 m; Fig. 2a). We found higher levels of butterfly species richness at the high altitudes (above 2000 m), which are characterised by lower productivity, relatively low plant richness and harsher weather conditions (e.g. winds; Shmida 1977) compared with lower elevations (<900 m; Fig. 2a). This supports our knowledge that butterfly ranges are often limited by factors other than the diversity and distribution of plants (Dennis and Shreeve 1991, Dennis et al. 1991, Quinn et al. 1997, Hawkins and Porter 2003) or by temperature and rainfall (Pollard 1988).

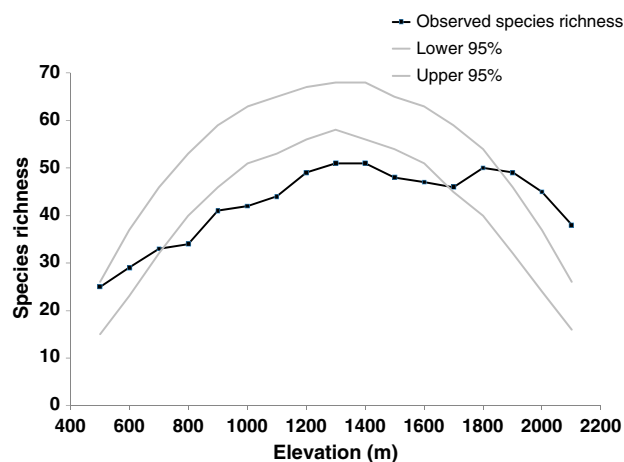


Figure 6. Mid domain analysis of the butterfly species richness. The upper and lower 95% confidence intervals were generated from 1000 Monte Carlo simulations.

Here, we examined the effect of the spatial extent at which the variability in NDVI was calculated. Interestingly, we found that the NDVI estimates that were based on the whole area of the elevation belt often provided better predictors of butterfly richness within each of the quadrats than the data from the quadrats themselves. It is not easy to conclude why this was found, but we can hypothesize that it results from the fact that scaling up when calculating NDVI better represented the relevant habitat as perceived by the butterflies (compare with Kumar et al. 2009). Because adult butterflies are mobile and move among host plants, which are not distributed in the area uniformly, this may better capture their preferences than local sampling of NDVI. Rowe and Lidgard (2009), following a detailed analysis of the effect of sampling methodology on patterns of elevation diversity, suggest that it may be advantageous to adopt more than a single spatial sampling method as empirical evidence because organisms relate to factors at a variety of spatial scales. This is especially true in the case of insects such as butterflies, in which the response of the different life stages may be quite different, with the adults being more mobile than the larval stages.

Multiple factors affect species diversity in mountains and its spatial variation along the elevation gradient, such as climate, soil type, water availability, snow cover and topographic heterogeneity (reviewed in Grytnes and McCain 2007). Additional factors that have been studied are area and the mid-domain effect (Grytnes and McCain 2007). Given that many factors can affect changes in diversity along elevation gradient, we find it interesting that such a large portion of the variation in butterfly diversity, and especially in richness and rarity, was explained by satellite-derived vegetation indices. Mid-domain was not an important factor in this system. After removing the effect of area on the relationship between NDVI and the diversity indices examined, NDVI remained a strong predictor of butterfly diversity when using the degree of change among adjacent belts. This suggests that the variation among belts in their productivity is a good indicator (or even surrogate) of spatial heterogeneity or other processes that shape diversity patterns across the mountain.

Range size rarity showed a strong negative correlation with both mean and SD of NDVI, whereas its relationship with the heterogeneity between elevation belts was somewhat weaker (Table 1). As we ascend the mountain into areas with lower vegetation cover, few or no trees, and with lower productivity, the proportion of rare species (those found in few elevation belts) increases. This is in

accordance with the prediction that the highest elevations, being more limited in area, more isolated from other areas and having conditions that require high levels of specialization (e.g. strong winds), will tend to show higher levels of rarity and endemism (this was also found for the range size rarity of plants on Mt Hermon; Levin et al. 2007). For locally rare species with smaller ranges in the mountain, both productivity and small-scale spatial heterogeneity in productivity are important. In our case, this may result from the fact that most of the locally-rare species are high-altitude butterflies that are not found elsewhere in Mt Hermon (Benyamini 2002, Pe'er and Benyamini 2008). Many butterfly species of the higher elevation belts reach the southern edge of their global distribution range on Mt Hermon, and comprise of peripheral populations (Benyamini 2002, Pe'er and Benyamini 2008). Lower NDVI values, indicating the lower productivity of high-altitude habitats and high local heterogeneity, are strongly correlated with the occurrence of unique species and high rarity. Species occurring in higher elevations are at higher risk in the face of climatic changes (Parmesan 2006 and references therein), as they occupy particularly small areas along mountain ranges. We should note, however, that our research was constrained to an elevation-range between 500 and 2200 m, and did not reach the summit of Mt Hermon, located in Syria at 2814 m. Thus, rarity patterns may be underestimated, as they are partly affected by the low number of elevation belts that were sampled above the tree-line (~1850–1900 m). Indeed, Nogués-Bravo et al. (2008) have shown that the different sampling extents along the elevation gradient can affect the relationships found between richness and productivity, which may partly result from the effect of under-sampled rare species. Reports from the uppermost sections of the mountain indicate that the area near the peak of Mt Hermon actually harbours several additional rare butterfly species (Benyamini 1993, 2002). However, different land-use practices (e.g. cutting of trees and overgrazing) in parts of Mt Hermon located in Syria and in Lebanon, beyond the study area, likely lead to a reduction in butterfly diversity and rarity there. It would be interesting to collaborate across the political borders and sample the upper areas of Mt Hermon.

In summary, we propose that estimates of local spatial heterogeneity in productivity based on remotely sensed vegetation indices may be useful in predicting butterfly richness along elevation gradients and should be examined in future studies. Such tools may be very useful in predicting and monitoring both plant richness (Levin et al. 2007) and animal richness in remote and inaccessible regions of high conservation importance. This is especially relevant in the face of the rapid climate changes and other environmental changes.

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References

- Alcock, J. 1987. Leks and hilltopping in insects. – *J. Nat. Hist.* 21: 319–328.
- Atauri, J. A. and de Lucio, J. V. 2001. The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. – *Landscape Ecol.* 16: 147–159.
- Auerbach, M. and Shmida, A. 1993. Vegetation change along an altitudinal gradient on Mt-Hermon, Israel – no evidence for discrete communities. – *J. Ecol.* 81: 25–33.
- Bailey, S. A. et al. 2004. Primary productivity and species richness: relationships among functional guilds, residency groups and vagility classes at multiple spatial scales. – *Ecography* 27: 207–217.
- Bawa, K. et al. 2002. Assessing biodiversity from space: an example from the Western Ghats, India. – *Conserv. Ecol.* 6: 7, <www.consecol.org/vol6/iss2/art7>.
- Ben-Dor, E. et al. 2005. Comparison between six model-based methods to retrieve surface reflectance and water vapor content from hyperspectral data: a case study using synthetic AVIRIS data. – Presented at International Conference on Optics and Optoelectronics – ICOL 2005, Dehradun, India.
- Benyamini, D. 1993. The butterflies of Mt Hermon (Lepidoptera, Rhopalocera and Hesperidae). – *Linn. Belg.* 14: 167–203.
- Benyamini, D. 2002. A field guide to the butterflies of Israel; including butterflies of Mt Hermon, Sinai and Jordan. – Keter Publ. House, Jerusalem.
- Blair, R. B. 1999. Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? – *Ecol. Appl.* 9: 164–170.
- Colwell, R. K. 2006. EstimateS: statistical estimation of species richness and shared species from samples. Version 8.0, user's guide and application. – <<http://purl.oclc.org/estimates>>.
- Colwell, R. K. and Hurtt, G. C. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. – *Am. Nat.* 144: 570–595.
- Colwell, R. K. and Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. – *Trends Ecol. Evol.* 15: 70–76.
- Colwell, R. K. et al. 2004. The mid-domain effect and species richness patterns: what have we learned so far? – *Am. Nat.* 163: E1–E23.
- Dennis, R. L. H. and Shreeve, T. G. 1991. Climatic change and the British butterfly fauna: opportunities and constraints. – *Biol. Conserv.* 55: 1–16.
- Dennis, R. L. H. et al. 1991. A multivariate approach to the determination of faunal structures among European butterfly species (Lepidoptera, Rhopalocera). – *Zool. J. Linn. Soc.* 101: 1–49.
- Dutilleul, P. 1993. Modifying the t test for assessing the correlation between two spatial processes. – *Biometrics* 49: 305–314.
- Ehrlich, P. R. and Wheye, A. 1988. Hilltopping butterflies revisited. – *Am. Nat.* 132: 460–461.
- Fleishman, E. et al. 2000. Upsides and downsides: contrasting topographic gradients in species richness and associated scenarios for climate change. – *J. Biogeogr.* 27: 1209–1219.
- Foody, G. M. and Cutler, M. E. J. 2006. Mapping the species richness and composition of tropical forests from remotely sensed data with neural networks. – *Ecol. Model.* 195: 37–42.
- Gaston, K. J. 1994. *Rarity*. – Chapman and Hall.
- Gillespie, T. W. et al. 2008. Measuring and modelling biodiversity from space. – *Prog. Phys. Geogr.* 32: 203–221.

- Grill, A. et al. 2005. Butterfly, spider, and plant communities in different land-use types in Sardinia, Italy. – *Biodivers. Conserv.* 14: 1281–1300.
- Grytnes, J. A. and McCain, C. M. 2007. Elevation patterns in species richness. – In: Levin, S. (ed.), *Encyclopedia of biodiversity*. Elsevier, pp. 1–8.
- Hall, J. K. et al. 1999. Test of the accuracy of the DEM of Israel – Geological Survey of Israel, Jerusalem.
- Hawkins, B. A. and Porter, E. E. 2003. Does herbivore diversity depend on plant diversity? The case of California butterflies. – *Am. Nat.* 161: 40–49.
- Huete, A. R. 1988. A soil-adjusted vegetation index (SAVI). – *Remote Sens. Environ.* 25: 295–309.
- Huete, A. et al. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. – *Remote Sens. Environ.* 83: 195–213.
- Izco, J. 1998. Types of rarity of plant communities. – *J. Veg. Sci.* 9: 641–646.
- Jetz, W. and Rahbek, C. 2002. Geographic range size and determinants of avian species richness. – *Science* 297: 1548–1551.
- Kark, S. and van Rensburg, B. J. 2006. Ecotones: marginal or central areas of transition? – *Isr. J. Ecol. Evol.* 52: 29–53.
- Kark, S. et al. 2007. The role of transitional areas as avian biodiversity centers. – *Global Ecol. Biogeogr.* 16: 187–196.
- Kark, S. et al. 2008. Global environmental priorities: making sense of remote sensing. – *Trends Ecol. Evol.* 23: 181–182.
- Kelly, L. and Debinski, D. M. 1998. Relationship of host plant density to size and abundance of the regal fritillary *Speyeria idalia* Drury (Nymphalidae). – *J. Lepidopterists' Soc.* 52: 262–276.
- Kerr, J. T. and Packer, L. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. – *Nature* 385: 252–254.
- Kerr, J. T. and Ostrovsky, M. 2003. From space to species: ecological applications for remote sensing. – *Trends Ecol. Evol.* 18: 205–299.
- Kerr, J. T. et al. 2001. Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. – *Proc. Natl Acad. Sci. USA* 98: 11365–11370.
- Kim, K. C. 1993. Biodiversity, conservation and inventory – why insects matter. – *Biodivers. Conserv.* 2: 191–214.
- Koleff, P. et al. 2003. Measuring beta diversity for presence-absence data. – *J. Anim. Ecol.* 72: 367–382.
- Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. – *Ecol. Appl.* 2: 203–217.
- Kühn, E. et al. 2008. Getting the public involved in butterfly conservation: lessons learned from a new monitoring scheme in Germany. – *Isr. J. Ecol. Evol.* 54: 89–103.
- Kumar, S. et al. 2009. Effects of spatial heterogeneity on butterfly species richness in Rocky Mountain National Park, CO, USA. – *Biodivers. Conserv.* 18: 739–763.
- Lennon, J. J. et al. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. – *J. Anim. Ecol.* 70: 966–979.
- Levin, N. et al. 2007. Predicting mountain plant richness and rarity from space using satellite-derived vegetation indices. – *Divers. Distrib.* 13: 692–703.
- Lillesand, T. M. and Kiefer, R. W. 1994. *Remote sensing and image interpretation*. – Wiley.
- Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. – *Global Ecol. Biogeogr.* 10: 3–13.
- McCain, C. M. 2004. The mid-domain effect applied to elevation gradients: species richness of small mammals in Costa Rica. – *J. Biogeogr.* 31: 19–31.
- Myers, N. et al. 2000. Biodiversity hotspots for conservation priorities. – *Nature* 403: 853–858.
- Nogués-Bravo, D. et al. 2008. Scale effects and human impact on the elevation species richness gradients. – *Nature* 453: 216–219.
- Nowicki, P. et al. 2008. Butterfly monitoring methods: the ideal and the real world. – *Isr. J. Ecol. Evol.* 54: 69–88.
- Oindo, B. O. 2002. Predicting mammal species richness and abundance using multi-temporal NDVI. – *Photogramm. Eng. Remote Sens.* 68: 623–629.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – *Annu. Rev. Ecol. Evol. Syst.* 37: 637–669.
- Parmesan, C. et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. – *Nature* 399: 579–583.
- Pe'er, G. and Benyamini, D. 2008. A template for publishing the “conservation chain” from problem identification to practical action, exemplified through the campaign for butterfly protection in Israel. – *Isr. J. Ecol. Evol.* 54: 19–39.
- Pe'er, G. and Settele, J. 2008a. The rare butterfly *Tomares nesimachus* (Lycaenidae) as a bioindicator for pollination services and ecosystem functioning in the north of Israel. – *Isr. J. Ecol. Evol.* 54: 111–136.
- Pe'er, G. and Settele, J. 2008b. Butterflies in and for conservation: trends and prospects. – *Isr. J. Ecol. Evol.* 54: 7–17.
- Pe'er, G. et al. 2004. Response to topography in a hilltopping butterfly and implications for modeling nonrandom dispersal. – *Anim. Behav.* 68: 825–839.
- Pettorelli, N. et al. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. – *Trends Ecol. Evol.* 20: 503–510.
- Pin Koh, L. and Sodhi, N. S. 2005. Importance of reserves, fragments, and parks for butterfly conservation in a tropical urban landscape. – *Ecol. Appl.* 14: 1695–1708.
- Pollard, E. 1977. A method for assessing changes in the abundance of butterflies. – *Biol. Conserv.* 12: 115–134.
- Pollard, E. 1988. Temperature, rainfall and butterfly numbers. – *J. Appl. Ecol.* 25: 819–828.
- Pollard, E. and Yates, T. 1993. *Monitoring butterflies for ecology and conservation*. – Chapman and Hall.
- Quinn, R. M. et al. 1997. Abundance–range size relationships of macrolepidoptera in Britain: the effects of taxonomy and life history variables. – *Ecol. Entomol.* 22: 453–461.
- Rahbek, C. 1995. The elevation gradient of species richness: a uniform pattern? – *Ecography* 18: 200–205.
- Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. – *Ecol. Lett.* 8: 224–239.
- Richter, R. 1998. Correction of satellite imagery over mountainous terrain. – *Appl. Optics* 37: 4004–4015.
- Rocchini, D. et al. 2010. Remotely sensed spectral heterogeneity as a proxy of species diversity: recent advances and open challenges. – *Ecol. Inform.* 5: 318–329.
- Rosenzweig, M. 1995. *Species diversity in space and time*. – Cambridge Univ. Press.
- Rouse, J. W. et al. 1973. Monitoring vegetation systems in the Great Plains with ERTS. – In: Freden, S. C. et al. (eds), *Third Earth Resources Technology Satellite-1 Symposium Technical presentations, section A, Vol. I*. National Aeronautics and Space Administration, Washington, DC, pp. 309–317.
- Rowe, R. J. and Lidgard, S. 2009. Elevation gradients and species richness: do methods change pattern perception? – *Global Ecol. Biogeogr.* 18: 163–177.
- Samways, M. J. 1989. Insect conservation and the disturbance landscape. – *Agric. Ecosyst. Environ.* 27: 183–194.
- Seto, K. C. et al. 2004. Linking spatial patterns of bird and butterfly species richness with Landsat TM derived NDVI. – *Int. J. Remote Sens.* 25: 4309–4324.

- Settele, J. et al. 2009. Ecology of butterflies in Europe. – Cambridge Univ. Press.
- Shields, O. 1967. Hilltopping: an ecological study of summit congregation behavior of butterflies on a southern California hill. – *J. Res. Lepidoptera* 6: 69–178.
- Shmida, A. 1977. A quantitative analysis of the Tragacanthic vegetation of Mt Hermon and its relation to environmental factors. – PhD thesis, The Hebrew Univ. of Jerusalem.
- Shmida, A. 1980. Vegetation and flora of Mt Hermon. – In: Shmida, A. and Livne, M. (eds), *Mt Hermon – nature and landscape*. Kibbutz Hameouchad, Tel Aviv, pp. 97–158.
- Shmida, A. and Wilson, M. V. 1985. Biological determinants of species diversity. – *J. Biogeogr.* 12: 1–20.
- Shochat, E. 1999. The effect of scrub fragmentation by planted woods on bird communities in the northern Negev. – PhD thesis, Ben-Gurion Univ. of the Negev, Beer-Sheva.
- Su, J. C. et al. 2004. Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. – *Conserv. Biol.* 18: 167–173.
- Thomas, J. A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. – *Phil. Trans. R. Soc. B* 360: 339–357.
- Thomas, J. A. et al. 2004. Comparative losses of British butterflies, birds and plants and the global extinction crisis. – *Science* 303: 1879–1881.
- Tucker, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. – *Remote Sens. Environ.* 8: 127–150.
- Tucker, C. J. and Sellers, P. J. 1986. Satellite remote-sensing of primary production. – *Int. J. Remote Sens.* 7: 1395–1416.
- van Rensburg, B. J. et al. 2009. Spatial congruence between ecotones and range restricted species: implications for conservation biogeography at the national scale. – *Divers. Distrib.* 15: 379–389.
- van Swaay, C. A. M. et al. 1997. Monitoring butterflies in the Netherlands and Flanders: the first results. – *J. Insect Conserv.* 1: 81–87.
- Walker, S. et al. 2003. Properties of ecotones: evidence from five ecotones objectively determined from a coastal vegetation gradient. – *J. Veg. Sci.* 14: 579–590.
- Williams, P. H. 2000. Some properties of rarity scores used in site quality assessment. – *Br. J. Entomol. Nat. Hist.* 13: 73–86.
- Williams, P. H. et al. 1996. A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. – *Conserv. Biol.* 10: 144–174.
- Wilson, M. V. and Shmida, A. 1984. Measuring beta diversity with presence-absence data. – *J. Ecol.* 72: 1055–1064.