University of South Bohemia
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Orchid diversity

Ph.D. Thesis

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Annotation:

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In this thesis I investigated the various factors that might determine species diversity, using mainly orchids as a model group. These factors were area, energy available, latitude and metapopulation interactions within a species.

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Declaration – Prohlášení

I hereby declare that I worked out this Ph.D. thesis on my own, or in collaboration with the co-authors of the presented papers and manuscript, and only using the cited literature.

I declare that in accordance with the Czech legal code § 47b law No. 111/1998 in its valid version, I consent to the publication of my Ph.D. thesis (in an edition made by removing marked parts archived by the Faculty of Science) in an electronic way in the public access to the STAG database run by the University of South Bohemia in České Budějovice on its web pages.

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Author contribution statement

Iva Schödelbauerová, author of this Ph.D. thesis, is the first author of tree papers (manuscripts) and one chapter in the book, and the second author of one chapter in the book and wrote a substantial part of these. Most of the raw data processing, as well as most of the statistical analyses were performed by her. David Roberts helped with "Species-area-energy relationships" (Paper I and Paper II), Anthony Dixon participated in "Inverse latitudinal gradient" (Paper III), Bishnu Bhattarai collected the orchid data in Nepal (Paper IV), Raymond Tremblay provided the raw data and advices regarding Lepanthes biology (Paper V), and Pavel Kindlmann as supervisor helped with all necessary things.

All co-authors hereby consent to the publication of the papers in the PhD. thesis of Iva Schödelbauerová and support it by their signatures:

Bishnu Bhattarai

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GENERAL INTRODUCTION

The Orchidaceae is one of the largest families of flowering plants, making up 10% of the flowering plant species in the world (Dressler 1981). The estimated number of orchid species varies from 12000 to 35000 (Fiveash 1974; Sanford 1974; Alphonso 1975; Hunt 1984; Heywood 1985; Dressler 1993). However, many of these species are rather locally distributed and/or generally rare (Tremblay 1997a; Koopowitz 2001; Zotz 2004; Benavides *et al.* 2005). Because of the continuing changes in land-use in both the tropics and the temperate zone, which frequently result in a considerable loss of suitable habitat, there is concern about the long-term conservation of many orchid species (e.g., Koopowitz 2001; Tremblay and Hutchings 2003; Vásquez *et al.* 2003; Wotavová *et al.* 2004).

For conservation it is important to know, what determines the number of species (species diversity). Determination of the factors that affect species diversity is an important topic in ecology (Huston 1994; Rosenzweig 1971, 1995) and has been studied at various levels, from local to regional. At the regional level, diversity has been related to area (species-area relationship; Arrhenius 1921; Gleason 1922; Williamson 1988; Palmer and White 1994; Rosenzweig 1995; Fridley *et al.* 2005; Drakare *et al.* 2006), available energy (species-energy relationship; e.g., Wright 1983; Currie 1991; Wylie and Curie 1993a,b; Rosenzweig 1995; Gaston 2000; Hawkins *et al.* 2003a; Pelkey *et al.* 2000; Evans *et al.* 2005; Storch *et al.* 2005), latitude (Pianka 1966; Rohde 1992; Rosenzweig and Sandlin 1997; Gaston and Blackburn 2000; Willig *et al.* 2003; Hillebrand 2004), landscape altitudinal complexity (Rahbek 1995), climate, productivity (Swift and Anderson 1994) or landscape heterogeneity (Turner 1987).

1) Species-area-energy relationship

On a global scale, the species-area relationship can be used to characterize the relationship between populations (metapopulations). The species-area relationship (SAR) is one of the few laws of ecology and has proved to be a useful tool in the study of biodiversity patterns (Lomolino 2001). Although the SAR was known at least as early as the eighteenth century, it was not until the 1920s that the relationship was mathematically quantified by Arrhenius (1921). The equation is $S = cA^z$, where S is the number of species in a given area A, and c

and z are constants (z is the slope of the line and c is the initial trajectory). SARs are often presented as log-log plots when the Arrhenius equation becomes: **log S = z *log A + log C**.

The SAR is used by conservation biologists in the study of habitat fragmentation (Turner *et al.* 1994; Brooks *et al.* 1997, 1999a,b; Cowlishaw 1999; Ney-Nifle and Mangel 2000) and also for ecological applications such as design of reserves (Gilpin and Diamond 1980; Higgs and Usher 1980) and for estimating species extinction rates (May *et al.* 1995; Pimm *et al.* 1995). The power law SAR has great significance in describing, in quantitative terms, what may be the most universally accepted ecological rule of thumb (MacArthur and Wilson 1976).

Area and available energy are major determinants of species richness. First, species richness increases with area – the species-area relationship (SAR; Arrhenius 1921; Gleason 1922; Williamson 1988; Rosenzweig 1995). Second, the energy available to an assemblage (i.e. that which it can turn into biomass) at a particular spatial resolution influences its species richness – the species-energy relationship (SER; e.g., Wright 1983; Currie 1991; Wylie and Curie 1993a,b; Rosenzweig 1995; Gaston 2000; Hawkins *et al.* 2003a; Pelkey *et al.* 2000; Evans *et al.* 2005; Storch *et al.* 2005). These two fundamental ecological patterns may be closely interrelated. Wright (1983) suggested that larger areas may contain more species as they have more resources that enable species populations to be larger, buffering them from extinction and promoting species richness (the 'area *per se*' hypothesis, according to Connor and McCoy 1979). Similarly, sites with more available energy may host more species because population densities are larger, this is often termed the more individuals hypothesis (Gaston 2000). Both the SAR and SER can be related to patterns of species abundance and occupancy. Although conclusive evidence that supports the more individuals hypothesis of the SER is not yet available (Currie *et al.* 2004; Evans *et al.* 2005), there is evidence that areas with higher energy availability host not only higher numbers of species, but also more individuals (Kaspari *et al.* 2003; Hurlbert 2004). Moreover, Bonn *et al.* (2004) report that there are on average higher species occupancies (i.e. proportion of sites occupied by each species) in areas where the availability of energy is highest.

The Normalized Difference Vegetation Index (NDVI) can be used as a measure of energy available to an assemblage. NDVI is strongly and positively correlated with the net primary productivity (Kerr and Ostrovsky 2003), and thus is a suitable measure of the energy available to consumers. NDVI derived from the visible and near infrared channel

reflectances (0.58 to 0.68 μm and 0.73 to 1.10 μm, respectively) and is highly correlated to surface vegetation. It is a dimensionless number with typical range from –0.200 to 0.800. Very low values of NDVI (0.1 and below) indicate barren areas of rock, sand or snow, moderate values shrub and grassland (0.2 to 0.3) and high values temperate and tropical rainforests (0.6 to 0.8). This data set is produced as part of the NOAA/NASA Pathfinder AVHRR Land program. The first AVHRR channel is in a part of the spectrum where chlorophyll causes considerable absorption of incoming radiation, and the second channel is in a spectral region where spongy mesophyll leaf structure leads to considerable reflectance. This contrast between responses of the two bands can be shown by a ratio transform; i.e., dividing one band by the other. The Normalized Difference Vegetation Index (NDVI) is one such ratio and is highly correlated with vegetation parameters, such as green-leaf biomass and green-leaf area. Hence, it is of considerable value for vegetation discrimination (Justice *et al.* 1985).

Storch *et al.* (2005) used avian species distribution data for South Africa and Lesotho and as expected, logarithmically transformed species richness was positively related both to log area and log NDVI for both avifaunas. The slope of the SER was lower for larger areas, and the slope of the SAR was lower in areas with high-energy availability. These results support the theory that high levels of energy availability depress the slope of the SAR by elevating species' occupancies. However, these results appear to disagree with some previous findings. Weiher (1999) report the opposite pattern, i.e., a positive relationship between productivity and the slope of the SAR so that the SAR has a higher slope in more productive areas. Soininen *et al.* (2007) report that the slope of SAR based on sample units of 11 km^2 increases with latitude. Koleff *et al.* (2003) conclude that very little is known about range distributions and regional species turnover in relation to latitude.

In many taxa, especially those confined to natural habitats that have decreased in area recently most of the species diversity is now concentrated in protected areas. The orchid family is a good example, as some of the enormous numbers of species are extremely susceptible to disturbance of their natural habitats (Kati *et al.* 2004; Padmawathe 2004; Flores-Palacios and Valencia-Díaz 2007; Jacquemyn *et al.* 2007). At present, protected areas in the agricultural/industrial landscape can be considered as habitat islands (Begon *et al.* 1990; Shriver *et al.* 2004; McDonald *et al.* 2008), i.e., islands of remnants of natural vegetation surrounded by a hostile landscape. For many species, including orchids, the

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surrounding landscape is uninhabitable (Forman 1995). Thus, instead of total area, often the size of protected areas may be more closely correlated with species richness. In Schödelbauerová *et al.* 2009 **(Paper II)** it is suggested that for orchids - on the large scale considered - area is always very important, latitude is more important than energy available and protected area gives a better fit than total area in most cases.

2) *Latitudinal and inverse latitudinal gradient*

Differences between habitats in the number of coexisting species per unit area fascinated early naturalists (Darwin 1859; von Humboldt [1828] 1993) and remain a central aspect of ecological research (Gaston and Blackburn 2000). No single pattern of biodiversity attracted ecologists more than increase in species richness towards the tropics (Pianka 1966; Rohde 1992; Rosenzweig 1995; Gaston and Blackburn 2000; Crawley and Harral 2001; Willig *et al.* 2003; Hillebrand 2004; Hawkins *et al.* 2006; Mittelbach *et al.* 2007). An obstacle to the search for the primary cause of this latitudinal gradient has been the ever-increasing number of hypotheses (Pianka 1966; Rohde 1992), their interdependence (Currie 1991; Gaston and Blackburn 2000) and the lack of rigorous falsification (Currie *et al.* 1999). Still, such latitudinal gradients in diversity exist and need to be accounted for. This could indicate that the basic pattern of species distribution is not the result of a single evolutionary or ecological process, but rather a complex of several factors (Bokma *et al.* 2001). It could also indicate that the bounded nature of global environments, even in the absence of any environmental gradients, produces equatorward increasing species richness patterns (Pielou 1977; Colwell and Hurtt 1994; Willig and Lyons 1998; review by Colwell and Lees 2000). In other words, the latitudinal gradient species richness might be partly a result of ecological and evolutionary processes, and partly a consequence of a combination of probability and the boundaries of landmasses in nature.

Explanations of the increase in species diversity towards the tropics

Mid-domain models use random placement of species geographical ranges in a domain (Earth) with hard boundaries (the poles) to predict a peak in diversity in the middle of this domain (equator) without invoking any ecological or evolutionary processes. Simulation and analytical modelling have shown that the random placement of species geographical ranges along a geographical gradient with hard boundaries (i.e. a domain)

produces a hump-shaped pattern of species richness, such that local species richness peak at the midpoint of the domain (Pineda 1993; Colwell and Hurtt 1994; Colwell and Lees 2000). Grytnes (2003) proposes four possible ecological models for the creation of the mid-domain effect:

1) Evolutionary model: a species may originate at any point within a domain. From this origin, the species may expand its range to adjacent areas, but not beyond the hard boundaries, even if it has the ecological potential to do so (see Bokma *et al.* 2001, for a similar model). The crucial point is that a species that originates outside the domain cannot expand its range over the hard boundaries and into the domain. One possible exception to this is that a propagule of a species from outside the domain might disperse into the domain causing the same species to establish within the domain (this will be the origin of this species within the domain) if such establishment is equally probable at any point within the domain. This means that areas close to the domain boundaries are not receiving more species from outside of the domain than any other point within the domain. This can happen if the distance between the domain and nearest suitable source of colonists is large relative to the size of the domain.

2) Source-sink model: this model may create the mid-domain effect if sink populations are commonly established from source populations that appear within the domain and if hard boundaries prevent establishment of sink populations from source populations outside the domain. The source-sink model may be particularly important for altitudinal gradients (Rahbek 1997; Kessler 2000; Lomolino 2001; Grytnes and Vetaas 2002). Here the geographical distance between very different ecological conditions outside the domain may be considerable (low probability of establishment of sink populations). The consequence is that source populations outside the domain cannot establish sink population inside the domain. The only exception to this is that source populations may establish sink populations inside the domain, if establishment of such populations is equally or almost equally (im) probable in the whole domain.

3) Dynamic-environment model: the environments of species are dynamic and so are the ranges of species. When the species adjust their distribution ranges following an environmental change (e.g. climatic changes) the species close to a hard boundary may face a problem as the hard boundary limits the possibilities for dispersal of the species. Hence, if the environmental conditions demanded by a species disappear from the domain, the species cannot migrate to another suitable area resulting in the extinction of species that

do not have part of their ranges inside the domain at all times (Vetaas and Grytnes 2002). This mechanism has also been offered as one of the explanations for Rapoport's rule (Brown 1995).

4) Range-size model: It has been hypothesized that species with small ranges have a higher probability of extinction (Jablonski 1986; Rosenzweig 1995). Close to the boundary, species ranges will tend to be smaller, as the sizes of some ranges are restricted by hard boundaries. Hence, a humped pattern results when more species go extinct close to the hard boundaries than towards the middle of the gradient.

Subsequent tests of the mid-domain model revealed high predictive power of such models for both global (Lyons and Willig 1997; Jetz and Rahbek 2001; Koleff and Gaston 2001) and regional data sets (Lees *et al.* 1999), whereas others found strong differences between predicted and observed diversity patterns (Bokma *et al.* 2001; Diniz-Filho *et al.* 2002). Lees *et al.* (1999) examined the latitudinal and elevational patterns of species richness of a group of butterflies (the subtribe Mycalesina – *cca.* 67 spp.), which does not exhibit such a monotonic pattern (the increase in the number of species from the poles towards the Equator, and from high elevations down to sea-level), either for empirical records or for interpolated species ranges. Instead, summation of their ranges generates a domed curve of species richness values approximately symmetrical around mid latitudes within the islands, a pattern most smoothly exhibited by the wider ranging and better known species, and a less symmetric curve peaking near mid elevations.

Bokma *et al.* (2001) created a simulation model, which suggests that random species distribution processes result in high species richness in the middle of a landmass. Species diversity increases towards the middle of a latitudinal domain in the absence of any geographical gradients in ecological and evolutionary processes. Their model predicts the highest species richness in the middle of larger areas rather than in the middle of the latitudinal stretch of a landmass, as predicted by earlier one-dimensional models (Willig and Lyons 1998). But in the case of the New World, their model predicts a two-peaked latitudinal pattern. The largest discrepancy with the real-world latitudinal diversity pattern is the low diversity predicted at mid-latitudes and the high diversity predicted at high latitudes. Therefore, two patterns emerge that need an ecological and/or evolutionary explanation: 1) the high extant diversity in Central America and 2) the low extant diversity in southern and central parts of North America. So, by using data on New World mammals, they found a high correlation between observed and predicted species richness

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in South America, but not Central America and North America. For mid-domain models, latitude represents the geometric constraint imposed on the range size of species. All other models use latitude as a surrogate variable for one or several factors co-varying with latitude.

Diniz-Filho *et al.* (2002) used a geostatistical approach to describe bi-dimensional spatial patterns in species richness of South American birds of prey (Falconiformes and Strigiformes) and indicate strong spatial patterns both across latitude and longitude, for the two groups. These patterns were then correlated with those predicted by a bi-dimensional null model constructed to take into account South America continental edges. Species richness of these two groups, especially that of the Falconiformes, seems to be strongly affected by biome type and shape, but it does not follow the simple null model based on random allocation of species ranges within continental boundaries. Also, the Andes affect the shape of the geographical ranges in South America and, consequently, bias the patterns of range overlap by chance alone, creating distinct biogeographical zones (Rapoport 1975; Graves 1988; Rahbek 1997; Ruggiero and Lawton 1998; Rahbek and Graves 2000, 2001).

Gradients of decreasing energy (and water) *supply* (Currie 1991; Allen *et al.* 2002) and *decreasing biome area* (Rosenzweig 1995) toward the poles are proposed as ultimate causes for the latitudinal diversity decline. Allen *et al.* (2002) argue that temperature influences the diversity of terrestrial and aquatic ectotherms primarily through its effects on the biochemical kinetics of metabolism. Metabolic rates, in turn, dictate resource requirements at the level of the individual and rates of resource supply required to maintain communities composed of many individuals. Allen *et al.* (2002) used data for terrestrial, freshwater, and marine taxa along latitudinal and altitudinal gradients to support their arguments. Their results support the hypothesis that elevated temperatures increase the standing stock of species by accelerating the biochemical reactions that control speciation rates (Rohde 1992).

Changes in the intensity or specificity of ecological interactions (competition, predation, parasitism) with latitude are also proposed as ultimate causes of the latitudinal trends in species diversity (Pianka 1966), but several recent contributions failed to observe consistent changes in interactions with latitude (Lambers *et al.* 2002; Ollerton and Cranmer 2002). Lambers *et al.* (2002) show that several temperate tree species experience density-dependent mortality between seed dispersal and seedling establishment, while ecologists have long postulated that density-dependent mortality maintains high tree diversity in the

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tropics (Janzen 1970; Coley and Barone 1996; Leigh 1999; Harms *et al*. 2000). The proposal that resources are divided more finely amongst a greater number of species in the tropics, compared to temperate communities (MacArthur 1972; Janzen 1973), suggests that tropical organisms should indeed be more ecologically specialised. However, the low species diversity at very high latitudes may also lead to apparent ecological specialisation in species interactions. In this case, the resulting latitudinal trend would be hump-backed – high specificity of interactions in the tropics and towards polar regions, with much lower specificity (greater generalisation) in temperate latitudes. Interestingly, the extremes of the gradient would show greater specialisation in interactions for diametrically opposite reasons – in the tropics because of high species diversity and consequently finer division of resources, in the polar areas because of low species diversity and therefore lack of opportunity for species to be more generalised. Ollerton and Cranmer (2002) assembled two independent data sets, which suggest that plant-pollinator interactions are not more ecologically specialised in the tropics compared to temperate latitudes. This is in contrast to the prevailing view that tropical ecological interactions tend towards higher specificity than their temperate counterparts. They used a data set of plant-flower visitor interactions in 35 communities at different latitudes and a data set on pollinators of various asclepiad species (subfamily Asclepiadoideae of the Apocynaceae sensu l. Endress and Bruyns 2000).

The effective evolutionary time hypothesis (Rohde 1992) assumes higher speciation rate in the tropics to be the major process increasing diversity at low latitudes. The higher diversification is based on energy being positively associated with mutation rates and negatively with generation time (Cardillo 1999), on temporal stability in geological time scales enhancing clade persistence (Jansson and Dynesius 2002) and on area size being positively associated with speciation rate (Losos and Schluter 2000). They show that *Anolis* lizards on Caribbean islands meet several expectations of the evolutionary theory. Within-island speciation exceeds immigration as a source of new species on all islands larger than 3000 km^2, whereas speciation is rare on smaller islands. Above this threshold island size, the rate of species proliferation increases with island area, a process that results principally from the positive effects of area on speciation rate. Also as expected, the slope of the species-area relationship jumps sharply above the threshold.

Rapoport's rule (Rapoport 1975, 1982) is the next general mechanism believed to regulate species diversity along the latitudinal continuum from the tropics to the poles.

Rapoport's rule predicts that organisms from low latitudes have narrower tolerances for climatic conditions than high-latitude species. Consequently, tropical latitudes appear as a finer mosaic of distinctive microclimates to a tropical organism than to temperate or polar organism (Stevens 1989). This pattern is explained (Stevens 1989, 1992) on the basis of climatic variation and tolerance ranges; high-latitude environments are expected to have a greater annual range of climatic conditions than low-latitude environments, therefore favouring the evolution of eurytolerant species, with larger geographic ranges than those evolved in the less variable, tropical environments. Thus, low-latitude organisms should be characterized by a broadening of climatic tolerance as compared to low-latitude organisms. As a consequence of a small geographic range, most low-latitude localities will have relatively more species near the margin of their geographic ranges than high-latitude sites. Populations near the margin, although poorly adapted to the local conditions, are not locally excluded because of the continuous arrival of migrants from areas, where the species does well, and thereby inflating species richness. Several reviews have made the point that greater habitat heterogeneity of tropical areas does not fully account for the gradient in species richness because even comparable habitat types support more species in tropical than in extratropical latitudes (MacArthur 1965, 1969; Whittaker 1969). The increased environmental sensitivity of low-latitude organisms does not result in an increase in the number of obvious ecotones in the tropics, but produces greater heterogeneity in the success of organisms exploiting a given location. The heterogeneity may allow for species coexistence that might otherwise be impossible (Stevens 1989). He also suggests that (i) tropical species with narrower geographical ranges have narrower environmental tolerances or narrow niches, (ii) their narrower tolerances would lead to greater spatial heterogeneity of their distributions, and (iii) a „rescue effect" operates such that patches where species do well supply individuals to patches, which cannot maintain viable populations. Several researchers (Connell 1978; Hubbell 1979, 1980; Huston 1979) have proposed a non-equilibrium hypothesis to account for the high species richness of tropical forests. In its usual form, this approach involves some kind of disturbance to the community. The problem for proponents of these explanations is that even in non-equilibrium conditions competitively inferior species are eventually become extinct in disturbance models (Hubbell 1980). Rapoport's rule should, in turn, influence SARs because in regions containing species with large ranges, the accumulation of species as area increases should be slower than in regions with higher rates of endemism (Stevens 1989; Arita and Rodríguez 2002). This suggests a connection between LDG and SAR

patterns: SARs should be steeper at lower latitudes and decline as the average species range size increases toward the poles (MacArthur 1965, 1969; Lyons and Willig 2002).

Niche breadth is also positively associated with latitude (the latitude-niche breadth hypothesis – MacArthur 1972) and niches become narrower toward the tropics. This idea has also been frequently considered as an explanation for the latitudinal patterns in species richness (Vazquez and Stevens 2004) that are described for all continents, except Antarctica, throughout much of geological time and for most higher taxa of plants and animals (Willig *et al.* 2003; Hillebrand 2004). MacArthur (1972) suggests that because of greater stability and lower seasonality in tropical than in temperate regions, populations at low latitudes should be more stable than populations at higher latitudes; in turn, greater population stability should allow narrower niches. He argued that populations of specialists should be more temporally variable than those of generalists and that tropical regions are less environmentally variable, have lower levels of abiotic stress, higher productivity and higher habitat heterogeneity than temperate regions. He also hypothesized that because of the lower environmental variability in the tropics there is a lower risk of the species there becoming extinct.

Some groups of organisms, however, show an opposite trend: a strong latitudinal decline in species diversity towards the tropics. These trends have been almost neglected in the literature and little is known about their underlying ecological and evolutionary causes. Therefore, the ecological explanations offered are usually specific to the group in question. In Kindlmann *et al.* (2006) **(Paper III)** the existing hypotheses explaining this phenomenon are summarized and the evidence that tends to favour each hypothesis is presented.

3) Orchid diversity in Chitwan

Several studies in Neotropical forests (e.g., Frei 1973) indicate that certain epiphyte species show marked preferences for particular species of trees (phorophyte), whereas in other studies little or no host specificity is recorded (Trapnell and Hamrick 2006, Zimmerman and Olmstead 1992). Generally, epiphytes occur on a number of different phorophytes, in variable frequencies (Benzing 1990) and different host specificities, the exclusive presence of one epiphyte species on one host species, was rarely observed (Tremblay *et al.* 1998). Possible mechanisms for host-tree or phorophyte specificity

involve microclimate (Callaway *et al*. 2002), tree architecture (Zotz and Andrade 2002), water retention capacity (Castro-Hernández *et al*. 1999; Callaway *et al*. 2002), bark sloughing, presence of certain bark chemicals (Frei and Dodson 1972), other bark characteristics (Benzing 1981), allelopathic components (Frei and Dodson 1972; Benzing 1990) and distribution of mycorrhizal fungal symbionts. Epiphytic orchids have mycotrophic nutrition (carbon, other nutrients and possibly water are supplied to the plant by mycorrhizal fungi) and require a mycorrhizal symbiont for seed germination (McKendrick *et al*. 2000, Otero *et al*. 2005).

Epiphytic communities are ideal systems for evaluating species-specific interactions. Epiphytes need trees for their survival but because the relationship is mainly in one direction, it is facilitative. Because trees appear to simply provide a substrate above the forest floor, the expectation is that these orchids will not be associated with particular species of trees (Callaway *et al.* 2002). However, many correlative studies have shown that epiphytes tend to be observed growing more frequently on certain species of trees (Johansson 1974; Benzing 1981; Bennett 1986; Ter Steege and Cornelissen 1989; Migenis and Ackerman 1993; Dejean *et al.* 1995; Kernan and Fowler 1995), and that various characteristics of tree species correlate with the presence and abundance of epiphytes (Frei and Dodson 1972; Schlesinger and Marks 1977).

Orchids in the Himalayan region have been studied over a long time (Duthie 1906; Banerji 1978, Amatya 1982; Paudyal 1982; Banerji and Pradha 1984), but there is neither data, nor any other information on orchids in the lowlands of Nepal, where most studies have focused on the higher animals and plants.

4) *The metapopulation concept*

In the past few years, the metapopulation concept has become widely and firmly established both in population biology and nature conservation, especially in the context of species protection in habitats, which are becoming increasingly fragmented (Hanski and Gilpin 1997). Habitat destruction and fragmentation have restricted an increasing number of plant species to small and isolated populations. Even in intact habitat remnants these populations face an increased risk of extinction because of environmental, demographic and genetic stochasticity. Random fluctuations in environmental conditions that affect survival and reproduction are considered to be the most important stochastic factor (Boyce

1992; Menges 1992), whereas demographic stochasticity, i.e., deviations from expected rates of survival and reproduction due to sampling error in finite populations, is considered to be of minor importance (Menges 1991).

The challenge of any population viability analysis is to predict future state of a population. Numbers of plants of many orchid species are declining. Changing this trend requires intervention and adoption of new management regimes, but it is necessary to have full knowledge of their potential effects. For small populations of endangered species the population decline may be irreversible. The potential consequence of a change in management for a population should, whenever possible, be subject to predictive modelling (Tremblay and Hutchings 2003). Predicting the number of individuals may be a desirable objective, but realistically for small populations predicting the likelihood that a population will go extinct within a specific period of time is more useful. The problem with small and isolated populations is that they are expected to have a higher probability of extinction because of higher demographic, environmental and /or genetic stochasticity (Goodman 1987; Menges 1991; Fisher and Matthies 1998). In isolated populations, genetic drift may eventually reduce genetic variation (Lacy 1987; Frankham 1996), especially because effective population sizes are usually much smaller than the number of reproductive individuals in a population (Frankham 1995). Populations with low genetic variability have a reduced potential to adapt to environmental changes (Ellstrand and Elam 1993). Reproduction of plants in small populations may also be negatively affected by a reduction in the diversity of incompatibility alleles (Byers 1995). Species are rarely distributed uniformly in space but are made up of separate populations, interconnected to varying degrees through dispersal. The clustering of individuals into local populations, the sizes of which vary in time and space, influences the genetic structure of a species. Genetic differences between local populations will evolve over time when there is little or no gene flow between them (Wright 1943, 1946). As a result of this spatial structure, the demography and genetics of populations will be a product not only of local environmental conditions but also processes operating at a regional scale (Husband and Barrett 1996). Few studies have examined, in detail, the distribution and demography of plants at a regional scale. These studies indicate that plants are never uniformly distributed, but rather occurred in clumps (Erickson 1943; Antonovics *et al.* 1994; Husband and Barrett 1996), even when the habitat appeared to be relatively homogenous (Carter and Prince 1988).

Terrestrial orchids produce tens of thousands of seeds during their lifetime (Arditti 1992; Willems *et al.* 2001), so even a small number of fruits should potentially yield a sufficient number of recruits. Seeds are small and light, which provides them with a highly efficient means of dispersal. Orchid seeds can be dispersed over great distances, colonizing islands 100s or 1000s of kilometers from the nearest seed source (Arditti and Ghani 2000). However, it is likely that the majority of orchid seed falls close to the mother plant (Dressler 1990). As their populations, on average, do not grow in numbers, one individual gives rise, on average, to only one offspring that achieves reproductive age. This illustrates the enormous mortality rates these species suffer during germination and the juvenile stages. The ability to successfully colonize a patch is likely to be dependent on a large number of variables. Newly colonized patches are usually small and small population sizes are innately uncertain, consequently in order to evaluate the probability of colonization are also needs to consider stochastic events. There are four types of stochastic variation that may influence colonization, demographic, environmental, genetic and catastrophes. In orchids, a number of demographic, environmental and catastrophic events may account for the observed patterns. Even though particular environmental conditions may be necessary for the colonization of a new site by orchids, nevertheless the most important factor is the presence of the appropriate fungi for seed germination. Orchid seeds lack endosperm and require mycorrhizal fungi for germination, at least until the protocorm becomes photosynthetic. Thus, empty patches close to occupied ones, may be unsuitable because they lack the necessary fungi for germination (Bayman *et al*. 2002). The likelihood of colonization can be also affected by the extent to which the substrate is covered by moss (Tremblay *et al*. 1998), quality and quantity of light (Fernández *et al*. 2003) or ambient humidity. So their effectiveness as colonizers is probably limited far more by their usually rather precise habitat requirements and by the necessary co-occurrence of their mycorrhizal associates, than dispersal.

Detailed demographic studies using stage-structured matrix models can reveal critical stages in the life cycle and provide the basis for the modelling of population dynamics (Hutchings 1991; Menges 1998). Sensitivity and elasticity analysis can be used to identify potential data shortages and management targets because changes in vital rates with high sensitivity or elasticity are likely to have the greatest influence on the population growth rate (Caswell 1978; de Kroon *el al.* 1986; Brault and Caswell 1993; Caswell 2000). When species have metapopulation structures, conservation efforts need to be directed towards

the preservation of suitable habitats. If metapopulation processes are weak, conservation efforts should be directed at existing populations (Tremblay *et al.* 2006). Population viability analysis (PVA) is used extensively in conservation biology to predict both the risk of extinction faced by populations and species and the efficacy of management strategies that seek to mitigate these threats (Shaffer 1981; Gilpin and Soulé 1986; Boyce 1992; Burgman *et al.* 1993; Possingham *et al.* 1993). Typically, information on population growth is obtained from tag-recapture data in which the numbers of organisms achieving the next stage (or size) or remaining in the current stage is recorded (Caswell 1989; Ebert 1999). In *Lepanthes* spp., survivorship (Tremblay 2000; Tremblay and Ackerman 2001) and reproductive effort are more highly correlated with developmental stage than age (Tremblay and Hutchings 2003). However, growth transitions for rare species are likely to be based on data that are few and scattered and small sample sizes can result in errors when calculating growth transitions.

SCOPE OF THE THESIS

In this thesis I investigated the various factors that might determine species diversity, using mainly orchids as a model group. These factors were area, energy available, latitude and metapopulation interactions within a species.

To determine the relative importance of total area, size of protected areas, energy available and latitude, data were collected on species richness of orchids for various countries worldwide, the influence of area was then factored out and the residuals then correlated with the mean Normalized Difference Vegetation Index (NDVI), as a measure of energy available at particular locations and latitude. This was done for both the total area and the size of the protected areas in the countries, in order to determine the better predictor **(Papers I and II)**.

Paper III indicates that not all species show a typical latitudinal gradient but that their abundance declines towards the tropics. These trends are rarely mentioned in the literature and little is known about their underlying ecological and evolutionary causes. Therefore, the ecological explanations proffered are usually specific to the group in question. This paper presents an account of the most important cases of inverse latitudinal gradients. The existing hypotheses explaining this phenomenon are summarized and the evidence that tends to favour each of these is presented.

Paper IV gives an account of the general status and distribution of orchids in one important lowland region, the Chitwan district. This includes the Chitwan National Park (CNP), Barandabhar corridor forest (BCF) and the Mahabharat range (MR), where the association of the orchids with particular species of common trees etc. was recorded. This paper introduces this topic and will be followed by a manuscript with more comprehensive analysis.

Paper V predicts population growth pattern based on monthly surveys over a period of more than 1.5 years. Conservation biologists need models that can predict population persistence and methods for determining the accuracy of the predictions (either of growth, reduction or stability). In addition, sensitivity and elasticity analyses were used to identify potential management targets because changes in vital rates with high sensitivity or elasticity may have the largest influence on the population growth rate. These populations were also re-censused 13 years later and the results evaluated in terms of whether the

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population changed as the model predicted, and whether 13 years is enough to achieve a stable distribution.

SUMMARY OF RESULTS AND DISCUSSION

Initially the null hypothesis that species richness increases with increasing NDVI was tested, but there was no significant trend. Because the influence of ln(mean NDVI) or ln(max NDVI) on species richness was very weak ln(area) was used as the next independent factor. Multiple regression with ln(species richness) as the dependent factor and ln(area) and ln(mean NDVI) or ln(max NDVI) as predictors indicate a significant influence of ln(mean NDVI) and ln(max NDVI) in Africa (positive trend) and Eurasia (negative trend). Data sets for the whole of America and the world did not reveal any trend. Because NDVI did not explain the variability in the data, mean latitude was used as the next independent factor. A significant influence of latitude was recorded in all regions, with species richness decreasing with latitude. Evident outliers (Somalia and Sudan in Africa; Eastern Karnataka in Eurasia; and Somalia, Sudan, Eastern Karnataka, Ethiopia and Morocco in the whole world data set) with large areas of uninhabitable land were excluded from the analyses. For the data set for the whole world latitude was used to demonstrate the decrease in species richness from the tropics to the pole **(Paper I)**.

Because the results of the first study were not as predicted the size of protected areas in a country and size of the total area were used to determine, which is the better predictor. When the Residual Sums of Squares (RSS) were compared protected area predicted the number of species better than the total area of the country for 3 out of 5 continents, the prediction for tropical America was almost the same and only for Europe was the total area a slightly better predictor. The explanation for Europe is that many European orchids thrive in unprotected agricultural meadows and are maintained by regular mowing (Janečková *et al.* 2006). Other species are confined to forests, which are usually not protected in Europe. In tropical America, only in a few countries are significant areas protected: Venezuela (34.4%), Belize (27.5%), French Guyana (14.4%), Surinam (11.3%) and Bolivia (11%); the mean for the remaining countries is 5.3% (The Environmental Information Portal, http://earthtrends.wri.org/searchable_db). The influence of ln(NDVI) on species richness, after the effect of total or protected area was removed, was again very weak and a positive trend was observed again for Africa, but this may be due to special geographical conditions: the two countries with the lowest species richness and NDVI (Sudan and Somalia) are extremely dry, so that most of the area lacks vegetation and is uninhabitable for orchids. The low orchid species richness here may also be due to insufficient research

due to the political situation. A negative correlation was observed for tropical America, while no significant correlation ($p > 0.05$) was found for any other continent. There is considerable empirical support for a positive correlation between species richness and the energy available (Waide *et al.* 1999; Mittelbach *et al.* 2001; Hawkins *et al.* 2003a,b; Storch *et al.* 2005). In our case, however, latitude was much better correlated with the residuals of orchid species richness normalized per unit area, Res_{tot} and Res_{prot}, than ln(NDVI). The explanation of the lack of a correlation between ln(NDVI) and Res_{tot}, and between ln(NDVI) and Res_{prot}, may be that on a small scale, energy availability may be important but on a large (continental) scale climate (dependent on latitude) takes priority. The following example may serve as an illustration: more species are expected to be found in a forest than a meadow at the same latitude and many more species in a tropical forest, than a temperate forest. The latter dependence overshadows the former. Thus latitude and energy available may be positively correlated (tropical vs. temperate forest), but the lack of a correlation between the amount of energy available and orchid species richness may occur, for example, if energy availability increases towards the tropics more slowly than the number of orchid species. The positive outliers are Malawi, Zambia and Zimbabwe in Africa and Mexico in America. The negative outliers are Ethiopia and Eritrea, Somalia and Sudan in Africa, Cambodia, Pakistan and Korean peninsula in Asia, and French Guyana and Surinam in South America. The reasons for these deviations from the trend may stem from (1) more extreme geographic conditions (e.g., the Ethiopia, Eritrea and Sudan and Pakistan are clearly mostly arid countries); (2) lack of intensive floristic research, which may be the case for Somalia and Cambodia – countries not favoured by orchidologists due to their current or former instability; (3) inverse targeting of specific countries for research: in Europe, where the correlation is very tight, Turkey – a frequent destination of orchid "hunters" – is far above Portugal, which is in a similar latitude, but has a lower orchid diversity. However, this could be an edge effect due to the Atlantic and less stable, oceanic climate. Alternatively, the high species richness as a function of "orchid hunters" could be the result of taxonomic inflation – taxonomic splitting. It would be interesting to explain why Malawi is so conspicuously above and French Guyana and Surinam below the regression line. Can topographical variability or the historical past, such as the British pastime of natural history collecting, explain the former and landscape flatness the latter deviation? **(Paper II)**.

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In some cases, species diversity of the group in question depends more strongly on some biotic or abiotic factor (e.g., energy available, abundance of a "keystone" predator) than on latitude: (1) Southern parts of North America are considerably drier and have accordingly a lower plant productivity, measured, for example, by the Normalized Difference Vegetation Index, NDVI, than more northern areas. That is why the species richness of the North American breeding birds also declines towards the south, which accords with the prediction of the species-energy relationship that there is a positive correlation between species richness and plant productivity. (2) The increase in species richness with latitude of invertebrates, protozoa and bacteria that inhabit the pitchers of *Sarracenia purpurea* L. can be explained by the important "keystone" role that predation plays in structuring this community. As the abundance of the top predator, a filter-feeding mosquito, decreases, a greater number of taxa in the lower trophic levels (protozoa and bacteria) are able to persist. (3) The inverse latitudinal pattern shown by seaweeds is the result of the coexistence along the coastlines of Peru and Chile of species with different geographic origins. This region is characterized by high endemism (32.3% of the flora) and a very unequal contribution of tropical (3.4%) and sub-Antarctic (34.4 %) species. The number of tropical species decreases towards the South Pole, while the sub-Antarctic elements increase. However, sometimes it is more difficult to account for the pattern. This is especially the case for ichneumonids and aphids for which three hypotheses are proposed. *The "resource fragmentation hypothesis"* (RFH) has been used to explain the inverse latitudinal trends in species richness of Ichneumonidae. It assumes that as species richness becomes very high, the increasing number of potential host species does not support an increasing richness of parasitoid species because each of the additional potential host species is too rare to be exploited by specialist parasitoids. To overcome resource fragmentation, tropical Ichneumonids must be more polyphagous, or better at finding rare hosts. *The "nasty host hypothesis"* (NHH) is based on the observation that toxicity is more common in tropical than in temperate plant communities and that plant allelochemicals in host tissue can injure immature parasitoids. Thus it is proposed that increased toxicity, accompanied by a great variety of toxins, may make hosts in the tropics less accessible to parasitoids, leading to the observed decline in species richness. *The "common host hypothesis"* (CHH) assumes that inverse latitudinal trends in species richness should be found in groups, in which species are characterized by five main attributes: (1) host specificity, (2) necessity to look for a host periodically, (3) random host search, (4) short time available to find a host and (5) the species richness of the group, to which their host

belongs, increases towards the tropics. Aphids are an ideal group, because they satisfy all these attributes. Most aphids feed on only one or a few species of plants, or host alternate between two plant species, a winter host and a summer host (1), and because of their enormous population growth rates, they frequently overexploit their host plants and then it is advantageous for individuals to fly off and seek hosts elsewhere (2), and their small size, they have little control of the direction of their flight, and therefore search for their host plant at random (3). It is advantageous for aphids to have short generation times. Thus migrant aphids have only a short time to search for a host plant (4). The species richness of plants, the group they feed on, increases towards the tropics (5) **(Paper III)**.

Paper IV indicates that in Chitwan there is almost no association between particular epiphytic orchid species and trees. In the temperate Mahabharat range (MR), there are 9 orchid species that were not found in the Chitwan National Park (CNP) and Barandabhar corridor forest (CF). These orchids (*Bulbophyllum secundum, Coelogyne nitida, Cymbidium iridioides, Dendrobium amoenum, Eria amica, Otochilus porrecta, Sunipia bicolor, Trudelia cristata* and one unknown orchid species) prefer cool or moderate temperatures, originate in the Himalayan region of India and Southeast Asia and can be found at altitudes of 600 – 2700 meters. In contrast, the CNP and the BCF host 7 orchid species that were not found in the MR: *Dendrobium anceps, Dendrobium primulinum, Gastrochilis bigibbus, Oberonia ensiformes, Oberonia falconeri* and *Oberonia myriantha*, which prefer warm or moderate conditions, originate from the Himalayan region of India, southeast Asia to Australia and can be found at altitudes of 100 – 1400 meters. In the BCF the orchids were associated with particular species of trees. In contrast, in the CNP the orchids are more generalist and were found on 8 different species of trees. The most common trees in the Barandabhar Corridor Forest were *Shorea robusta* (48 orchid species in Shorea forest and 42 in mixed hardwood forest), *Lagestroemia parviflora* (36), *Cleistocalyx operculata* (34 in Shorea forest and 35 in Riverine forest), *Bombyx ceiba* (28) and *Gaultheria fragrantissima* (28). In the Chitwan National Park, the most common trees were again *Shorea robusta* (45 in Shorea forest and 43 in Mixed hardwood forest), *Bombyx ceiba* (42), *Trewia nudiflora* (41), *Lagestroemia parviflora* (37) and *Cleistocalyx operculata* (36). In the Mahabharat range the number of orchids recorded on *Castanopsis tribuloides* was 42, on *Shorea robusta* 26 in Hill Shorea forest and 41 in mixed hardwood forest, on *Rhododendron arboretum* 35 and on *Schima wallichii* 34 in Mixed hardwood forest and 33 in Rhododendron forest. The most abundant orchid species in BCF were

Acampe papillosa and *Luisia micrantha* that was mostly found on *Shorea robusta* and *Acampe rigida* on *Gaultheria fragrantissina*. In CNP the most abundant orchids were species *Luisia micrantha*, *Acampe rigida* and *Aerides multiflora* that were mostly found on *Shorea robusta*. In MR the most abundant orchid species were *Eria amica* and *Coelogyne flaccida* on *Schima wallichii* and *Coelogyne cristata* on *Castanopsis tribuloides*.

To determine whether it is possible to predict population persistence over a period of 13 years, a total of 381 individuals of *Lepanthes rubripetala* in six populations were marked and observed every month from June 1994 to January 1996 at Rio Grande within the Yunque National Forest, Puerto Rico. These populations were monitored again in June 2007. Of the six populations of *L. rubripetala* surveyed one went extinct (population 4) during the period between 1994 and 2007, while almost all the other populations had changed size, either increasing (population 2, 5) or decreasing (population 1, 2, 6). Similar patterns were observed also in other epiphytes - growth (Zotz 2005; Zotz *et al.* 2005) or shrinking of populations (Mondragón *et al.* 2004; Tremblay 1997b; Zotz 2005). The predicted stable stage distribution based on the data from 1994 was similar for all populations, which should consist mainly of reproductive adults. Except for population 2 in 1994 and population 3 in 2007, the stage distribution of all populations in both these years differed from the stable stage distribution. As in case of *L. caritensis* (Tremblay 1997b) the stable stage of the populations was skewed towards adults. However, in Winkler 2007, the small stages (seedling and juvenile stages) dominated the stable stage distribution in *C. sessiliflora*, *T. deppeana*, *T. multicaulis*, *T. juncea* and *T. punctulata*. Observed stage distribution differed significantly from the stable one in all species except of *C. sessiliflora*. The same was observed for the epiphytes *L. speciosa* (Hernández-Apolinar 1992) and *T. brachycaulos* (Mondragón *et al.* 2004) where young offshoots predominated, and in *W. sanguinolenta* (Zotz *et al.* 2005). The deviations from the stable age structure in most of our populations might be because orchids produce many (>1000) seeds per fruit. This may result in strongly stochastic recruitment events, which transcend in the structure of the population. The confidence intervals (CI) of the population growth rate estimated from transition matrices using the 1994 data all overlap 1, which suggests that none of the predicted population growth rates, λ_{pred}, is significantly different from one. The observed population growth rate (the change in population size between 1994 and 2007 were all within the 95% CI and close to the estimated mean except for population 4, which went extinct. The ability to predict the final population size depends on the transition matrices

and the variance of the transition elements adequately representing the general growth pattern of the population. In addition, the population growth rate depends on the carrying capacity of the habitat. In four populations, the predicted outcome was close to that observed (population 1, 3, 4, 5). All simulations for populations 2 and 6 predicted very small population size after 13 years with a very high probability of extinction but the final population sizes were larger then predicted. Population 4, which had a low probability of persistence, went extinct. The extinction of population 4 may occur commonly in these orchids as a result of environmental conditions and small population size. In population 4, a flood resulted in the loss of all the adults, but most of the juveniles and seedlings survived to the end of the 1994 survey. However, it is likely that high mortality of juveniles and seedlings resulted in extinction of the population. Another population of *L. rubripetala* growing along the Rio Grande de Patillas in the Carite State Forest became extinct as a result of a flash flood in the first month of the 1994 survey. In most simulations, independent of the maximum carrying capacity used, the lower 95% CI included extinction. A priori determination of the most likely carrying capacity for each population resulted in the value most similar to the simulation results **(Paper V)**.

GENERAL CONCLUSIONS

Paper I indicates that orchid species richness does not increase with increasing NDVI, but significantly decreases with increasing latitude and that there is no difference between northern and southern hemisphere in this respect. **Paper II** shows that, at the large scale considered, area is always very important, latitude is more important than energy available and the size of protected areas gives a better fit than the total area in most cases. This implies that to preserve biodiversity conservation efforts should be directed at maximizing the size of the protected areas in each country.

Certain taxonomic groups do not follow the usual trend of increasing species richness from the poles to the tropics. One explanation for this is that it is a consequence of the constraints imposed by the way of life of the group. A more comprehensive explanation was necessary in the case of Ichneumonids, where the *"resource fragmentation hypothesis"* is used, and in the case of aphids the diversity can be explained by the *"common host hypothesis"*. The empirical data for several groups indicate that the CHH can explain several inverse latitudinal gradients (e.g., psyllids and coccids). Nevertheless, the variability of nature makes it likely that this is not the only explanation **(Paper III)**.

In Chitwan the epiphytic orchids are not associated with particular species of trees **(Paper IV)**.

The main result of this study, using demographic data on *Lepanthes rubripetala* **(Paper V),** is that it is possible to make a long-term prediction of the growth rate of an orchid population, as the population growth rates as far as 13 years ahead, which is about eight times the life span of the species, were successfully predicted. This encouraging result lends support for using of matrix models for population viability analysis of natural orchid populations. However, a large number of variables may affect the accuracy of the transition probabilities, including small sample size, stochastic events, variation in vital rates as a consequence of density dependent processes and variation among years/surveys.

CONSERVATION IMPLICATIONS

One important finding of **papers I and II** is that the size of protected areas is a better predictor of orchid diversity than the total area of a country. Thus it is important to maximize the size of the protected areas in each country in order to preserve most of its biodiversity. The close correlation between the size of protected areas and orchid species diversity shows that many endangered orchid species might be saved from extinction just by increasing the size of protected areas of suitable habitats and their strict protection. Habitat protection is particularly necessary for plant groups with special habitat requirements, like orchids. Logically, the reverse is also true as any reduction in the size of undisturbed natural areas will result in the extinction of many species, as shown here for orchids.

If average temperature is plotted on the x-axis instead of latitude, these regressions may serve as a rough prediction of what might happen during global warming. Our results suggest that the orchid diversity in temperate regions might increase, but other factors might obscure this prediction. For example, while this prediction might be correct for South America, it is unlikely to hold in highly industrialized and fragmented landscapes in the northern hemisphere (Europe, North America).

Another aspect of conservation that emerges from our research is the significance of the outliers in our regressions (see Fig. 1). Once those outliers that can be attributed to geographic conditions and inverse targeting of specific countries for research have been identified, then there is a need to consider whether the other outliers are for countries that are understudied. This may well be the case for Somalia and Cambodia in Africa and Portugal in Europe. Thus our global analysis of orchid species diversity in various countries can pinpoint understudied countries. Interestingly, Ecuador and Costa Rica (positive outliers) have many more orchid species per unit area than the less studied Bolivia (on the trend line), even though all three countries are in the tropics and have an enormous altitudinal variation. That the little research done there is the reason for the relative apparent lack of orchid species in Bolivia was confirmed by Vásquez *et al.* (2003).

Analyses, similar to those presented here, of other plant and animal groups can indicate more effective uses of resources for conservation, especially when money is limiting.

The results of the predictive modelling (**Paper V**) can be used for exploring the effects of new management regimes, especially when considering small populations of endangered species, for which a change of management could result in extinction. The predictions of matrix models are based on population numbers and therefore do not take into account external perturbations, which may negatively affect the prediction. This might have been the case for our populations, which are often subject to disturbances like hurricanes, flush floods etc., which sweep away the whole or part of the population. Thus such unpredictable effects have to be taken into account in the viability analyses.

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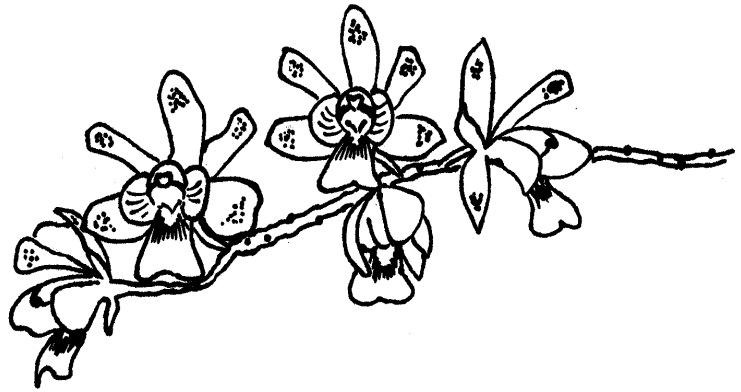
Paper I

The species-area-energy relationship in orchids

Schödelbauerová, I., Roberts, D. and Kindlmann, P.

Abstract

Area, energy available and latitude are the main factors influencing species richness: (1) species richness increases with area – the species-area relationship (SAR); (2) according to the species-energy relationship (SER) the energy available to an assemblage (i.e. that to which it can turn into biomass) at a particular spatial resolution influences the species richness; (3) there are more species per unit area in the tropics than in the temperate regions. To test the relative importance of area, energy available and latitude on species richness, we have collected data on species richness of orchids for various areas in the world and calculated the mean Normalizes Difference Vegetation Index (NDVI) as a measure of energy availability in these areas. We show that area considered is always very important, and that latitude is more important than energy available.

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Paper II

Size of protected areas is the main determinant of species diversity in orchids

SCHÖDELBAUEROVÁ, I., ROBERTS, D. AND KINDLMANN, P.

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Abstract

Efficient allocation of conservation resources will be achieved only if the priorities for biodiversity conservation – the "hotspots" – are correctly defined. To achieve this we need to pinpoint the main determinants of species diversity. Area, energy available and latitude are thought to be the most important determinants of species richness. Area is clearly the most important, but the relative importance of the other two is uncertain. To test the relative importance of energy available and latitude, data on the species richness of orchids was collected for various countries in the world, the influence of area factored out and the residuals correlated with energy available at these countries and with latitude. This was performed for both total area and that of the protected areas at the 67 countries from 5 continents, in order to determine, which gives a better prediction. We show that – at the large scale considered – area is always very important, latitude is more important than energy available and the size of the protected areas gives a better fit than the total area in most cases. This implies that conservation efforts should be directed to maximizing the size of the protected areas in each country.

Key words: NDVI, Orchidaceae, protected area, species area, species richness.
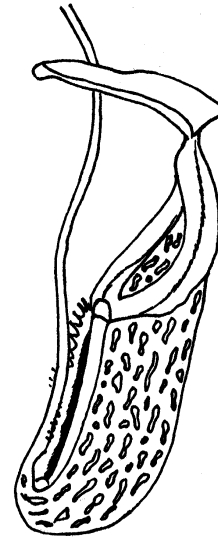
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Paper III

Inverse latitudinal gradient in species diversity

KINDLMANN, P., SCHÖDELBAUEROVÁ, I. AND DIXON, A.F.G.

Shortened version for web presentation

KINDLMANN, P., SCHÖDELBAUEROVÁ, I. AND DIXON, A.F.G. (2006). Inverse latitudinal gradient in species diversity. *In:* Storch D. and Marquet P.A. (eds.). *Scaling Biodiversity*. Cambridge University Press, Cambridge, UK, 2007, pp. 246-257

Abstract

No single pattern of biodiversity has attracted ecologists more than the observed increase in species richness from the poles to the tropics. An obstacle in the search for the primary cause of this latitudinal gradient is the ever-increasing number of hypotheses, their interdependence and lack of rigorous falsification. However, the general decline in species richness with latitude was commonly observed.

Some groups of organisms, however, show an opposite trend: a strong latitudinal decline in species diversity towards the tropics. These trends have been almost neglected in the literature and little is known about their underlying ecological and evolutionary causes. Therefore, the ecological explanations proffered are usually specific to the group in question. Here an account of the most important cases of inverse latitudinal gradients is given. The existing hypotheses explaining this phenomenon are summarized and the evidence that tends to favor one of these is presented.
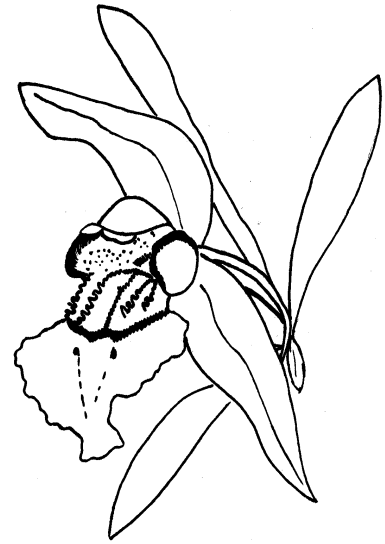
Paper IV

Orchid diversity in the Chitwan district

Schödelbauerová, I., Bhattarai, B. and Kindlmann, P.

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Abstract

Although the orchids in the Himalayan region are generally well known there is little or no information on the orchids in the lowlands of Nepal. The aim of this paper is to shed light on the general status and distribution of orchids in one important lowland region, the Chitwan district. The study area included the Chitwan National Park (CNP), Barandabhar corridor forest (BCF) and the Mahabharat range (MR). The orchids in the trees, on rocks and on the ground were recorded along a total of 200 line transects: 40 in the BCF, 105 in the CNP and 55 in the MR. From the beginning of each transect, the first 50 trees within ten meters of the transect line were sampled. In addition, all terrestrial orchids and species of trees within ten meters of the transect line were also recorded. There was no association between the orchid and specific species of trees. There were 9 orchid species in the MR that did not occur in the CNP and BCF, and 7 in the CNP and BCF that did not occur in the MR. In the BCF, the orchids occurred on average on 4 different trees. In contrast, in the CNP the orchids occurred on average on 8 different trees.

Keywords: orchids, species-abundance, Nepal
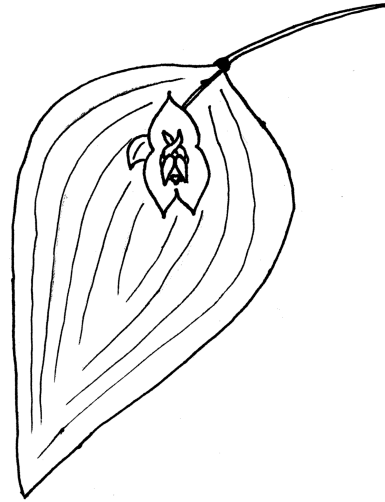
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Paper V

Prediction vs. reality: Can a model predict population persistence 13 years later?

SCHÖDELBAUEROVÁ, I., TREMBLAY, R. AND KINDLMANN, P.

Shortened version for web presentation

Abstract

The challenge of conservation biology is to make models that predict population dynamics and have a high probability of accurately tracking population change (increase, decrease, constancy). In this study we modeled 6 small populations of an epiphytic orchid using a Lefkovitch type analysis to predict population growth pattern based on monthly surveys for approximately 1.5 years. In addition, sensitivity and elasticity analyses were used to identify life stages with high sensitivity or elasticity that have the largest influence on population growth rate. We re-censused the populations 13 years after the first study and compared the structure of the populations to predictions based on the earlier census data. One objective was to determine if populations had achieved a stable size distribution over the 13 years period. Population growth rate models suggested that all populations should have persisted. Effective population growth rates were similar to those expected except for one where the population went extinct. The prediction slightly (but not significantly) overestimated the actual population growth rates of some populations. Elasticity analysis revealed that the adult stage is critical in the life cycle. The observed stage distributions of the populations were not stable at the beginning of the survey and neither were they after 13 years. We suggest that this might be caused by external perturbations that result in unequal mortality between life stages and stochastic recruitment events. The ability of the matrices to predict population size approximately eight generations in the future is encouraging and warrants the continued use of these approaches for PVA.

Key words: *Lepanthes rubripetala*; matrix models; re-census; transition matrix, PVA.

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