Variation in species richness and spatial turnover among different vegetation types along an elevation gradient in east Nepal

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The relationship between plant species richness and spatial turnover is sought along the elevation gradient in southeastern part of Nepal. Data were collected from field sampling (plot size 20 x 50 m²) to cover all three physiognomic type of vegetation i.e. open, shrub dominated and forest. In each 100 m elevation band, two plots were made in each vegetation type controlling both area and sampling efforts. The species richness and spatial turnover is regressed against elevation by means of Generalised Linear Model. The species richness in each vegetation types as well as combined has similar unimodal relationship along the elevation gradient shown by significant second order polynomial. The maximum species richness occurred at mid-elevation 600-900 m a.s.l. The spatial turnover and elevation also exhibits a trend indicated by significant second order polynomial, but it is an inverse unimodal. The species richness and spatial turnover have highly significant negative relationship. The high species turnover was observed towards the ends of gradient, and low at the middle. All vegetation types have similar pattern for species richness and spatial turnover, which may indicates same underlying control upon them.

Keyword: Species richness, spatial turnover, vegetation types, generalised linear model

Species are not equally distributed; some regions are richer in species than others. Thus, there is a gradient on species distribution. The latitudinal and elevational gradients are most well studied biogeographical patterns (Pianka, 1966; Whittaker *et al.*, 2001). Generally species richness is lower at higher elevation. The elevation gradients in diversity may differ between plant groups (Bhattarai and Vetaas, 2003). Different lifeforms are dominant upon different vegetation types, whereas, tree dominates forest, herbaceous vegetation dominates open land and intermediate land type is dominated by shrubby vegetation. Thus, elevation gradient on species richness along different vegetation types might be an interesting topic in macro-ecology. However literatures pertinent to this topic is rare.

Local gradients in species richness produced spatial turnover (cf. Harrison *et al.*, 1992). Pattern in species richness and spatial turnover are major issues in macro-ecology (Blackburn and Gaston, 1996; Lennon *et al.*, 2001). In literature species richness and turnover are treated separately but they are logically inseparable and interact through changes in spatial scale (Lennon *et al.*, 2001).

Natural forests are decreasing due to increasing human population in Himalayan region. Some of the forests in Himalaya have already been cleared and turned into shrub and grassland before estimation of species richness. In other hand, some open lands are also turned in to close forest by afforestation and conservation measures. Thus, lots of change on natural vegetation is a common phenomenon everywhere in the world. By comparing species richness pattern among different vegetation types along the elevation gradient we can generate information whether the replaced vegetation exhibits some fundamental underlying control, which can have potential applications in conservation practices.

Many different measures based on species richness and occurrences have been developed. These measure include species richness, alpha diversity, beta diversity and gamma diversity (Whittaker *et al.*, 2001). The studies of Whittaker (1960, 1972, 1977), MacArthur (1965, 1972), Wilson and Shmida (1984) and others have established importance of these measures. The alpha diversity is species richness within local patches of a given vegetation or land type (within-habitat diversity i.e. plot richness). Local species richness may

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or may not equal to alpha diversity, depending upon how fine is the spatial resolution of the localities concerned and how heterogeneous they are (Whittaker, 1960, 1972). Spatial turnover is an extent of species replacement or biotic change along environmental gradients (Whittaker, 1972). The spatial structure is equated frequently with beta diversity (Koleff and Gaston, 2002). Defining spatial turnover following Whitatker's (1960) original definition of beta diversity (i.e. regional richness/ local richness) is employed here. However, the combine influence of alpha and beta diversity referred to gamma diversity or total species richness (Brown and Lomolino, 1998).

Despite wide application of these terms, studies on the relationship between species richness and spatial turnover among the different vegetation along the elevation gradient has been surprisingly low. Both measures are important issues for conservation matters as reserve design. Therefore the present study aims to address the following basic questions about spatial structure of pant assemblage along the elevation gradient: (i) is there a relationship between species richness and spatial turnover? and (ii) how species richness and spatial turnover are varying among vegetation types along the elevation gradient?

Methods

Site description

The study was carried out in southeastern (26° 42' N; 87° 16' E to 26° 59' N; 87 °21' E) Nepal, (Fig. 1). The study transect is situated in the Terai and part of the Mahabharat range. The Siwalik is a sub-Himalayan range (c. 1300 m a.s.l.), which rises beyond plain land of Terai and is the youngest in the formation of the mountain system (Manandhar, 1999), but in the eastern Nepal where this study was carried out there is no exiestence of separate Siwalik mountain due to its merging into Mahabharat range (Pandey, 1995). The lesser Himalayas are called Mahabharat range (maximum ca. 3000 m.a.s.l.), which is immediately to the north of Siwalik range.

Nepal has monsoon climate with dry periods in winter and wet periods in summer. The monsoon is hot and humid, wet summers and mild warm dry winters up to 1000 m a.s.l., but in the Mahabharat range between 1000-2000 m a.s.l. there is a warm temperate monsoon climate with warm and wet summers and cool and dry winters. Mean annual temperature at 100 m a.s.l. is 24.7 °C and declines by 0.53 °C per 100 m elevation (adiabatic lapse rate in the studied transect), and the mean annual precipitation is 2001 mm (see Bhattarai and Vetaas, 2003, Table 1). Cloud zones influence the vegetation of mountains, which starts above c. 1400 m.a.s.l. and occurs frequently at c. 2000 m.a.s.l. in the lesser Himalayas, whereas cloud formation is normally between 2500-3200 m.a.s.l. in the greater Himalayas (Dobremez, 1976).

Plot design and vegetation sampling

The field sampling was carried out in summer (Jun-July) 2001. An imaginary transect line was made in a north-south direction from 100 to 1500 m.a.s.l. Six plots (50 x 20 m) were made in each fifteen 100 m elevation band. The plot size 0.1 ha is very common
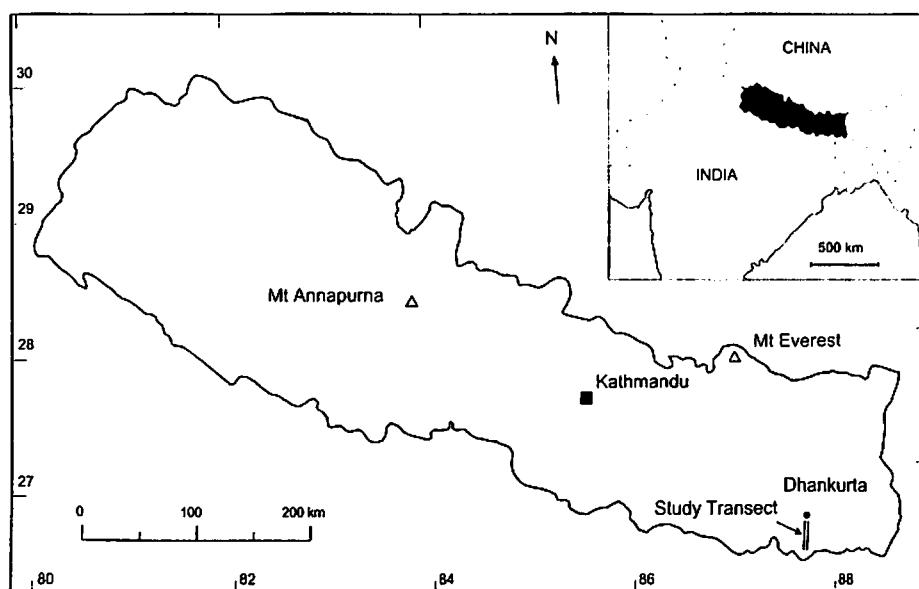

Fig. 1 Location of study transect in east Nepal

in such study and has been used in several such studies (e.g. Whittaker, 1963, 1966; Whittaker and Woodwell, 1969; Whittaker and Niering, 1975; Bhattarai and Vetaas, 2003).

Three different categories of vegetation open, shrub dominated and forest were sampled. Two plots each were in open herb-dominated vegetation, laid shrub-dominated vegetation, and in the close forest, which facilitates biogeographical comparison of species richness among vegetation types (see Bhattarai and Vetaas, 2003). There is no continuous band of each vegetation type along the elevation gradient so plots were selected subjectively in each 100 m elevation band according to availability of vegetation types. All vascular plant species, including pteridophytes were recorded. Elevation was recorded by altimeter. Each plot (50 x 20 m) was sampled by equal efforts (2-4 hours by 4 persons) to control both sampling effort and area (Rahbek, 1997; Lomolino, 2001).

Statistical analysis and autocorrelation

Detrended correspondence analysis (DCA; Hill and Gauch 1980), with detrending by segments and non-linear rescaling was used for total data set as well as data from each vegetation type to describe the difference in species composition and estimate the length of gradient in SD-units (Hill, 1973).

A Generalized Linear Model (GLM; McCullagh and Nelder, 1989; Dobson, 1990) was used to relate total species richness as well as species richness of each vegetation type to elevation. The species richness is discrete data (counts) and may have a Poisson distribution of error (McCullagh and Nelder, 1989), which requires a logarithmic link. The assumption was found reasonable after checking the residuals. Significance test was carried out by using "F" due to over dispersion of the models (Crawley, 2002).

Beta diversity was calculated by formula established by Whittaker (1960) which is most widely used in ecological research (Wilson and Shmida 1984), $\beta_w = S/\alpha - 1$, where S is the total number of species

recorded in the system (i.e. whole gradient), and α is the average number of species recoded within the community samples (i.e. each elevation band). The beta diversity (β_w) as species turnover between two elevation bands, two terms are used synonymously in the present study. I use the term richness as the number of species presents in each 100 m elevation bands (Peet, 1974).

The number of species in each 100-m bands is a variable which can exhibits spatial autocorrelation (Tobler, 1969), which means that species richness in two nearby elevation bands on average more similar than species richness in two different bands (Bhattarai and Vetaas, 2003). The autocorrelated variable is a problem mainly when explicit causal factors are being tested (Legendre, 1993; Lennon 2000). In this study I am not testing any causal factors but only want to generate hypothesis, so no separate autocorrelation test was performed.

Result

Species composition

There are total 966 species in all 90 plots of three vegetation types along the whole transect, among them 672 species are found in open vegetation, 655 in shrub dominated vegetation and 663 species in forest. The mean species numbers are 98, 102 and 92 in open, shrub and forest respectively. Even though, the variance is greater in forest (Fig. 2) compared to open and shrub land, mean species richness in each vegetation types is not significantly different. The length of gradient is almost similar with 3.75, 3.67, 3.68 SD units for open, shrub and forest respectively. When all data set were combined (all vegetation types included) the length of gradient was almost the same (i.e. 3.80 in SD unit).

When species richness of each vegetation type is regressed against elevation. The polynomial first (1) and second (2) order were tested against null model and each other. The deviance explained indicates percentage of total (null) deviance.

Table 1: Summary of regression statistics

Vegetation type	Polynomial order	Degree of freedom	Residual Deviance	%-deviance explained	P-value
Species richness in open land	2	12	34.74	53	<0.011
Species richness in shrub land	2	12	24.02	41	<0.040
Species richness in forest	2	12	91.08	40	<0.050
Combined	2	12	19.99	52	<0.012

Species richness pattern among vegetation types

There is a significant unimodal relationship between species richness and elevation in each vegetation type along the elevation gradient (Fig. 4, Table 1). Similar unimodal relationship between species richness and elevation is also observed when data sets from three vegetations are combined but optimum point and intercept are slightly different. Open has intercept 4.58; shrub has 4.62 and forest has 4.51. Open land has optimum richness at 800-900 m.a.s.l. shrub has optimum richness at 600-800, forest has optimum richness at 800-900 m.a.s.l.

Spatial turnover and species richness

There is a significant trend on spatial turnover (beta diversity) along the elevation gradient. The pattern of spatial turnover along the elevation gradient is shown in (Fig. 5). There is a strong significant negative correlation between species richness and spatial turnover (open r= -0.74, shrub r= -0.98, forest r= -0.95, total r=-0.89) (Fig.6). The correlation between unique species richness to mean species richness is also high (r=0.72). The spatial pattern is inverse unimodal in all vegetation types, higher turnover observed at lower and higher elevation. The pattern of spatial turnover or betadiversity in each vegetation types when combined with all data sets from each vegetation types showed statistically significant on second order polynomial regression (Table 2). High species richness bands at the middle of the gradient are found to be with low spatial turnover.

When beta diversity of each vegetation type is regressed against elevation. The polynomial first (1) and second (2) order were tested against null and each other. The deviance explained indicates percentage of total (null) deviance.

Discussion

Vegetation type and species richness

The species richness in each vegetation type attained a peak at mid elevation. The unimodal pattern observed in each vegetation types along the elevation gradient indicates consistency on species richness in all vegetation types (Fig. 4). This may indicates that all vegetation types have same underlying control even though some are natural and some are replaced vegetation of original types. Mean species richness among vegetation types is not significantly different which may indicates that two plots of each vegetation type have constancy on species composition along the elevation gradient. Three vegetation types are homogeneous in species composition is also indicated by almost similar gradient length in SD unit, 3.75 for open, 3.67 for shrub and 3.68 for forest. The open land has slightly longer gradient length as compared to others two. Generally shorter gradient length in open land as compared to others is expected due to domination of herbaceous species, which are more widespread in species composition and less sensitive to higher elevation (Bhattarai and Vetaas unpublished), so that longer gradient found in open land is rather the opposite. The longer gradient in open land might be associated with more disturbances than shrubby and forest vegetation type by grazing and other anthropogenic factors which can create microenvironment to colonize new species (Hoopes and Harrison, 1998). Dispersal of propagule from core area to local habitat, mass effect (Shmida and Whittaker, 1981) increase species richness in general but its influence on beta diversity or community gradient i.e. coenocline depends upon the properties of the system. If surrounding habitat is homogenous, mass effect decreases beta diversity because of homogenizing effect of expanded species ranges (Shmida and Wilson, 1985).

Beta diversity is increased by mass effect if surrounding habitat is heterogeneous and immigration of species occurs from beyond the extremes of the gradient (Wilson and Shmida, 1984; Shmida and Wilson, 1985). The study area is part of Himalayan elevation (longest mountain range in the world) gradient, so that migration of species to colonise in an open land is possible from regional species pool beyond 1500 m a.s.l. which can justify the longer gradient in open land as compare to others.

Table 2. Summary of regression statistics

Vegetation type	Polynomial order	Degree of fredom	Residual Deviance	%-deviance explained	P-value
Open betadiversity	2	12	8.79	58	<0.005
Shrub betadiversity	2	12	5.92	36	p=0.07
Forest betadiversity	2	12	25.15	53	<0.010
Combined	2	12	2.15	51	<0.014

If one compares this study with latitudinal gradient, it is equivalent to a macro scale study where temperature varies 7-8° centigrade between two end of gradients so local process such as topography, grazing and land use process may have less influence on species richness relationship in such a study.

The maximum species richness is found between 600-900 m a.s.l. which is middle of the gradient. The mid elevation peak on species richness is a common pattern (Rahbek, 1995, 1997). Terborgh (1977) argued that emerging hump-shaped relationship between species richness and elevation because of hot spot in resources. Shmida and Wilson (1985) claimed that the higher species richness at mid elevation associated to mass effect and ecological equivalency. The mid elevation receives input on species richness from either direction.
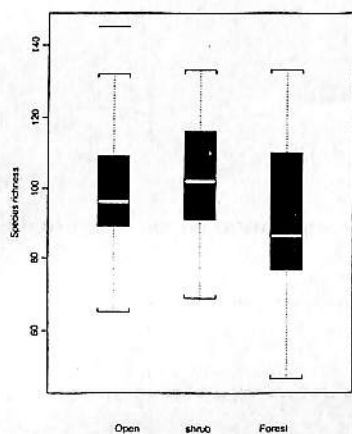

Fig. 2 Box plots showing variation in species richness across three vegetation types.
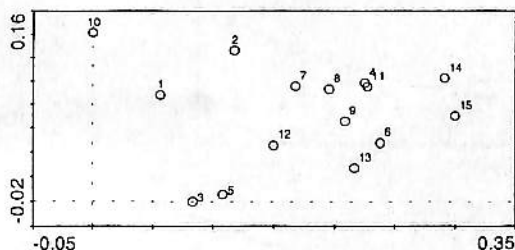

Fig. 3 DCA diagramme shows the position of 15 different 100 m elevation bands. Along the DAC axis 1 there is gradient from Terai to Mountain top (1500 m).

On species richness-elevation relationship, sampling efforts and area exert strong influence (Rahbek, 1995; Lomolino, 2001). Terborgh (1977) found a spurious pattern from his non-standardised sampling data. Rahbek (1995) made compilation of literature on species richness elevation relationship and found only 21% of studies have standardised their area and

sampling efforts. I have standardised my sampling by doing fieldwork in same season with equal plot size, and equal efforts by same persons. Therefore there is no doubt upon observed pattern between species richness and elevation.

Species turnover and richness gradients

There is a gradient on richness (Fig. 3) and strong negative relationship between species richness and spatial turnover or beta diversity (Fig. 6). The turnover i.e. beta diversity has significant pattern along the elevation gradient. There is higher beta diversity at lower species richness band and vice versa, indicate that higher richness areas are associated with more species in common with neighbouring bands. Austrheim (2002) also found more similarity on species at mid elevations. My result supports Lennon et al. (2001), who also found negative relationship between species richness and turnover. Beta diversity is a measures of differentiation diversity, the higher species richness at midelevation is not due to higher beta diversity. The lower and upper elevation bands have high turnover because of different species composition. The turnover between two elevation bands is a measure of the difference between the lists of species present in each band. Turnover consisits of species continuity, gain and loss (Lennon et al., 2001). I argued that the low turnover associated at high species richness site might be due to higher species gain rather than species loss. But at lower and upper elevation band there is a more random mixture of species.

Rosenzweig (1997) has defined spatial turnover as the slope of the species-area relation. The concept of spatial turnover is intimately linked to the notion of change of species, both gain and loss along the ecological gradient (Whittaker, 1972). Study area relationship has shortcomings as a measure of turnover because it focuses solely on species net gain with increasing area; species loss in the additional area is effectively invisible (cf. Lennon et al., 2002). To study spatial turnover it is necessary to consider explicitly gain and loss of species in space. Spatial turnover is a differentiation diversity or between-habitat diversity (MacArthur, 1965).

Ecological interpretation of diversity and its measurements has historically been simple species richness within sample i.e. alpha diversity results from niche differentiation among species and beta diversity from species response to a range of habitats
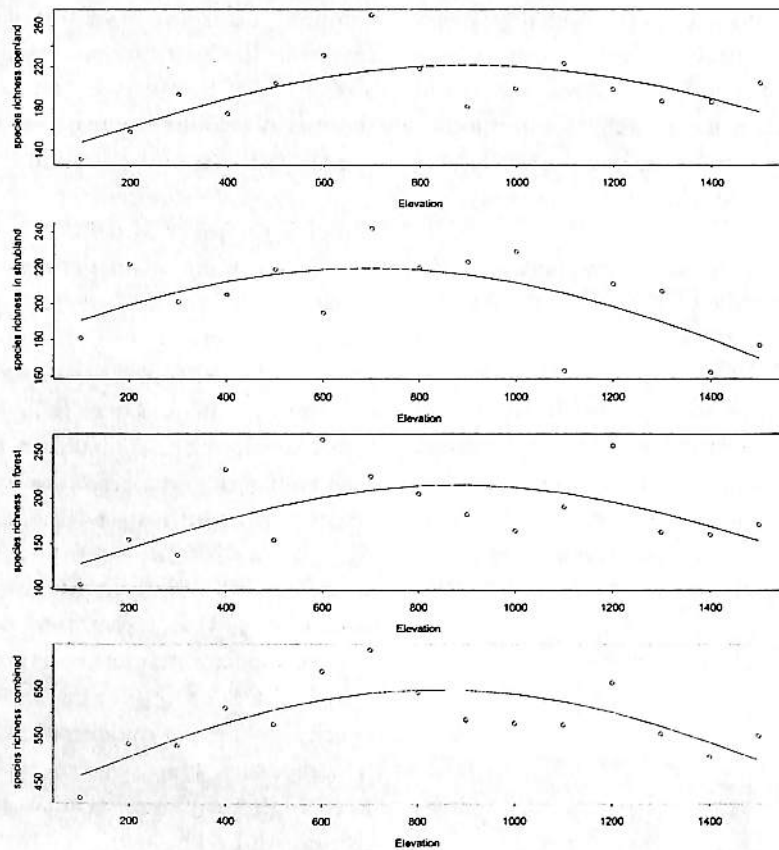
Fig. 4 Relationship between species richness and elevation in different vegetation types. The fitted lines are based on significant second order term in Genralized Linear Models.
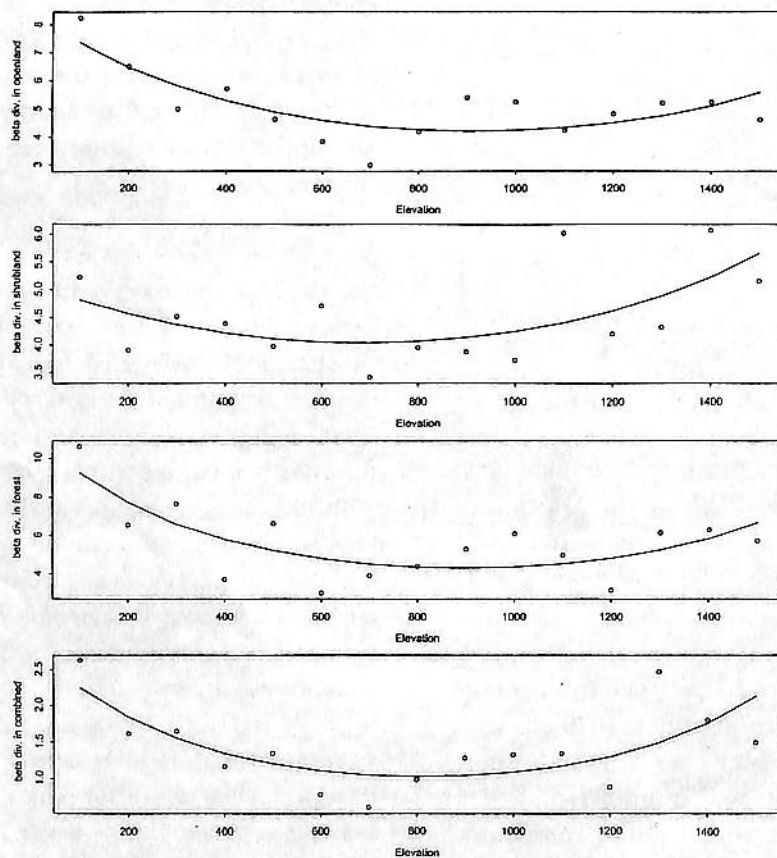

Fig. 5 Relationship between beta diversity or spatial turnover and elevation in different vegetation types. The fitted lines are based on significant second order term in Genralized Linear Models.
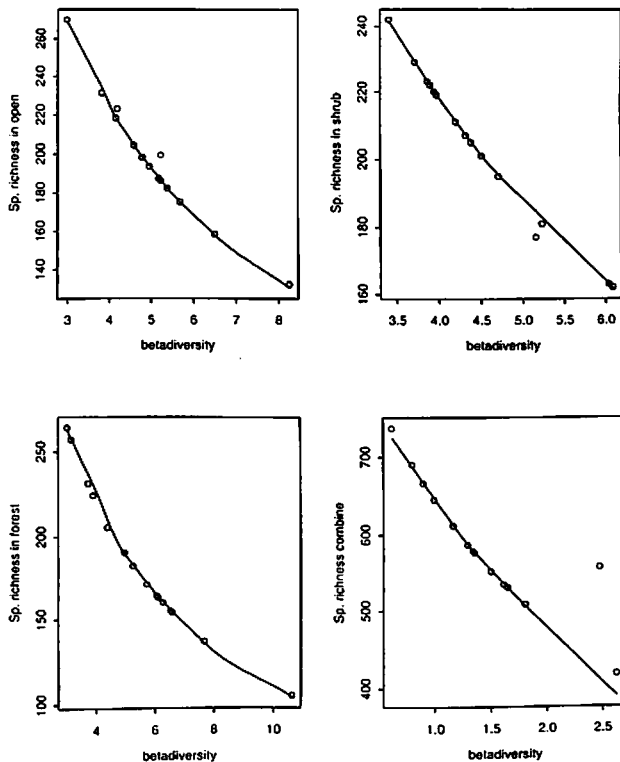
Fig. 6 Relationship between species richness and beta diversity (spatial turnover) in different vegetation types along the elevation gradient.

(Whittaker 1960, 1966, 1972, MacArthur 1965, 1972, Terborg 1973). Beta diversity alone does not explain much regarding richer or poorer diversity in a space but it may shows habitat difference, which is important issue on conservation. But beta diversity and species richness provide diversity pattern of a landscape. Even though two concepts seems rather independent but should not be separated in biodiversity study.

Species pool and turnover

Species pool, species richness, species turnover and autocorrelation are related ecological phenomenon, which determine diversity pattern along the ecological gradient (cf. Zobel, 1997). Low turnover between two sites indicate that two sites share similar species which is a phenomenon of spatial autocorrelation (cf. Lenon *et al.*, 2001). The mid elevation (600-900 m a.s.l.) have higher species richness with lower turnover indicates that adjacent mid elevation bands to contain increasingly large proportion of the local species pool. Therefore there is a low turnover rate at high species area simply because of less vacant for difference in species composition when higher proportion of the species pool is already present (Lenon *et al.*, 2001).

In clusion, this study shows that different vegetation types along the elevation gradient have similar pattern in species richness and sptial turnover, which may indicate that similar underlying factors may control upon the spatial distribution of species. These results generate a hypothesis that, to explore the species richness pattern one can sample any type of vegetation along the elevational gradient. This hypothesis needs to be tested by further study, which can have potential application in conservation and species introduction.

Acknowledgment

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