

Predicting mountain plant richness and rarity from space using satellite-derived vegetation indices

Noam Levin^{1,2}, Avi Shmida³, Oded Levanoni⁴, Hagit Tamari⁴ and Salit Kark^{4†*}

¹Department of Geography and Environmental Development, Ben-Gurion University of the Negev, Beer Sheva 84105, Israel, ²The Centre for Remote Sensing and Spatial Information Science (CRSSIS), The School of Geography, Planning and Architecture, St. Lucia Campus, University of Queensland, Brisbane, QLD 4072, Australia, ³The Israel Plant Information Center (ROTEM), Department of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem, Jerusalem 91904, Israel, ⁴The Biodiversity Research Group, Department of Evolution, Systematics and Ecology, The Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem, 91904 Israel

*Correspondence: Dr Salit Kark, The Biodiversity Research Group, Department of Evolution, Systematics and Ecology, The Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem, 91904 Israel.

E-mail: salit@hebrew.edu

†Present address: The Ecology Centre, School of Integrative Biology, Goddard Building, University of Queensland, St. Lucia, Brisbane, QLD, 4072 Australia.

ABSTRACT

Can species richness and rarity be predicted from space? If satellite-derived vegetation indices can provide us with accurate predictions of richness and rarity in an area, they can serve as an excellent tool in diversity and conservation research, especially in inaccessible areas. The increasing availability of high-resolution satellite images is enabling us to study this question more carefully. We sampled plant richness and rarity in 34 quadrats (1000 m²) along an elevation gradient between 300 and 2200 m focusing on Mount Hermon as a case study. We then used 10 Landsat, Aster, and QuickBird satellite images ranging over several seasons, going up to very high resolutions, to examine the relationship between plant richness, rarity, and vegetation indices calculated from the images. We used the normalized difference vegetation index (NDVI), one of the most commonly used vegetation indexes, which is strongly correlated to primary production both globally and locally (in more seasonal and in drier and/or colder environments that have wide ranges of NDVI values). All images showed a positive significant correlation between NDVI and both plant species richness and percentage tree cover (with R^2 as high as 0.87 between NDVI and total plant richness and 0.89 for annual plant richness). The high resolution images enabled us to examine spatial heterogeneity in NDVI within our quadrats. Plant richness was significantly correlated with the standard deviation of NDVI values (but not with their coefficient of variation) within quadrats and between images. Contrary to richness, relative range size rarity was negatively correlated with NDVI in all images, this result being significant in most cases. Thus, given that they are validated by fieldwork, satellite-derived indices can shed light on richness and even rarity patterns in mountains, many of which are important biodiversity centres.

Keywords

Mountains, NDVI, plants, rarity, remote sensing, richness.

INTRODUCTION

In recent years, our understanding of the relationships between energy, productivity, and species richness patterns has advanced substantially. However, quantification of energy is often based on surrogates such as climate and rainfall. The recent advancement in the availability of high-resolution satellite images (Fritz, 1999) and of global Landsat images that are now freely available on the Web (NASA's Geocover data set; Tucker *et al.*, 2004) is now enabling us to directly estimate productivity using vegetation indices, and to examine the relationships between these estimates and biodiversity patterns (Turner *et al.*, 2003). Nevertheless, very little work has been done to examine these relationships in mountain regions, where access to large parts of the region is limited. Thus, our understanding of the patterns and conclusions are almost

always based on a very small sample of the area. A tool that could aid in mapping and predicting patterns of species richness and rarity over large areas at a relatively low cost that can be validated with fieldwork could be highly valuable.

A large body of research has focused on changes in species richness and rarity along elevation gradients in mountains, identifying a range of patterns (Lomolino, 2001). Among these, one of the most widely documented pattern is a unimodal one, showing peak species richness at mid-elevations. This pattern has been related to ecological and evolutionary factors, as well as to area size and geometrical constraints, such as the mid-domain effect (e.g. Shmida & Wilson, 1985; Auerbach & Shmida, 1993; Lomolino, 2001; Grytnes & Vetaas, 2002; Vetaas & Grytnes, 2002; Kattan & Franco, 2004; McCain, 2004; Rowe, 2005). However, fieldwork on which these models are based is often limited to

very small portions of the area compared to the landscape as a whole. This is especially true in mountainous regions, where access to large parts of the area is limited, dangerous, and costly due to steep terrain, climate, and other limiting factors.

Recently, the availability of satellite-derived vegetation indices increased, making it feasible to study all parts of the globe up to a resolution of 30 m (Pettorelli *et al.*, 2005). Satellite-derived vegetation indices, such as the Normalized Difference Vegetation Index (NDVI, see Methods) (Tucker, 1979; Pettorelli *et al.*, 2005) have been shown to be useful estimates of productivity and can also be used to quantify vegetation-related spatial heterogeneity, two important factors shaping biodiversity patterns (Tucker & Sellers, 1986; Nichols *et al.*, 1998; O'Brien *et al.*, 2000; Mittelbach *et al.*, 2001; Benayas & Scheiner, 2002; Rocchini *et al.*, 2004). On a global scale, NDVI is closely related to net and gross primary productivity. However, local models of NDVI seem to be more accurate in more seasonal and in drier and/or colder environments with wider ranges of NDVI values (except in extremely arid deserts). Local NDVI-based models are less reliable when limited to less seasonal vegetation types, especially tropical or other evergreen forests (Box *et al.*, 1989). Recent work suggests that NDVI is positively correlated with richness levels in different groups. However, most studies to date have shown relatively low correlations between NDVI and plant richness (with R^2 values usually below 0.5) (e.g. Gould, 2000; Bawa *et al.*, 2002; Oindo & Skidmore, 2002; Fairbanks & McGwire, 2004; Rocchini *et al.*, 2004; Gillespie, 2005). This is likely because the images used were either of low spatial resolution (e.g. NOAA AVHRR at 1 km), focused on a subset of the plant species or were restricted to a single date. However, with current advances in technology and data availability over the Web, Landsat images are currently freely available at a resolution of 30 m globally (Tucker *et al.*, 2004), and more detailed images, up to a resolution of dozens of centimetres, can be bought from commercial companies with satellites such as Ikonos (since 1999), QuickBird (since 2001), and OrbView (since 2003). Combined with large-scale and freely available databases of other environmental variables (e.g. temperature and rainfall), these enable us to better understand the relationship between biodiversity and energy, as estimated using remotely sensed measures of productivity (Mittelbach *et al.*, 2003).

Our aims here were to: (1) test the relationship between NDVI values (average and variability) and species richness and rarity; (2) test whether such a relationship, if found, holds for sensors at several spatial scales, and (3) test whether this relationship holds when examined over different seasons.

We here test the hypothesis that plant richness and satellite-derived levels of NDVI will be positively correlated, and that plant richness will be positively correlated with the spatial variation of NDVI within quadrats. The relationship between rarity and NDVI has rarely been examined in earlier studies and was more difficult to predict (Lauver & Whistler, 1993). We predicted that the relationship with NDVI will be stronger for species richness than for rarity, as rare species are not expected to follow the same patterns as common species (Hill & Keddy, 1992) and are often related to the occurrence of unique habitats (Nilsson

et al., 1988; Lauver & Whistler, 1993) limiting our ability to accurately predict their distribution (Karl *et al.*, 2002). However, if such a relationship between rarity and NDVI is found, it may have important implications for conservation purposes.

We examined our hypotheses focusing on Mount Hermon (Fig. 1) in the Middle East as a case study. The Hermon is one of the richest and most unique locations in Israel (Shmida & Sinai, 1980), which is itself a biodiversity hotspot (Medail & Quezel, 1999) within the Mediterranean Basin, one of 25 highest ranking global biodiversity hotspots (Myers *et al.*, 2000). The Hermon has also recently been defined as an area of imminent species extinction (Ricketts *et al.*, 2005). Thus, besides serving as a case study for examining the potential of remote sensing tools that can later be applied to many other parts of the globe, the results of this study can be used and translated for regional trans-boundary conservation purposes.

MATERIALS AND METHODS

Study area

Mount Hermon, located in NE Israel (33°25' N, 35°48' E) along the border with Lebanon and Syria (Fig. 1), is part of the Anti-Lebanon Mountains, which are isolated from the main mountain chains of the Middle East, Asia, and Europe (Shmida, 1977). The Hermon is an elongated anticline that extends NE–SW over 35 km and rises from 300 to 2814 m a.s.l. over a 13-km distance on its SW side, where our study area is located (the highest point in the Israeli part of the Hermon is at 2224 m). The parent material is homogeneous, hard Jurassic limestone forming Terra Rossa soil, and the terrain is characterized by steep rocky Karst slopes (Auerbach & Shmida, 1993). The climate is Mediterranean, with rainy, cold winters, and hot, dry summers. Temperature decreases while solar radiation and precipitation increase with elevation (Shmida, 1977). Precipitation ranges from 600 to 1500 mm per year, and above 1500 m consists mostly of snow (Shmida, 1977). The major snow event usually occurs in the first half of January. During the spring, snow patches remain only at elevations above 1900 m.

Three main vegetation belts have been defined in earlier studies of Mount Hermon (Shmida, 1977, 1980). These include the (1) evergreen Mediterranean maquis (300–1200 m); (2) the xeromontane open forest (1200–1900 m), and (3) the subalpine Tragacanthic belt (1900–2814 m; elevations based on Shmida, 1977). The Israeli part of the Hermon ranges covers approximately 7300 ha, most of which is a nature reserve since 1972. Whereas today there are only few settlements on the Israeli side of the Hermon, there are at least 35 known sites of historical seasonal and permanent settlements (Dar, 1978) (Fig. 1). The area has a long history of grazing by cattle, goat and sheep, which continues today.

Field sampling of plants

In order to reduce the spatial variation resulting from the effect of slope, all sampling sites were chosen on SW facing slopes. In addition, we preselected for sampling only locations with tree

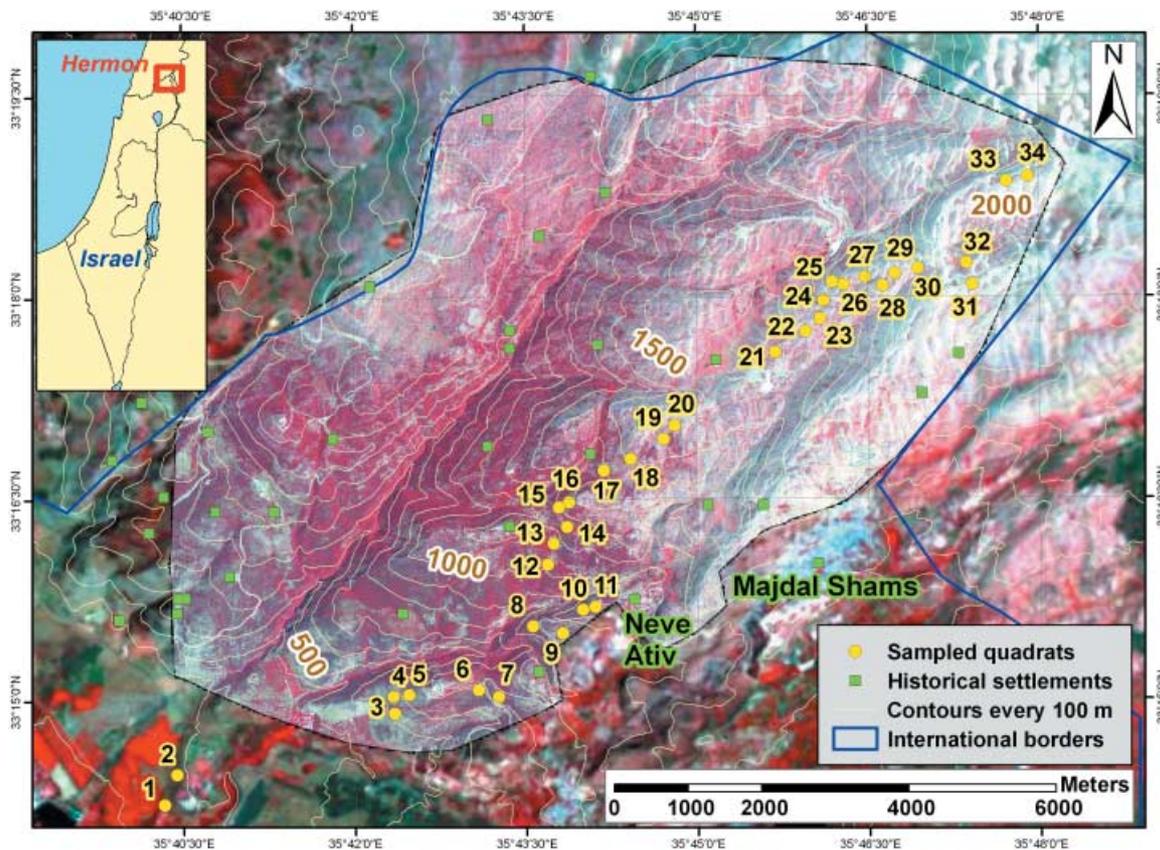


Figure 1 Location map of the study area and field samples: the locations and names of the 34 field samples of vegetation are shown by yellow circles (see online publication for colour content) on a QuickBird satellite image from 26 May 2004 (and a Landsat image from 21 May 2000 for the two lowest elevation locations outside the QuickBird coverage) when there are almost no snow patches left (vegetation is shown in red in this image), with contour elevation at intervals of 100 m. Distribution of historical settlements is marked in green squares based on Dar (1978). Of these, only Neve Ativ and Majdal Shams are currently populated.

cover under 50%, slopes between 30 and 60% steep, and no more than 30% rock cover, located as far as possible from roads, ski areas, and army bases. We sampled 34 quadrats along the elevation gradient ranging between 300 and 2200 m (Fig. 1, Table 1). In order to assist in objectively selecting quadrats for sampling that are representative of their elevation belt, we used the satellite images in the sampling design stage. For each 50-m elevation belt between 300 and 2200 m, we calculated the average NDVI value (from the QuickBird image of May 2004) of all 0.1 ha quadrats on SW facing slopes in the belt. This was done for the total area of the Israeli part of Mount Hermon. We then selected for detailed plant sampling 50 × 20 m (1000 m²) grid squares along a transect that had NDVI values closest to the average of the elevation belt. Several of these locations were later slightly (several meters maximum) relocated in the field due to logistical constraints. Plant sampling was conducted following Whittaker's plant diversity sampling method (Shmida, 1984). All plants in the 20 × 50 m quadrat were then thoroughly sampled. Sampling usually took between 2 and 4 h per quadrat, depending on its richness. All sampling was performed between April and May 2005 by AS, at the time of peak flowering in each elevation (Table 1). AS also visually estimated the percentage cover of trees within each

0.1 ha quadrat. This enabled us to identify and record all plant species except for some of the autumn geophytes. The field quadrat locations were determined using Garmin eTrex Legend GPS (4-m accuracy) (Garmin International Inc., Olathe, KS, USA) measurements of three points along the central axis (at 0, 25, and 50 m) of the quadrats. These were then checked and corrected if needed using a 1-m orthophoto.

For each quadrat, we calculated the total vascular plant species richness, as well as the perennial and annual plant richness (Table 1). Quantifying rarity within a mountain is not trivial, as it can be measured following several estimates (Izco, 1998). Because we are here interested in the relative range size rarity within the mountain area (asking how limited plants are to specific elevation belts), rather than in rarity over their whole distribution range, we decided to use an estimate that enables us to quantify the rarity of the species in each quadrat, as compared with other quadrats. An estimate called 'range size rarity' has been used in many recent studies, for example in the selection of biodiversity hotspots by Myers *et al.* (2000). Range size rarity (RSR) is calculated as the sum of the inverse of the range sizes of all the species occurring in each quadrat (*sensu* Williams *et al.*, 1996; Williams, 2000) (Table 1). We estimated range size as the

Table 1 Summary of characteristics and data from the 1000 m² quadrats sampled in the field.

Quadrat number on Fig. 1	Sampling date	Elevation (m)	Plant richness	% annual species	Relative range size rarity	Percentage tree cover
1	9/4/05	259	95	79%	0.192	20%
2	9/4/05	275	128	76%	0.224	15%
3	8/4/05	517	118	68%	0.127	15%
4	8/4/05	571	120	70%	0.148	15%
5	8/4/05	645	111	70%	0.123	20%
6	15/4/05	695	146	62%	0.136	15%
7	15/4/05	728	142	70%	0.174	20%
8	15/4/05	863	164	65%	0.162	20%
9	16/4/05	868	153	67%	0.133	20%
10	16/4/05	946	142	64%	0.139	5%
11	16/4/05	972	165	62%	0.143	15%
12	29/4/05	1000	139	67%	0.137	20%
13	29/4/05	1070	134	69%	0.133	25%
14	29/4/05	1150	131	72%	0.106	20%
15	29/4/05	1200	139	63%	0.135	15%
16	8/5/05	1275	161	68%	0.147	15%
17	30/4/05	1300	140	62%	0.129	15%
18	30/4/05	1400	131	60%	0.112	15%
19	30/4/05	1430	128	48%	0.126	15%
20	30/4/05	1490	117	62%	0.106	15%
21	8/5/05	1515	124	54%	0.136	15%
22	8/5/05	1595	118	58%	0.126	10%
23	9/5/05	1645	95	32%	0.165	6%
24	9/5/05	1673	101	53%	0.132	7%
25	8/5/05	1740	89	31%	0.179	5%
26	9/5/05	1802	87	33%	0.152	1%
27	26/5/05	1860	74	27%	0.144	3%
28	26/5/05	1895	75	17%	0.152	1%
29	26/5/05	1920	73	14%	0.184	1%
30	26/5/05	1945	74	19%	0.219	0%
31	9/5/05	2060	54	20%	0.179	0%
32	27/5/05	2080	52	29%	0.232	0%
33	27/5/05	2140	39	23%	0.181	0%
34	27/5/05	2150	62	24%	0.343	0%

number of quadrats in which the species occurred out of the 34 quadrats sampled along the elevation gradient. Due to the correlation between species richness and range size rarity in our samples (see Results), we used a modified version of this estimate, which we call relative range size rarity (RRSR). We calculated it by dividing the RSR for each quadrat by the number of species sampled in the quadrat. This estimate, also called mean RSR was proposed by Williams *et al.* (1996). Because richness and RSR are linearly related in our case, we were able to apply this measure across the whole elevation gradient.

A mid-domain effect is expected where landmass boundaries such as mountaintops restrict species ranges and the simple overlap of many, variously sized ranges creates a peak in species richness at mid-elevations (Colwell & Hurtt, 1994). To examine the mid-domain effect, we grouped each two sampling quadrats into intervals of 100 m. We then ran 1000 Monte Carlo simulations without replacement to compare the species richness data with

predictions of a null model that simulates species richness curves based on empirical range sizes (between 300 and 2200 m). We compared our results with 95% simulation prediction curves (intervals) generated by the simulations. This was done based on analytical stochastic models (Colwell & Hurtt, 1994), using the Mid-Domain Null program (McCain, 2004).

Processing satellite imagery

We collected 10 Landsat (path 174, row 37), Aster, and QuickBird satellite images representing different seasons and spatial resolutions (Table 2). To obtain images from all seasons, we compiled the images from a period of five consecutive years (see Wulder *et al.*, 2004 regarding the advantages of using off-year over off-season imagery for classification) (Table 2). All satellite images were radiometrically and atmospherically corrected following Chavez (1996), as implemented in Idrisi GIS. We corrected the

Table 2 Summary of information on the satellite images used in the study and the correlation for each image between NDVI as estimated from the image and plant richness and relative range size rarity as sampled in the field. Due to the continuous snow cover, image 2 was removed from most analyses (see Methods).

Image number	Sensor	Snow distribution	Date	Sun azimuth	Sun zenith	Spearman correlation between NDVI and plant richness	Spearman correlation between NDVI and plant relative range size rarity
1	Landsat 7 ETM +	No snow cover	07/08/99	116.6	28.6	0.874***	-0.516**
2	Landsat 7 ETM +	Continuous snow cover down to 1250–1400 m	14/01/00	151.6	58.6	0.502**	0.036
3	Landsat 7 ETM +	Patches of snow in wind protected east facing slopes, mostly above 2000 m	21/05/00	116.9	24.0	0.931***	-0.468**
4	Landsat 7 ETM +	Few patches of snow in wind protected east facing slopes, mostly above 2200 m	22/06/00	108.4	23.3	0.876***	-0.469**
5	Landsat 7 ETM +	Semi-continuous snow cover down to 1900 m	08/03/02	140.9	45.9	0.828***	-0.500**
6	Aster	Few patches of snow in wind protected east facing slopes, mostly above 2300 m	24/05/01	131.4	17.7	0.896***	-0.497**
7	Aster	No snow cover	09/10/02	161.1	41.3	0.870***	-0.505**
8	Aster	No snow cover	21/10/03	161.1	45.6	0.871***	-0.503**
9	QuickBird	Very few patches of snow in wind protected valleys, mostly above 2000 m	02/07/03	111.1	22.2	0.820***	-0.484**
10	QuickBird	Few patches of snow in wind protected valleys, mostly above 2000 m	26/05/04	124.2	19.1	0.753***	-0.546**

** $P < 0.01$; *** $P < 0.001$.

images for shading effects caused by the topography following Smith *et al.* (1980), using a Digital Elevation Model (DEM) obtained from the Survey of Israel (Hall *et al.*, 1999). We used vegetation indices based on band ratios, which compensate for some of the topographical effects (Riano *et al.*, 2003).

We calculated NDVI, one of the earliest satellite-derived 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 (Pettorelli *et al.*, 2005). We compared the performance of NDVI with that of the soil adjusted vegetation index (SAVI), which is less affected by differences in the soil background than NDVI (Huete, 1988). The NDVI and SAVI were calculated as follows:

$$\text{NDVI} = (\text{NIR} - \text{R}) / (\text{NIR} + \text{R}) \quad (1)$$

$$\text{SAVI} = (\text{NIR} - \text{R}) / (\text{NIR} + \text{R} + \text{L}) * (1 + \text{L}) \quad (2)$$

where NIR = value in the near infrared band of an image pixel, R = value in the red band of an image pixel, and L = a constant soil adjustment factor (we used an intermediate value of 0.5 following Huete, 1988).

All satellite images were rectified to the Israel New Grid at a spatial resolution of 25 m of the DEM, using control points identified on a 1-m resolution colour orthophoto.

NDVI and SAVI were calculated from each of the 10 images for each of the 34 field-sampled quadrats. For the highest resolution (2.4 m) QuickBird images, we also calculated the average, standard deviation (SD), and coefficient of variation (CV) of the vegetation indices within each quadrat. To minimize noise caused by snow cover in the winter images, we excluded from our analysis the fully snow-covered parts of Mt. Hermon. Because the January 2000 image had full snow cover down to an elevation of about 1250–1400 m and could not be analysed for NDVI, we excluded it from further analyses. In our detailed analyses, we focused on the NDVI, as it was found to perform better than SAVI. For analysing spatial heterogeneity, we used the high-resolution (QuickBird) image of May, as it enabled us to examine within-quadrat variation and also corresponded with the mid-season of both sampling and of flowering (Table 2).

Statistical analyses

Variables were checked for normality using the Shapiro–Wilk W -test as implemented in STATISTICA 7.1 (1984–2005; StatSoft,

Inc., Tulsa, OK, USA). Because some variables did not show a normal distribution, we applied where needed the nonparametric Spearman correlation to test for correlation between remotely sensed variables and field estimates of richness and rarity.

RESULTS

Plant richness and NDVI patterns along the gradient

Overall, 574 plant species were sampled in the field along the elevation gradient. Within quadrats, plant richness varied from a minimum of 39 to a maximum of 165 plant species per 0.1 ha quadrat (Table 1), the latter being one of the highest species per area ratios ever detected in Mediterranean regions around the world (Keeley & Fotheringham, 2003; A. Shmida, unpublished data). Plant richness as sampled in the field (in 0.1 ha quadrats, Fig. 1) showed a hump-shaped pattern with elevation ($R^2_{\text{quadratic}} = 0.89$, $n = 34$, $P < 0.001$) (Fig. 2a). Peak plant richness was found between 900 m and 1275 m. However, species richness plotted against elevation did not show a strong mid-domain effect. Only 21% of our 100 m elevation belts fell within the 95% prediction curves of the model based on the 1000 simulations of the Mid-Domain Null, and the shape of the sampled plant richness was not symmetric as predicted by the simulated curves (Fig. 2b).

Annual plant richness showed a hump-shaped pattern along the elevation gradient ($R^2_{\text{quadratic}} = 0.88$, $n = 34$, $P < 0.001$), very similar to that of total species richness. Perennial species richness showed a weaker hump shape ($R^2_{\text{quadratic}} = 0.49$), with peak richness found at somewhat higher elevations (~1500 m). Annual species dominated the community up to 1500 m, and from there upwards perennial species became the majority of the plants, comprising about 80% of the flora at 2000 m (compared with only 25% at 250 m). Relative range size rarity showed a U-shaped correlation with elevation ($R^2_{\text{quadratic}} = 0.59$, $n = 34$, $P < 0.001$), with lowest levels at 1150 m and 1490 m, and highest levels at 2080 m and 2150 m (data in Table 1).

Average NDVI values ranged between 0.18 and 0.35 (for all images), where the lowest values (below 0.1) were obtained mostly for snow covered areas in winter time or for bare rocky areas, and highest NDVI values (above 0.5) were mainly obtained below 1300 m in March (beginning of spring season in the lower parts of the mountain). A hump-shaped pattern was obtained when NDVI was plotted against elevation ($R^2_{\text{quadratic}} = 0.80$, $n = 34$, $P < 0.001$) (Fig. 2c) for mid-spring, whereas a monotonic decreasing linear relationship showed an R^2 of 0.55). Percentage tree cover in the sampled quadrats ranged between 15 and 25% up to 1500 m, whereas from 1925 m upwards no trees were present.

The relationship between richness, rarity, and NDVI

In support of the hypotheses, we found in all our images a strong and positive relationship between average NDVI in each quadrat and plant species richness as sampled in the field (Table 2). NDVI values explained between 57–87% of the variation in total plant species richness (Table 2), regardless of the time of year when the image was taken, the sensor, or the spatial resolution of

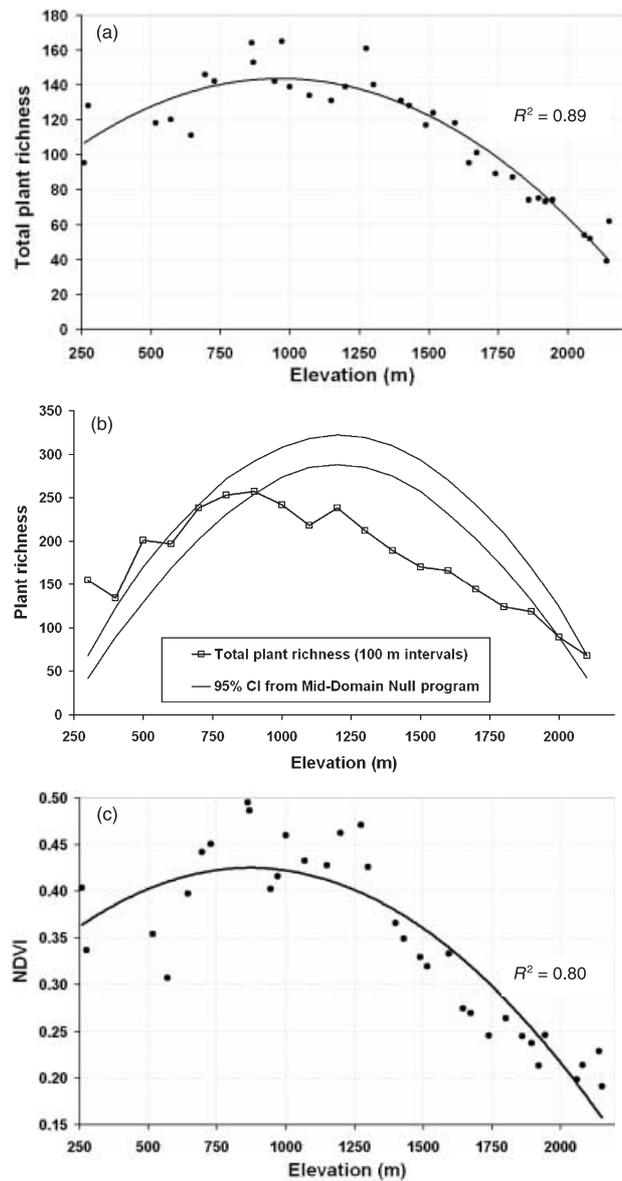


Figure 2 (a) Plant richness as sampled in the 1000 m² quadrats as a function of elevation along with a second-order polynomial fit. (b) Species richness curves (lines with data points for the 100 m intervals), and the 95% confidence intervals (CI) curves generated by the program Mid-Domain Null (1000 simulations each sampled without replacement; McCain, 2004). Analysis was done using empirical range sizes and simulated range midpoints. (c) Mean NDVI (21 May 2000 Landsat image) within the 1000 m² quadrats as a function of elevation.

the image. The corresponding figures for SAVI explained 47–82% of the variation in total and annual plant richness. This relationship was the strongest in the spring image (May 2000 Landsat image) ($R^2 = 0.87$, $P < 0.001$, $n = 34$; Fig. 3a). This relationship became even stronger (by an average of 4%) in all images when analysed separately for field-sampled annual plant richness, reaching a maximum for the May 2000 image ($R^2 = 0.89$, $P < 0.001$, $n = 34$). However, perennial plant richness was not significantly

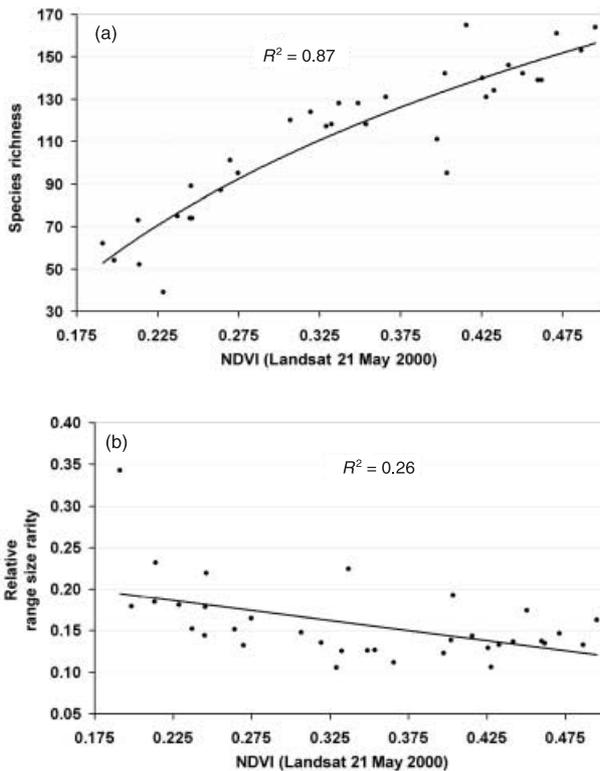


Figure 3 The relationship between NDVI as calculated from the 21 May 2000 Landsat image and: (a) field-derived estimates of plant species richness in the 1000 m² quadrats (R^2 value is between log NDVI and plant richness); (b) relative range size rarity of plant species in the 1000 m² quadrats.

correlated with average values of NDVI. In addition, NDVI was positively correlated with percent tree cover, explaining up to 78% of the variation for the spring Landsat image of March.

On the contrary, relative range size rarity was negatively correlated with NDVI values in all images, this relationship being significant for most images (see Table 2; Fig. 3b). Plant species richness was negatively correlated with relative range size rarity ($R^2 = 0.21$, $P < 0.01$, $n = 34$, after log transformation of both variables).

Because we used very high-resolution images (QuickBird), we could calculate the spatial variation in NDVI among pixels within our sampled quadrats, each 1000 m² quadrat having between 150 and 180 pixels (depending on its orientation relative to the north). The SD of NDVI values within the quadrats was significantly correlated with total plant species richness ($R^2 = 0.58$, $n = 32$, $P < 0.001$; Fig. 4) as well as with annual plant richness ($R^2 = 0.63$, $n = 32$, $P < 0.001$). However, the coefficient of variation (CV) of NDVI within the quadrats was not correlated with plant richness. This may be due to the correlation between the values of average NDVI and SD of NDVI within the quadrats ($R^2 = 0.74$, $n = 32$, $P < 0.001$). Temporal variability in mean NDVI values (i.e. between the satellite images) showed a hump-shaped relationship with both total and annual plant richness ($R^2 = 0.40$ and 0.59, respectively; $n = 34$, $P < 0.001$; Fig. 5a,b) when calculated

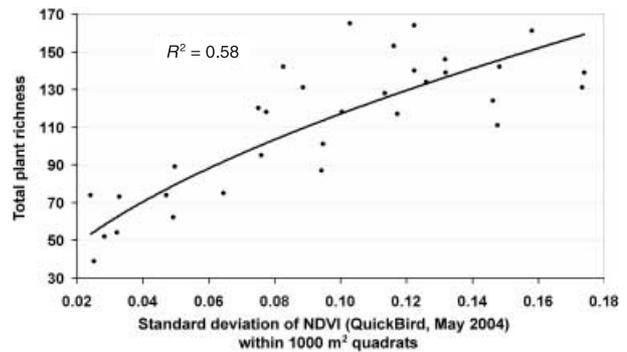


Figure 4 The relationship between field-derived estimates of plant species richness (in the 1000 m² quadrats) and the standard deviation of NDVI within the quadrats (26 May 2004 QuickBird image). R^2 value is between log SD of NDVI and log plant richness.

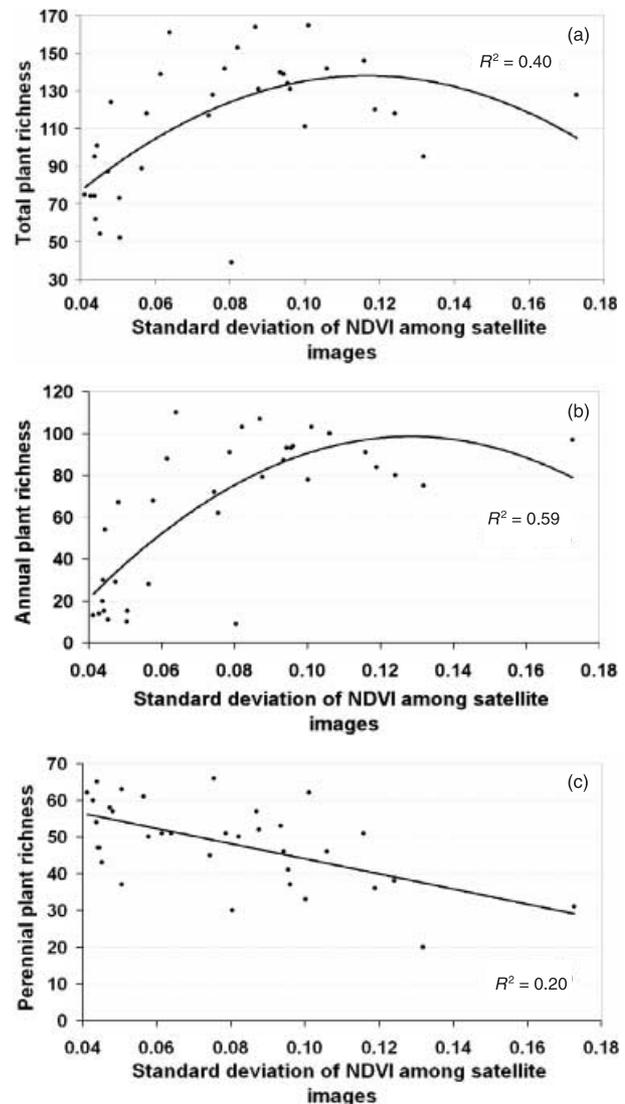


Figure 5 The relationship between the standard deviation of NDVI of the 10 satellite images and (a) total plant richness, (b) annual plant richness, and (c) perennial plant richness.

using the SD. These hump-shaped relationships became even stronger when an outlier quadrat that had especially high temporal variation (located at an elevation of 275 m) was excluded from the analysis ($R^2 = 0.47$ and 0.62 for total and annual plant richness, respectively). However, the coefficient of variation (CV) of NDVI between the images was not correlated with total or annual plant richness. Perennial plant richness was negatively (and significantly) correlated with temporal variability in NDVI values when calculated using the SD ($R^2 = 0.20$, $n = 34$, $P = 0.01$; Fig. 5c) but not with the CV of NDVI between the images.

DISCUSSION

Remote sensing as a predictor of biodiversity

A range of high-resolution satellite images covering different seasons and spatial scales were used in this study to compare the results derived from remote sensing analyses with those of detailed field sampling of plants collected as part of the same study and sampled within the same quadrats. This enabled us to compare field-sampled plant richness and rarity with both the mean NDVI (and SAVI) and the spatial variability in NDVI within 0.1 ha quadrats across the altitudinal gradient. Average NDVI values were strongly correlated with percentage tree cover, and both the average and the SD of NDVI in space were positively correlated with total species richness, and especially with annual plant richness, as sampled in the field. However, as the CV of NDVI was not significantly correlated with plant richness, it may be concluded that productivity (e.g. percentage tree cover), rather than habitat variability (heterogeneity) was a more important factor in explaining species richness. In addition, using 10 different images at spatial resolutions ranging between 2.4 and 30 m, we find generality in the patterns. All images showed similar relationships between NDVI and plant richness, with the strongest relationships found for the spring month of May, where 87% of the variation in plant richness was explained by NDVI. The strong correlation that we found between NDVI and species richness, regardless of the time of year the image was taken, the sensor or the spatial resolution, testifies to the stability and reliability of satellite image-derived vegetation indices for scientific and practical applications, when combined with field sampling. The fact that we can explain up to 87% of the variation in plant richness as sampled in the field using indices derived from satellite images, has great promise. Clearly, satellite images cannot replace fieldwork aimed at understanding the community composition, detecting alien species or studying the distribution of specific rare species, although recent studies suggest that they can assist in determining community composition (Hurlbert & Haskell, 2003; Feeley *et al.*, 2005; Lassau *et al.*, 2005).

As predicted, rarity is less strongly related to NDVI than richness, but interestingly, also shows clear relationships. When examining the range size rarity after standardizing for richness using the relative range size rarity estimate (RRSR), we find that as we move up the mountain into areas with less vegetation cover, lower productivity, and lower NDVI values, the proportion of

rare species increases. Thus, we find that RRSR and NDVI are negatively, and mostly significantly, correlated. This finding goes hand in hand with the prediction that higher elevations, being smaller in their area and more isolated from other populations and from humans, will tend to show higher levels of rarity and endemism (Lomolino, 2001). Had we been able to sample all the way to the Hermon peak at 2814 m, we expect that the patterns would have become even stronger due to the fact that the uppermost parts of the Hermon have even more rare species. While remote sensing tools cannot identify specific rare species and their traits in most cases, they are a promising tool for helping predict rarity patterns.

NDVI as an estimate of primary productivity

Why do we find such strong correlation between plant richness and NDVI values? Two main factors are expected to shape this correlation — productivity and heterogeneity. NDVI correlates strongly with plant biomass and with net primary productivity (NPP), the difference between carbon fixed by photosynthesis and carbon lost to autotrophic respiration (Evans *et al.*, 2005). As such, it is one of the best and most direct available estimates for ecosystem productivity, especially in more seasonal and in drier and/or colder environments with wider ranges of NDVI values (Box *et al.*, 1989; Oindo & Skidmore, 2002; Hurlbert & Haskell, 2003; Kerr & Ostrovsky, 2003; Pettorelli *et al.*, 2005). It is a useful proxy for photosynthetic energy absorption, which is in turn, controlled by fractional canopy cover, leaf area index (LAI), leaf angle, and leaf optics. Fractional cover and LAI are of maximum importance in arid/semiarid/Mediterranean systems with canopies < 50% cover and can be accurately monitored using remote sensing methods (Elmore *et al.*, 2000).

Productivity–richness relationships

The relationship between energy, productivity, and species richness is an extensively studied topic in ecology and has been tested at multiple spatial scales and ecological systems (Evans *et al.*, 2005). Many studies strongly support the hypothesis that energy correlates positively with species richness. This relationship is considered as one of relatively few universal ecological laws (Huston, 1994; Rosenzweig, 1995), though we have not yet reached a full understanding of the processes shaping these patterns (reviewed in Evans *et al.*, 2005). It is also not yet totally clear whether similar processes shape patterns seen in latitudinal vs. altitudinal gradients (Stevens, 1992; Rahbek, 1995; Sanders, 2002; Sanders *et al.*, 2003). The two most common relationships found between richness and energy include (1) a unimodal hump-shaped pattern, initially increasing, peaking at intermediate energy levels and then declining at higher energy levels (Colwell & Hurlbert, 1994; Colwell & Lees, 2000; Lomolino, 2001) and (2) a positive relationship, showing monotonically increasing richness with increasing energy (Tilman, 1982; Rosenzweig & Abramsky, 1993; Rosenzweig, 1995; Waide *et al.*, 1999; Mittelbach *et al.*, 2001; Whittaker & Heegaard, 2003; see Evans *et al.*, 2005 and references therein).

In mountains, studies conducted on ecologically diverse species and in widely separated geographical regions reveal hump-shaped patterns of richness along elevation gradients in many cases, with peak richness occurring at intermediate elevations (reviewed by Lomolino, 2001). The locations of the richness peaks, while varying substantially among mountain ranges, often occur in ecotonal areas of transition between communities (Lomolino, 2001). The peak richness at mid-elevations has been explained by several hypotheses (reviewed in Rahbek, 1995). For example, the productivity hypothesis suggests that productivity is the driving force behind patterns in richness and that elevation merely serves as a surrogate for productivity (Rosenzweig & Abramsky, 1993). Another hypothesis relates to the interaction between the response of species to daily temperatures, photosynthesis rates, and respiratory rates for plants (Janzen, 1973; Sanders, 2002). An additional hypothesis proposes that distributions are limited by climatic severity and reduced availability of resources at upper elevations, and by biotic factors (e.g. predation) at lower elevations (reviewed in Sanders, 2002). An alternative hypothesis suggests that lower elevations have lower species richness due to human-related activities, such as fragmentation, agriculture, and introduction of alien species (Lomolino, 2001; Sanders, 2002). Other factors contributing to the pattern, such as the area effect and the mid-domain effect, explained by geometric constraints within a bounded region (Colwell & Lees, 2000), have been suggested and are discussed in the literature (Rahbek, 1997; Sanders, 2002; Sanders *et al.*, 2003). Our data support the linear relationship between richness and productivity in mountains, as proposed by the productivity hypothesis, showing little support for the mid-domain null model effect.

In systems other than mountains, various relationships have been reported in recent studies between NDVI and species richness, including a positive (Gillespie, 2005), a hump-shaped (Fairbanks & McGwire, 2004), and a negative relationship (Oindo & Skidmore, 2002). For SD or coefficient of variation of NDVI in space and/or time, these patterns include a positive relationship (Gould, 2000; Oindo & Skidmore, 2002; Fairbanks & McGwire, 2004) or a negative relationship (Gillespie, 2005). In our study, we found a positive relationship between NDVI and richness. Had our plant samples included also quadrats covering dense maquis (chaparral), we expect that the observed relationship would have been unimodal, initially increasing, but later decreasing again. This is because in woody areas, such as Mediterranean maquis, NDVI values are higher than in shrubland areas (Asner, 1998). However, species richness in dense Mediterranean maquis is lower than that found in more open areas and shrublands (Shmida, 1985). Therefore, it is expected that when closed maquis areas will be included, the full range of the relationship between NDVI and species richness in Mount Hermon and other Mediterranean ecosystems will show a hump-shaped pattern, the most common relationship observed between species richness and productivity (Mittelbach *et al.*, 2001). We expect that strong correlations as we found for Mt. Hermon between NDVI and plant richness will occur mainly in high mountains where several vegetation belts occur, covering a wide range of NDVI values. NDVI is more sensitive to low and medium values of the LAI

values and becomes saturated for high LAI values (usually above 3) (Birky, 2001; Wang *et al.*, 2005) as well as for high NPP values (Asner *et al.*, 2004). Therefore, in very dense and less seasonal vegetation areas, this tool may be less useful (Box *et al.*, 1989). Our results suggest that the spatial variation in NDVI within quadrats is positively related to the number of species that occur in the quadrat. However, when we examine the coefficient of variation in NDVI, which standardizes the variability within each quadrat by the mean NDVI, the estimate does not appear to be correlated with richness. Thus, it may be that productivity, rather than heterogeneity, is the major factor shaping the patterns of plant richness. Had our plant samples included also quadrats covering dense maquis, we expect that the observed relationship between the CV of NDVI and plant (and especially annual plant) richness would have been positive, as species richness in dense Mediterranean maquis is lower than that found in more open areas and shrublands (Shmida, 1985).

Our results were different for annual vs. perennial plants. Temporal variability in NDVI showed a hump-shaped correlation with both total and annual plant richness, but was negatively correlated with perennial plant richness. As none of our plant samples were collected in areas fully covered by trees, most of the variability in species richness was related to that of annual plant species. These comprise the majority of plant species up to an elevation of 1500 m, and the variability in their spectral response over the year is greater than that found in most perennial plant species, excluding deciduous trees (Karnieli, 2003). The differences in the patterns between annuals and perennials may result from the fact that the trees in the lower elevations of Mt. Hermon up to c. 1200 m are evergreen, while those in the higher elevations, and especially in the xero-montane forest, are deciduous. As the temporal variability explained plant richness mostly when using the SD (and not the CV) of NDVI values between the images, it may be concluded again that the main factor explaining plant richness in this system is its productivity.

Conservation implications

Quantifying biodiversity and studying its changes in space and time are labour intensive and expensive, and often spatially restricted, a fact that leads to many gaps in the databases on which our ecological knowledge and conservation decisions are made. This is especially true for mountainous regions, which are often not only species rich, but also hold endemic species and species at risk of extinction (Millennium Ecosystem Assessment, 2003; Ricketts *et al.*, 2005). As such, mountains show up as high-priority conservation hotspots in many cases. For example, among the 34 hotspots recently defined by Conservation International (<http://www.conservation.org/xp/CIWEB/regions/priorityareas/hotspots.xml>), at least one high-priority hotspot in every continent occurs in mountains and, in some cases such as Europe and Central Asia, almost all biodiversity hotspots are located in mountainous regions. Our results suggest that satellite images can be a very useful complementary tool in mountain ecology and biodiversity research, especially for covering large and inaccessible areas, comparing spatial scales and analysing temporal

trends. This approach may be very useful as part of the process of evaluating and predicting plant richness and rarity in mountains at regional and global scales, which is an important component in biodiversity estimation.

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