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Perspectives on Variation in Species Richness

Area, Energy and Habitat Heterogeneity

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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston Ylistönrinteellä salissa YAA303
helmikuun 18. päivänä 2011 kello 12.

Academic dissertation to be publicly discussed, by permission of
the Faculty of Mathematics and Science of the University of Jyväskylä,
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UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2011

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Cover picture: Lake Pieni Luotojärvi in Kivijärvi is a home for 15 dragonfly species
including protected Leucorrhinia albifrons and L. caudalis. Photo by Aili-Maria Sorjanen.

ABSTRACT

Species richness (i.e. number of species) tends to differ from one area to another. Two major patterns observed in the nature are 1) species-area relationship which states that larger areas contain usually larger species richness, and 2) species-energy relationship which postulates that the amount of energy encompassed in the area determines species richness. Even though both of these relationships may result from multiple mechanisms, which may be also intertwined, for instance through heterogeneity of habitats, they are not often studied simultaneously. In addition to broaden our theoretic knowledge understanding the mechanisms that produce species richness could help us to protect biodiversity. I studied the effects of area, energy, and habitat heterogeneity on species richness and related adjacent mechanisms in three taxa. My results showed that bird species richness was determined mainly by total energy (measured as tree volume and growth) in an area through its effects on the number of individuals. Bird species richness was further limited by the density of energy and its spatial dispersion, most likely because increased habitat heterogeneity benefits specialists. Also aquatic macrophyte species richness was determined by a multiple of factors and one of them was potential productivity (a measure of energy). Whilst potential productivity increased species richness, species turnover showed a unimodal relationship with it. Thus, potential productivity may decrease the regional species diversity as the species turnover between lakes may be reduced. Finally, dragonfly (Odonata) species richness was determined by habitat heterogeneity (measured as aquatic macrophyte species density), and the relationship was shaped by just a handful of common species. My results help to build up the theoretic knowledge about the mechanisms behind species richness patterns and have important implications for species conservation.

Keywords: Aquatic macrophytes; birds; dragonflies; species-area relationship; species-energy relationship; species number.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-IV.

I Honkanen, M., Roberge J.-M., Rajasärkkä, A. & Mönkkönen, M. 2010. Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. Global Ecology and Biogeography 19: 61-71.

II Honkanen, M., Roberge J.-M., Rajasärkkä, A. & Mönkkönen, M. Energy and its spatial dispersion limit species richness of boreal forest birds. Submitted manuscript.

III Honkanen, M., Kanninen, A., Alahuhta, J., Meissner, K., Liljeroos, K. & Mönkkönen, M. Potential productivity as a determinant of aquatic macrophyte species richness and turnover in boreal lakes. Manuscript.

IV Honkanen, M., Sorjanen, A.-M. & Mönkkönen, M. 2010. Deconstructing responses of dragonfly species richness to area, nutrients, water plant species diversity and forestry. Oecologia (accepted).

The table shows the contributions to the original papers. Smaller contributions are stated in the acknowledgements of the original papers

	I	II	III	IV
Original idea	MM, MH, JMR	JMR, MH, MM	KM, MH, MM	MH
Data	AR	AR	AK, JA, KL	MH, AMS
Analyses	MH, JMR	MH	MH	MH
Writing	MH, JMR, MM	MH, JMR, MM	MH, MM, AK, JA, KM	MH, MM

MH = Merja Honkanen, MM = Mikko Mönkkönen, JMR = Jean-Michel Roberge, AR = Ari Rajasärkkä, JA = Janne Alahuhta, AK = Antti Kanninen, KM = Kristian Meissner, KL = Katri Liljeroos, AMS = Aili-Maria Sorjanen

1 INTRODUCTION

1.1 Patterns of species richness

Though the exact number of species on Earth can be disputed, it is clear that there is an uneven distribution of these species across the planet. But why? It seems that the simplest questions are not the easiest to answer since the issue has puzzled ecologist over decades and the debate continues. The distribution of species richness (number of species) is far from random and researchers have put forward a myriad of factors, including historical, evolutional and ecological variables to explain the differences in number of species between areas. Here I focus on two major species richness patterns observed throughout the planet: species-area and species-energy relationships.

1.2 Species-area relationship (SAR)

One of the most striking patterns observed in nature is the so called species-area relationship (SAR): the larger the area, the more species it contains. The oldest figure of species-area curve can be traced back to 1859 (Rosenzweig 1995) and the pattern was later formalized mathematically by Arrhenius (1921) and Gleason (1922). Since then, SAR has been found to be one of the most robust and general patterns in ecology (Connor and McCoy 1979, Rosenzweig 1995) and has invoked a considerable amount of attention. On the theoretical side, researchers have concentrated on how to model SAR correctly, and what are the ecological and statistical interpretations of the parameters used in those various models (e.g. Preston 1962a, b, MacArthur and Wilson 1963, 1967, Gould 1979, Martin 1981, Lomolino 1989, 2000, He and Legendre 1996). In addition, SAR has proven to have several practical implications in conservation biology (Rosenzweig 2004). For instance, it has been used as a tool to predict changes in species richness, in relation to changes in habitat area (Pimm and Askins 1995, Hanski 2000), and has been brought to bear the debate whether we should have

single large or several small nature reserves (Gilpin and Diamond 1980, Higgs and Usher 1980).

Why do SARs occur then? There are three mechanisms why increasing area should result in increased species richness (i.e. number of species in a certain area) (Connor and McCoy 1979). Preston (1962a, b) showed that species richness increases as a power function of the number of individuals. If individuals are randomly positioned in space, increasing area would lead to increasing number of individuals, and consequently species, just by random sampling. According to Connor and McCoy (1979) the idea that SAR results purely from a sampling phenomenon should be considered as a null hypothesis and other hypotheses invoking biological processes should be considered alternatives. In addition to the random sampling hypothesis, there are two other biological mechanisms that explain SAR. First, large areas may have higher probability of colonization and lower probability of extinction due to increased population sizes (MacArthur and Wilson 1963, 1967). Second, larger areas may include more habitat types. As species differ in their habitat requirements this should lead to increased species richness.

Indeed, habitat heterogeneity has been shown to be an important determinant of species richness (Tews *et al.* 2004), whether it increases with area or not. In contrast, teasing apart the effects of area *per se* and habitat heterogeneity has been proven difficult. One of the reasons is simply that habitat heterogeneity is hard to define, and an appropriate measure is likely to depend on the taxon in question. Moreover, area and habitat heterogeneity are usually correlated (e.g. Kallimanis *et al.* 2008) and the two hypotheses are not mutually exclusive. Thus, both area and habitat heterogeneity can have effects on species richness, whether independently and/or simultaneously (Ricklefs and Lovette 1999, Kallimanis *et al.* 2008).

1.3 Species-energy relationship (SER)

1.3.1 Species richness and energy

Another obvious pattern of species richness is the decreasing number of species toward the Earth's poles. The phenomenon was observed already in 1808 by Alexander von Humboldt (Hawkins 2001). Since then increasing species richness with decreasing latitude has been documented for a wide variety of taxa (Fischer 1960, Pianka 1966, Hillebrand 2004). The latitudinal pattern of species richness may be a result of several processes (Fischer 1960, Pianka 1966, Mittelbach *et al.* 2007). One of these factors is energy.

The role of energy in shaping species richness patterns came about in late-1950's (Hutchinson 1959, Brown 1981) and it was later formalized by Wright (1983) as a species-energy theory which states that the more energy an area contains, the more species it is able to sustain. Thus the positive relationship between species richness and energy is formed (species-energy relationship;

SER). According to Wright (1983) SAR would be just a special case of SER and larger areas have more species just because they encompass a larger amount of energy. Indeed, energy-related variables tend to explain large scale species richness patterns well (Waide *et al.* 1999, Mittelbach *et al.* 2001, Hawkins *et al.* 2003a, b, Whittaker *et al.* 2007) and seem to perform better in explaining those patterns than area or its counterpart, habitat heterogeneity (Field *et al.* 2009).

1.3.2 Defining energy

In order to study SERs one has to define what energy really means. In his original paper, Wright (1983) defines available energy as 'the rate at which resources available to the species of interest are produced'. The obvious breadth of this definition has resulted in a variety of interpretations. For instance, the meta-analysis by Field *et al*. (2009) exemplifies 19 different measures of climate or productivity (the words themselves referring to energy).

Different meanings of energy occurring in the literature can be summarized to three different forms of energy: 1) light (or more specifically photosynthetically active radiation, which is the fraction of the visible spectrum between 400 and 700 nm); 2) temperature; and 3) Gibbs free energy released from reduced organic compounds when they are oxidized during intermediary metabolism (Clarke and Gaston 2006, Clarke 2007). In practice light and temperature are often lumped together as kinetic (Allen *et al.* 2007) or solar (Evans *et al.* 2005d) energy; whereas, Gibbs free energy is considered to be potential (Allen *et al.* 2007), or more colloquially, productive (Evans *et al.* 2005d) energy (or productivity). The important aspect following the definitions of energy, is that plants and animals use different energy forms. Only plants are able to utilize sunlight whereas animals use chemical energy. By contrast, both plants and animals are affected by temperature through its effects on organisms' metabolic rate.

Because of obvious difficulties, experiments that directly manipulate energy levels are quite rare (but see Srivastava and Lawton 1998, Hurlbert 2006). Hence, the energy measures used are rarely direct measures of available energy for specific organisms but rather represent different kinds of proxies; for instance, actual or potential evapotranspiration, biomass, temperature, normalized difference vegetation index, etc. This calls for considerable care in study design, because inappropriate proxies for energy may lead to erroneous conclusions. For instance, several authors have used plant biomass as a measure of energy for plants (Mittelbach *et al.* 2001). Within the theoretical framework presented above, this seems highly inappropriate and may lead to spurious conclusions of the general shape of SER (Gillman and Wright 2006, Whittaker 2010).

1.3.3 Mechanisms

1.3.3.1 Mechanistic basis of SER

Nowadays, the interest of studies concerning large scale species richness patterns has largely shifted from describing the patterns to revealing the underlying mechanisms. This makes the distinction between different energy measures especially important because mechanisms through which energy may affect species richness most likely depend on the energy form (Evans *et al.* 2005d, Clarke and Gaston 2006). Also, it must be borne in mind that the relevance of different mechanisms may differ according to spatial scale (Evans *et al.* 2005d). The following introduction to different mechanisms resulting from light, temperature, and productive energy is not meant to be exhaustive but aims to present the wideness of the theoretical framework concentrating on the most important/studied mechanisms.

1.3.3.2 Light and temperature

Plants need light to produce sugars through photosynthesis. At small scales the effect of light on species richness has been rigorously demonstrated by Hautier *et al.* (2009), who showed that decreasing species richness after eutrophication in grass communities was prevented by adding light in the under-storey. However, at larger scales plant diversity is distributed far more unequally than would be predicted from the availability of the light alone (Clarke and Gaston 2006). The reason for this mismatch is partly due to the water requirement in photosynthesis. Thus, strong correlations between plant species richness and climatic variables involving water and temperature have been found (e.g. Francis and Currie 2003).

But why should temperature be a better explanatory variable than light, especially if these two are intercorrelated? The direct effects of temperature on species richness have been emphasized by several different hypotheses. Apparently the first hypothesis put forward to explain latitudinal species richness gradient involved temperature: in 1808 von Humboldt reasoned that just a few species might be tolerant for freezing (Hawkins 2001). In modern days the ideas behind von Humboldt's hypothesis has taken multiple forms. For example, the physiological tolerance hypothesis (Currie *et al.* 2004) and the range limitation hypothesis (Evans *et al.* 2005a) state that fewer species can physiologically tolerate conditions in low-energy areas (i.e. cold and/or dry) than in high-energy areas (warm and wet). In contrast, Lennon *et al.* (2000), as the basis of their thermoregulatory loads hypothesis, argued that in warm regions individuals use less energy in their thermoregulation and therefore can allocate more energy for growth and reproduction. This results in higher population densities which are less vulnerable to extinction. Although the previous hypotheses refer to slightly different phenomena they have an underlying tenet that warmer habitats are easier place to live than cold ones. However, neither Currie *et al.* (2004) nor Lennon *et al.* (2000) found the predictions of their hypotheses to be fulfilled. More importantly, all of the

hypotheses leave one central question unanswered: why should more species be adapted to high-energy areas (Evans *et al.* 2005d)?

A possible answer to this question might be given by the evolutionary speed hypothesis (Rohde 1992, Allen *et al.* 2002, 2006). It predicts that temperature affects speciation and extinction rates: high temperature results in faster speciation rates and slower extinction rates. This hypothesis makes several key assumptions but the current knowledge seems to be inconsistent and/or insufficient in order to fully reject or by contrast, strongly support the hypothesis (Evans and Gaston 2005, Evans *et al.* 2005d, Clarke and Gaston 2006). Thus more research on the topic is clearly needed.

1.3.3.3 Productive energy

Increased productive energy has been hypothesised to promote species richness through several pathways: via increasing food chain lengths (Oksanen *et al.* 1981, Fretwell 1987), by enhancing species recovery from disturbances (Huston 1979), increasing the number of predators resulting from lowered competitive exclusion among prey species (Paine 1966, Evans *et al.* 2005d), or by enabling species to concentrate on fewer resources and thus reduce their niche breadth overlap allowing more species to coexist (Evans *et al.* 2005d).

The hypothesis that has probably gained the most attention is the so called more individuals hypothesis (MIH; Srivastava and Lawton 1998). MIH is an equivalent for MacArthur's & Wilson's (1963, 1967) island biogeography theory in the sense that areas with increased productive energy are supposed to be able to sustain larger population sizes which are less vulnerable to extinction. Although MIH is intuitively appealing, its predictions have seldom shown to be fulfilled (Srivastava and Lawton 1998, Currie *et al.* 2004, Evans *et al.* 2005a, b, c, 2006, 2008, Hurlbert and Jetz 2010, McGlynn *et al.* 2010, but see Kaspari *et al.* 2000, Mönkkönen *et al.* 2006). Moreover, the sampling hypothesis, where more individuals are sampled in an increased area, has its equivalent in species-energy framework: larger amounts of productive energy may support larger numbers of individuals, which could represent larger number of species, just by chance (Evans *et al.* 2005d). Random sampling and MIH are similar in that they both predict species richness resulting from increased number of individual but they have an important difference: MIH predicts that increased number of individuals results in increased species richness due to reduced extinction events. Thus, in order to rigorously test MIH one must take energy-based sampling hypothesis into account. An increase in the number of individuals as a consequence of increased energy, does not prove that MIH is working. Indeed, the energy-based sampling hypothesis has gained support (Carnicer *et al.* 2008, Evans *et al.* 2008) but can not fully account for SERs.

Increased productive energy may increase the local abundance of rare resources, combinations of resources, and conditions that are required by specialist species (Abrams 1995). An increased variety of resources may be considered as an essential part of habitat heterogeneity. Therefore high-energy areas may be better able to sustain niche position specialists (Abrams 1995,

Evans *et al.* 2005d). In contrast to niche breadth specialists, which use relatively narrow resource range, niche position specialists use relatively rare resources i.e. atypical resources for a particular community (Gregory and Gaston 2000). A growing number of studies suggest that some kind of niche specialization is at least partly responsible for correlated species richness with energy (Srivastava and Lawton 1998, Hurlbert 2004, Evans *et al.* 2006, Mason *et al.* 2008, Hurlbert and Jetz 2010).

Allen *et al.* (2007) have taken an integrated approach into the mechanisms behind SER: a metabolic theory of ecology. This theory states that both kinetic and potential energy play important roles in regulating species richness. Specifically, the theory proposes that thermal kinetic energy (i.e. environmental temperature) affects biodiversity through its effects on cellular- and individual-level processes, and chemical potential energy affects species richness through its effects on community abundance (Allen *et al.* 2007). Moreover, both of the energy forms regulate species richness since they affect speciation rates. Increase temperature is proposed to increase the rates of genetic divergence among species populations (Allen *et al.* 2006), whereas increased potential energy will increase the abundance of individuals by increasing the total rates of population subdivision (Allen *et al.* 2007). Thus, the metabolic theory of ecology is consistent with both evolutionary speed hypothesis and MIH whilst combining them with ideas from neutral theory of biodiversity (Hubbell 2001). Although there are clearly some challenges and caveats in the current metabolic theory of ecology (Allen *et al.* 2007) it is a step towards an integrative understanding of the mechanisms producing the observed SERs (Stegen *et al.* 2009).

1.3.4 Forms of the species-energy relationship

Despite the amount of studies related to SER a considerable disagreement exist over what is the general form of the SER (Waide *et al.* 1999, Mittelbach *et al.* 2001, 2003, Whittaker *et al.* 2001, Whittaker and Heegaard 2003, Gillman and Wright 2006). In contrast to species richness and area, which virtually always show a positive correlation (Connor and McCoy 1979), SERs have been observed to show multiple forms. SERs may form positive, negative, hump-shaped or U-shaped relationships, and sometimes there is no relationship at all. Particularly the hump-shaped relationship (i.e. at first species richness increases and then declines after the peak) has got a lot of attention leading some authors to refer it as the 'true' (Rosenzweig 1995) or the 'ubiquitous' (Huston and Deangelis 1994) form of SER. However the generality of a unimodal pattern may be partly misconceived, as a positive or negative relationship can always be interpreted to represent just a part of the pattern (see for instance Pärtel *et al.* 2007). Unfortunately all meta-analyses investigating the general form of SER (Mittelbach *et al.* 2001, Gillman and Wright 2006, Pärtel *et al.* 2007) have resulted in highly divergent outcomes. These meta-analyses have been shown to suffer from serious flaws compromising their reliability (Whittaker 2010).

A great deal of the confusion around the shape of SER may arise from the failure to understand the significance of spatial scale (Rahbek 2005, Whittaker 2010). Spatial scale consists of three things (Whittaker *et al.* 2001): (1) grain which refers to sampling unit, (2) focus which is the inference space used in analysis (which in some cases equals and is often used as a synonym to grain) and (3) extent which refers to geographic area within which the data set is embedded. Usually the extent of the study is discussed in studies of SERs but the importance of grain is overlooked (Whittaker 2010). However, both grain and extent are likely to affect SERs. First, the form of the SER may change as the grain of the study changes (Whittaker *et al.* 2001, Chase and Leibold 2002, Whittaker and Heegaard 2003, Chalcraft *et al.* 2004, 2008, Whittaker 2010). Indeed, larger grain sizes have often been found to result in monotonically positive SER, whereas more various forms of SER have been found at smaller grains. Second, different mechanisms are likely to act at different grains and extents (Evans *et al.* 2005d). Thus in order to gain meaningful results from the SER study, or even more importantly when comparing different studies, the work should be placed in an explicit scale framework in terms of both grain and extent (Whittaker 2010).

1.3.5 Energy and species composition

Species richness is by no means the only measure describing species assemblages. Two similar areas may differ drastically in their species composition. The species richness may be similar although the individual species types found within may differ. Alternatively, two areas may have different levels of species richness, yet the species types overlap between the two areas. To put it formally, regional species richness (γ-diversity, sensu Whittaker 1960) consists of local species richness (α-diversity) and species compositional variation/turnover among the sites (β-diversity) (see Tuomisto 2010a, b, for a recent review of β-diversity). Thus high regional species richness can be achieved if every site has high local species richness or if species differ among localities.

Though equally important, the patterns of species richness has received considerable amount of attention, species turnover has received far less effort (Gaston *et al.* 2007). Although, the issue is closely related to the scale-dependency of SERs. As already stated, the form of SER has been observed to change with the scale. For instance, Chase and Leibold (2002) showed that the relationship between primary productivity (a measure of productive energy) and local species richness was hump-shaped, whilst the relationship between primary productivity and regional species richness was positive. Thus, species compositional differences must have increased with productivity. Indeed, increasing species dissimilarity with increasing energy has often been observed (Chase and Leibold 2002, Harrison *et al.* 2006, Bai *et al.* 2007, Gardezi and Gonzalez 2008, He and Zhang 2009, Chase 2010), although unimodal (Chalcraft *et al.* 2004) and negative (Bonn *et al.* 2004) relationships have been found.

The mechanisms behind increasing species turnover with increasing productivity are not clear but several different mechanisms have been proposed. First, high-productivity areas may have higher heterogeneity in environmental factors (including productivity itself), which may enhance species richness. However, this has not been observed in a few studies addressing the question (Chase and Leibold 2002, Harrison *et al.* 2006). Chase (2010) showed that a species pool that could potentially live in low-productivity sites was more or less nested within the pool of high-energy species, plus different stochastic events such as colonization history increased with increasing productivity. Hence, increasingly random species assemblages with increasing primary productivity led inevitably to higher dissimilarity among sites (Chase 2010).

Increased harshness of environmental conditions can decrease site similarity by filtering out species that can not tolerate such conditions from a regional species pool (Chase 2007). For instance, the effect of nutrient enrichment was dependent on the initial productivity state of the site: nitrogen enrichment increased dissimilarity at low-energy sites and decreased it in high-energy site (Chalcraft *et al.* 2008). Thus, high nitrogen concentrations could be considered as a harsh environmental condition to which few species are adapted. It is easy to imagine why drought (Chase 2007) or very high nitrogen loading (Chalcraft *et al.* 2008) can be considered as a 'harsh' condition. However, if we use the same terminology to low productivity we end up back to the basic question: why are more species are adapted to high-productivity than to low-productivity conditions?

1.4   Area, energy or habitat heterogeneity?

Although Wright (1983) originally tried to refine MacArthur's and Wilson's (1963, 1967) theory of island biogeography by simply replacing 'area' by 'total available energy', effects of area and energy are seldom studied simultaneously (but see Storch *et al.* 2005, 2007, Hurlbert 2006, Kalmar and Currie 2006, Hurlbert and Jetz 2010). Usually studies of SER are based on equal-area grid data that focus on the variation in energy whilst controlling the effect of area. Moreover, studies that have integrated SAR and SER have often gone about the problem by using also grid-base data but with multiple grid sizes (Storch *et al.* 2005, 2007). These studies come quite close to the scale-shifting issue discussed earlier (for example Evans *et al.* 2008). A quite different analytic approach is to add the area as an explanatory variable to the analysis, together with energy (e.g. Kalmar and Currie 2006). Although the energy-related variables tend to be more strongly correlated with taxon richness than area or habitat heterogeneity (Field *et al.* 2009), it does not mean that area and/or habitat heterogeneity do not have any effect on species richness.

In shaping species richness patterns area and energy are theoretically related in several different ways. First, increasing area can, and usually does,

increase the amount of energy available for species. Secondly, area and energy can also be linked through their effects on habitat heterogeneity. Both area and energy may increase habitat heterogeneity but it seems energy benefits species richness more (Hurlbert and Jetz 2010). This complexity suggests that it would be beneficial to study the effects of area, energy, and habitat heterogeneity simultaneously.

1.5   Aim of the thesis

The scientific literature concerning patterns of species richness in their relation to area, energy, and related factors is enormous. However, despite the ongoing work over 100 years our knowledge of the mechanisms producing the basic patterns of biodiversity is still incomplete. Because of the actions of humankind we are now on the crest of the 6th extinction wave. Thus it is more important than ever to reveal the mechanisms behind patterns of species richness. Not purely for theoretic knowledge, a mechanistic understanding of the causes of species diversity could help us to predict the consequences of our actions and give us tools to protect biodiversity (Kerr *et al.* 2007). Moreover, the effects of area, energy, and habitat heterogeneity may be intertwined. The general aim of my thesis is twofold: 1) to dissect the effects of area, energy, and habitat heterogeneity on species richness, and 2) provide information about the mechanisms behind species richness patterns.

2 STUDY QUESTIONS AND HYPOTHESES

The four studies included in the thesis in concert provide a wide perspective on species richness patterns occurring in boreal landscapes. Despite the common theoretical background, I have chosen to study the subject from different angles: the studies are conducted at different spatial scales, with different organisms, and each of the paper takes a slightly different point of view to the subject. The first of the studies address boreal forest bird species richness in Finnish forested nature reserves. I began with the following question:

1. Is the main determinant of bird species richness area, energy, habitat heterogeneity or a combination of these factors (I)?

Although at larger scales energy tends to be a superior explanatory factor for species richness (Field *et al.* 2009), it is by no means self-evident that it would always override the effects of area and habitat heterogeneity. Moreover, the effects of the three factors may be intertwined, and this synergism is seldom addressed. Answering this basic question about the nature of species richness pattern also allowed me to develop the study further by asking:

2. What is the mechanism(s) producing species richness (I)?

It has become clear by now that the mechanisms producing variation in species richness are still not fully understood. Hence, I identified 12 different potential mechanisms causing increase in species richness with increasing area, energy, and/or habitat heterogeneity, and developed unique predictions for these mechanisms and tested them explicitly. This was (partly) done by the so called deconstructive approach (Marquet *et al.* 2004) which recognizes that species differ from each other and may respond in different ways to changes in the environment. Thus decomposing richness into smaller subsets of species that are internally more homogenous can help to reveal the mechanisms producing species richness patterns (Evans *et al.* 2006, Terribile *et al.* 2009). For instance, MIH predicts that rare species respond stronger to increasing energy than

common ones (see reasoning in paper I). The deconstructive approach is used throughout the studies in the thesis but it is especially important in paper I.

In the second study I concentrated on the relationship between area and energy on species richness. I formalized a hypothesis which suggests that an area's ability to support species is dependent not only on the total energy it contains, but also on the spatial dispersion of energy, defined here as the mean energy density and its spatial variation. In other words, the same amount of total energy may be distributed within a large area resulting in low mean energy density or within a small area consequently resulting in a high mean energy density. The distinction between total energy and mean energy density in area is rarely made, basically because the studies are often conducted in the grid-based framework where the area is held constant. Thus my question was:

3. Does density of energy and its spatial dispersion limit species richness and if so, by what mechanism (II)?

Energy density and its spatial variation may influence species richness through two mechanisms which need not to be mutually exclusive. First, energy should be sufficiently concentrated in space so that it can fulfil the organisms' metabolic requirements. As home range size is approximately proportional to body mass and energy requirements scale with body mass as power of 0.75 (Peters 1986), small-bodied animals cannot gather sufficient amounts of energy where the spatial density of energy is too low. In contrast large-bodied species are likely to be primarily limited by the total amount of energy in the area (Bokma 2004). Therefore, small-bodied species should primarily respond to energy density and large-bodies species to total energy availability. Second, increased mean energy density or its spatial variation may increase the local abundance of rare resources or combinations of resources and conditions that are required by specialist species (Abrams 1995).

Specifically, in order to answer my question I tested 1) whether energy density and its spatial variation are better predictors of species richness than the total amount of energy in the area. To dissect between the two possible underlying mechanisms, I tested the following predictions: 2) Small-bodied species respond more strongly than large-bodied species to mean energy density, whereas the opposite is true for the total amount of energy; 3) Both aspects of the spatial dispersion of energy (mean energy density and its variation) influence species richness: first, more resources – including rare resource types – are likely to occur where mean energy density is high, which benefits specialists. Second, some species are specialized on exceptionally high energy densities whereas others are specialized on low energy densities, and hence species richness increases also with increasing spatial variation in energy density.

In the third study I studied the relationship between potential productivity (i.e. the availability of limiting nutrients) and aquatic macrophyte species richness and turnover in boreal lakes. The beginning question was:

4. Is the main determinant of aquatic macrophyte species richness: area, energy, non-nutrient related water quality, or a combination of these factors (III)?

All of the factors have been shown to have an effect on species richness but their relative importance, and particularly the form of species-energy relationship seem to vary (Dodson *et al.* 2000, Jeppesen *et al.* 2000, Heino 2002). This is likely due to the fact that different life-form groups of aquatic macrophytes react differently to increasing productivity (Jeppesen *et al.* 2000, Edvardsen and Økland 2006), and differ in their use of the littoral habitat, as well as response to other environmental factors (Toivonen and Huttunen 1995, Lacoul and Freedman 2006). Thus, it is relevant to study the species richness of these particular life-form groups separately.

I predicted that species richness of different life-forms may react differently to some of the study variables and the relative number of species belonging to each life-form group then determines the response of total species richness to explanatory variable in question. Thus, I formalized specific predictions for responses of each of the life-form groups.

Studying the relationship between energy availability and species turnover could improve our understanding of regional and local diversity dynamics. Thus, I continued with the question:

5. How is species compositional turnover related to productivity (III)?

The simplest hypothesis explaining the relationship between productivity and compositional turnover is the random sampling mechanism. It predicts decreasing turnover rates with increasing productivity: low productivity areas tend to foster very few individuals (a small fraction of total species pool), and thus pure random sampling mechanism may result in high turnover rates between two sites of low productivity as they both have just few individuals. With increasing sample size such random effects become moderate. However, also hypotheses invoking biological mechanisms can be related to explain the relationship between species turnover and energy: the more individuals hypothesis (Srivastava & Lawton 1998) predicts that with increasing productivity individual species became more abundant and therefore can maintain viable populations, thus leading to decreasing turnover with productivity. A contrasting prediction can be derived from niche specialization hypothesis whereby higher levels of productivity enable individual species to become more specialized in resource use resulting in higher turnover rate among sites at higher levels of productivity (Bonn *et al.* 2004). Finally, purely stochastic processes such as ecological drift, dispersal limitation, priority effects, and differential colonization/extinction dynamics across localities may result in higher compositional turnover rates at higher levels of productivity (Chase 2010). Thus, I addressed if the relationship is negative as predicted by the random sampling and the more individuals hypotheses, or positive as predicted by the niche specialization hypothesis and stochastic processes, and

whether it follows the variation in species richness. A unimodal pattern of compositional turnover would indicate that several mechanisms operate simultaneously.

The fourth study concerns dragonfly (Odonata) species richness in boreal forest ponds. Again, I began with dissecting the effects of area, energy, and habitat heterogeneity on species richness by asking:

6. Is the main determinant of dragonfly species richness area, energy, habitat heterogeneity or a combination of these factors (IV)?

All of the three factors have been shown to affect dragonfly species richness but their relative importance is unclear. Moreover, answering the previous question is a prerequisite for answering the next, perhaps more interesting question:

7. Do the individual species respond to the same environmental variable (area, energy, habitat availability) than species richness and which species determine the observed species richness pattern (IV)?

Thus, I took the deconstructive approach to its extreme (Terribile *et al.* 2009): I modeled the occupancies of individual species. The reasoning behind this was that it is not clear whether species richness patterns arise from consistent responses of individual species to area, energy, and habitat availability, or if the overall pattern is merely due to responses of a few dominating species.

I set up two competing hypotheses: 1) rare species respond strongly to the same environmental variable as the total species richness and thus determine the relationship, and 2) more common species respond consistently to environmental variables and are the main drivers of species richness patterns. Dissecting between the two hypotheses is of importance as it is often assumed that variation in species richness is primarily due to presence/absence of rare species rather than more ubiquitous common species. These results have important conservation implications because species richness has been a commonly used proxy in conservation site selection projects (Prendergast *et al.* 1993).

3 MATERIALS AND METHODS

3.1 Study species and variables

3.1.1 Birds (I, II)

I used breeding bird line transect census data (Järvinen and Väisänen 1975) from 104 forested nature reserves in Finland. The data were collected by the state forest enterprise Metsähallitus during years 1976-2006 and they represent geographical variation from 60°11′ to 67°46′N and 22°10′ to 31°16′E. I restricted the species pool to birds having forest as a main habitat type (77 species). These species were further grouped based on their recovery ability, abundance, trophic status, habitat use and migratory behavior in order to dissect between competing hypotheses.

For each reserve, I used two different productive energy measures: tree volume (m^3) and growth (m^3 y^{-1}). Tree volume mirrors the standing tree biomass. Larger tree biomass implies larger production of many critical resources for birds, such as invertebrate prey, seeds, and nesting sites. By contrast, tree growth measures annual increment of tree biomass, i.e. instant productive energy. From these energy measures I derived total energy availability (I) and total energy density (I, II) for each reserve. As a solar energy measure I used degree days (the sum of the degrees above + 5 °C for all days during the growing season) and area was defined as forested area in the reserve. As measures of habitat heterogeneity I used structural habitat heterogeneity i.e. the number of different types of stands present in the reserve (I, II), and spatial variation in energy density within a site (II).

3.1.2 Aquatic macrophytes (III)

I used aquatic macrophyte species from 67 lakes situated in Eastern Finland (61°9′ to 63°51′N; 25°41′ to 30°45′E). Data were collected by regional environmental authorities using a transect method (Kuoppala *et al.* 2008) during the growing seasons of 2002 - 2008. Total of 105 aquatic macrophyte species

were recorded. In addition to studying total species richness of aquatic macrophytes, I considered the species richness of different life-forms separately.

As measures of available habitat area I used shoreline length and Secchi depth which reflects water transparency. I used degree days as a measure of solar energy, and total nitrogen (TN) and total phosphorus (TP) as proxies for (potential) productive energy because these nutrients have been shown to be limiting factors in freshwater systems (Elser *et al.* 2007). Additionally, water pH, conductivity and alkalinity were included into analyses due to their great potential for shaping aquatic macrophyte communities (Toivonen and Huttunen 1995, Vestergaard and Sand-Jensen 2000).

3.1.3 Dragonflies (IV)

I sampled 26 forest ponds and small lakes situated in Central Finland (61°36' to 63°17'N; 24°40' to 26°11'E). I sampled the ponds for dragonfly (Odonata) larvae twice during summer 2007, with a water-net and searched the shoreline for dragonfly exuviae (the larval skin that leaves behind when a dragonfly emerges). The sampling effort was standardized according to shoreline length which was also considered as a measure of area (habitat available for larvae).

Aquatic plant species richness could represent habitat heterogeneity for dragonflies as they use vegetation for various actions in all life-stages (Buchwald 1992, Corbet 2004). I sampled aquatic plants by a transect reaching from the shoreline towards the center of the pond as far as the vegetation did, and the number of transects was standardized according to shoreline length. As in study III, I used TP and TN as proxies for productive energy of ponds. Additionally, I measured water pH since it has been showed to have an effect on dragonfly species community (Johansson and Brodin 2003). Although solar energy has been found to affect dragonfly species richness (Heino 2002, Keil *et al.* 2008) due to limited range of temperature (a result from a restricted extent of the study) it was not considered in the current study.

3.2 Statistical analyses

Throughout the studies I used an information theoretic approach in analyzing the data (Burnham and Anderson 2002). First, I developed a set of candidate models explaining species richness. There different explanatory variables were regressed against species richness (i.e. number of species), or species richness of certain species groups (I, III). Inclusion of the variables in the models was based on the different competing hypotheses, as was the use of specific species groups. As spatial autocorrelation may violate the assumption of residual independence (Legendre and Legendre 1998), I used simultaneous autoregression (I, III) or spatial partial regression models (II) to account for the spatial structure in the data of large scale studies.

I used Akaike Information Criterion (AIC) to compare the alternative models (Burnham and Anderson 2002). The AIC method is based on likelihood, but it encourages parsimony (i.e. models with as few parameters as necessary) by imposing a penalty according the number of parameters included. The model with the smallest value of AIC is considered to have the most support given the data. If there is no apparent best model in the set (which is often the case) differences in AIC values among competing models (ΔAIC) enable a more comprehensive interpretation of the results. These differences are usually calculated between each individual model (i) and the model with the smallest AIC ($\Delta AIC_i = AIC_i - AIC_{min}$). It is generally considered that models differing less than 2 have a substantial level of empirical support, 4 through 7 substantially less support, and greater than 10 essentially no support (Burnham and Anderson 2002). However, rather than restricting oneself to this quite simplistic view inferences can be drawn from the whole model set easily by calculating model-averaged parameter estimates for different variables to compare their effects on species richness (III, IV; Burnham and Anderson 2002).

In studies II and IV, I wanted to test individual species responses to different environmental variables. In study II, I did this by fitting a binary logistic regression model. On the other hand, to gain individual dragonfly species responses I used single-season occupancy models which use repeated surveys of ponds to estimate occupancy and detection probabilities (MacKenzie *et al.* 2002, IV).

I emphasized earlier the importance of an explicit scale framework for both grain and extent. Bringing the variation into our analyses might seem contradictory; however, the amount of sampling conducted was relative to area (I, II, IV) or the sampled area was included in the analyses (III). Moreover, random sampling was taken into account by using residuals from observed vs. randomised species richness as a response variable (I), including number of individuals (II, IV) or in the models.

The spatial autoregression models, spatial partial and binary logistic regressions were built using SAM 3.0 (Rangel *et al.* 2006), single-season occupancy models were calculated with Presence (MacKenzie *et al.* 2006), species similarity indexes were calculated with 'vegan' package in R (R Development Core Team, 2010), and other analyses were performed with SPSS 16.0 (SPSS Inc., Chicago, IL, USA).

4 RESULTS AND DISCUSSION

4.1 Bird species richness (I, II)

Tree volume and growth (proxies for productive energy) explained boreal forest bird species richness better than area or structural habitat heterogeneity, the relationship being monotonically positive (I). This shows that productive energy overrides the effects of area and habitat heterogeneity in the study system and is in line with several studies showing the importance of productive energy for bird species richness (e.g. Wright 1983, Storch *et al.* 2005, Mönkkönen *et al.* 2006, Hurlbert and Jetz 2010). Solar energy, which has been previously shown to be an important variable for bird species richness (Hawkins *et al.* 2003a, b, Evans *et al.* 2005a), did not play a significant role in explaining species richness. The difference arises most likely from the rather restricted spatial extent of my study: when variation of solar energy is not considerable it can not be a very good predictor of variation of species richness either.

Random sampling was the main mechanism through which productive energy affected species richness. The high-energy areas harbored increased number of individuals, which consequently represented higher number of species. Together with previous studies (Carnicer *et al.* 2008, Evans *et al.* 2008), finding support for a random sampling mechanism calls for controlling random sampling in order to reveal other mechanisms producing SER. Indeed, when controlled for, it appeared that random sampling was not sufficient to explain all of the variance in species richness and thus multiple mechanisms are likely to take a part in shaping SERs (Carnicer *et al.* 2008, Evans *et al.* 2008).

After taking into account the random sampling mechanism, total productive energy in an area had a positive effect on species richness. While the size of the area had a negative effect (I), meaning that for a given area larger areas fostered fewer species. Thus an area's ability to support species may not be dependent only on the total amount of energy it contains but also the density of productive energy (energy per area unit). In contrast to our predictions metabolic constraints were not likely to explain the relationship between

species richness and energy density. Small-bodied species were found not to be limited by productive energy density and total productive energy content did not limit the occurrence of large-bodied species (II). Thus it seems that increased productive energy density increased habitat heterogeneity, which benefits specialist species. Also, there was considerable variation among species in their response to increased mean energy density (II): some species responded positively, some negatively and others did not react at all. Moreover, the variation in mean productive energy density within a site, a measure of habitat heterogeneity, was associated with increasing species richness (II). A model with random sampling accounted for found that productive energy density and its variation explained over 80 % variation in species richness (II). Thus most species would find their habitat from a high-energy site that included a lot of variation in energy density within the site.

It has long been recognized that bird diversity responds positively to increasing complexity in vegetation structure within stands due to the addition of different foraging guilds (Willson 1974). Vegetation structure and complexity tends to increase within plant species richness which in turn has been shown to be linked to the global energy gradient (Francis and Currie 2003, Kreft and Jetz 2007). Indeed, climatic factors may influence bird species richness through vegetation structural complexity rather than directly (Kissling *et al.* 2008). However, for some species increased habitat heterogeneity may mean increased fragmentation (Tews *et al.* 2004). This was also apparent in our data as some species reacted negatively to increased variation in energy density (II).

Also, tree volume explained species richness better than tree growth (II). Tree volume is an energy measure directly reflecting the standing tree biomass, which supports a very large proportion of the resources critical to forest birds (food, nest sites, cover, etc.). By contrast, tree growth reflects the annual increment of tree biomass, without consideration of standing stock. For example, a young forest with little tree biomass may have a faster tree growth than a tall forest containing a large tree biomass. Hence, standing tree biomass, by reflecting the availability of resources, is a more useful energy measure than the rate of tree growth for predicting bird species richness.

Overall, my results showed that the boreal forest bird species richness of Finnish forested protected areas is mainly governed by total volume of trees, a measure of productive energy in the reserve. An increase in productive energy increased the number of individuals in the reserve which in turn resulted in elevated species richness. Additional increases in species richness were through spatial dispersion of productive energy which most likely benefited specialist species. My results fit well with earlier studies showing that energy affects avian species richness through increasing number of individuals. But abundance does not predict species richness perfectly, and at least part of the additional increase in species richness results from increased habitat heterogeneity with energy (Hurlbert 2004, Hurlbert and Jetz 2010). Hence, area, energy, and habitat heterogeneity seem to be intertwined both in theory and in practice.

4.2 Aquatic macrophyte species richness (III)

The main determinants of aquatic macrophyte species richness were: shoreline length (a proxy for habitat area), potential productivity, and non-nutrient related water quality. Together these three variables explained 60 % of the variation of total species richness. As predicted, the relative importance of individual variables depended on the specific life-form group studied.

The positive effect of area (shoreline length) has usually been explained through habitat heterogeneity. Since larger lakes have more microhabitats, more species will be able to find a suitable habitat as area increases (Rørslett 1991, Toivonen and Huttunen 1995). Due to restrictions of the data, habitat heterogeneity was not included in my study and thus the specific mechanism is left open to speculation. However, as the total transect length sampled in a lake was taken into account in analyses, random sampling is unlikely to generate the result.

My results provide further support for the importance of potential productivity to species richness. Contrary to the fact that unimodal SERs have been found in water environments (Dodson *et al.* 2000) the effect of potential productivity on macrophyte species richness was positive. In addition, non-nutrient related water quality affected species richness particularly strongly. These effects may be partly due to pH, whichis strongly correlated with humus concentration, that in turn is known to be an important determinant of aquatic macrophyte species richness in Finland. Lakes with low pH are highly humic and consequently display low species richness. Unfortunately, I was unable to include humic content into the analyses due to the high amount of missing cases.

Contrary to my predictions the measure of solar energy, degree days, had no effect on species richness. As increasing latitude (which obviously has a strong correlation with degree days) has been previously found to decrease species richness of aquatic macrophytes in boreal areas (Heino 2002, Heino and Toivonen 2008), the poor predicting ability of degree days may be a result of the relatively small variation in the variable due to the limited regional extent of the study.

Regardless of the specific life-form group and contrary to numerous studies (Chase and Leibold 2002, Harrison *et al.* 2006, Bai *et al.* 2007, Gardezi and Gonzalez 2008, He and Zhang 2009, Chase 2010) species turnover showed a unimodal response to potential productivity (TN and TP availability). Lakes with high potential productivity and high species richness were similar to each other, as were lakes with low potential productivity and low species richness. In contrast, lakes of intermediate productivity had high species compositional turnover. This indicates that neither the random sampling hypothesis, the more individuals hypothesis, the niche specialization hypothesis, nor the stochastic processes, which all predict linear relationships, are exclusively capable of explaining the results. Several mechanisms are likely involved.

However, there was a strong increasing phase in species compositional turnover with increasing productivity. Thus the niche specialization hypothesis and/or stochastic processes may be involved. Increased harshness of the environment, such as low productivity or excessive nutrient richness, can act as an environmental filter allowing only species tolerating these harsh conditions to exist (Chase 2007, 2010). This process, filtering off species from the regional species pool, may result in homogenized species compositions at both ends of the productivity spectrum. The decreasing phase of species turnover was due to six lakes with very high levels of potential productivity. These lakes are located in drainage basins with much higher cover of agricultural land than average. Thus, it may be that the aquatic macrophyte flora of the study is poorly adapted to human-induced eutrophic conditions, limiting the number of species capable of occupying the highly eutrophic lakes.

In conclusion, although the level of potential productivity may increase local species richness (i.e. within a lake), it may also decrease the regional species diversity as species turnover between the lakes may be reduced. This probably results from anthropogenic eutrophication, which may cause regional impoverishment of aquatic macrophyte species diversity. Regional homogenization of species diversity following excessive nutrient content poses a serious threat to freshwater diversity (Donohue *et al.* 2009).

4.3 Dragonfly species richness (IV)

Dragonfly species richness was largely determined by the density of aquatic plant species. This was not surprising since the positive connection between species richness of aquatic plants and dragonflies has earlier been shown shown at multiple scales (Sahlén 1999, Heino 2002, Keil *et al.* 2008). The mechanistic reason for this pattern is, however, obscure. Although dragonflies do not directly feed on plants they do use water vegetation for multiple purposes during different life-stages (Buchwald 1992, Corbet 2004). Despite that only a few dragonflies directly depend on some specific plant species (*Aeshna viridis* and its tight connection with *Stratiotes aloides* being the only example in Finland) it may be that increasing amount of plant species allows more dragonfly species to find their optimal habitat in a pond. On the other hand, rather than focusing on some specific plant species, dragonflies may prefer emergent, floating or submerged vegetation (Sahlén 2006). It is likely that the number of these life-forms increases with increasing plant species richness, which then benefits dragonfly species richness. My results suggest that aquatic macrophytes are important for creating different structures and habitats for other organism groups (III, Crowder and Cooper 1982, Gilinsky 1984) and, more generally, stress the importance of habitat heterogeneity as a driver of species richness (Tews *et al.* 2004).

Additionally water pH was an important determinant of dragonfly species richness: species richness increased with diminishing water acidity. Also earlier

studies have shown water acidity to be an important variable explaining dragonfly community composition (Johansson and Brodin 2003). Dragonfly larvae are relatively tolerant to changes in pH (although the evidence is rather controversial, see Corbet 2004). Consequently pH may seldom be the proximate factor determining the species distribution (Corbet 2004). Thus, it has been suggested that the effect of pH is indirectly mediated by fish predators (Eriksson *et al.* 1980, Bendell and McNicol 1987). Indeed, presence of fish strongly determines relative abundances of species in dragonfly communities (McPeek 1990, Johansson *et al.* 2006) and may have a positive, but relatively small effect on dragonfly species richness (Johansson *et al.* 2006). Although I suspect that fish occurred in most of the study ponds and thus it is unlikely that my main results were biased due to unknown fish presence, different fish species and their abundance may affect dragonflies differently (Wittwer *et al.* 2010). Unfortunately, I do not have data to evaluate such an effect in the study ponds.

Shoreline length (or pond area) has earlier been shown to affect dragonfly species richness (Oertli *et al.* 2002) but I did not find such a relationship. Moreover, main water nutrients, TN and TP, had a negligible effect on dragonfly species richness. This was not a big surprise since dragonflies are not directly dependent on these nutrients. In order to test rigorously the relationship between productive energy and dragonfly species richness a more direct measure of resources available for dragonflies should be used. This could be, for instance, the biomass of invertebrate fauna. Thus, my result emphasizes the need for careful selection of the variables used as proxies for energy. However, given the strong relationship between aquatic macrophyte species richness and nutrient availability (III), one might have been expected an indirect effect of nutrients on dragonfly species richness. On the other hand, I did not find any correlation between nutrient availability and aquatic plant species density.

Individual dragonfly species had various responses to shoreline length, nutrient availability, pH, and aquatic macrophyte. However, the 6 species showing the strongest relationship with aquatic plant density, representing 25 % of the total species richness, and shaped the entire relationship between species richness and aquatic plant species density. By contrast the 9 rarest species (which make 37.5 % of total species richness) did not have a considerable effect on species richness patterns. Earlier studies have shown that common species tend to shape species richness patterns (Jetz and Rahbek 2002, Lennon *et al.* 2004) and that common species also show stronger correlations with environmental variables than do rare ones (Jetz and Rahbek 2002, Evans *et al.* 2005b, I). The reason for this may partly be purely statistical (Šizling *et al.* 2009). Although I was not able to remove all these possible statistical artifacts it seems that in addition to being common a species need to response strongly to the environmental factor in question in order to shape species richness patterns.

5 CONCLUSIONS AND IMPLICATIONS

5.1 Conclusions

I conclude by answering the questions presented in the 'Study questions and hypotheses'. My results showed that boreal forest bird species richness was largely determined by productive energy (measured as total tree volume and growth) in the nature reserve (I). The main mechanism producing the relationship was energy-based random sampling whereby an increase in productive energy increased the number of individuals in the reserve, which in turn resulted in elevated species richness (I). Thus Connor's and McCoy's (1979) view that sampling phenomenon as an explanation for SAR should be considered as a null hypothesis and other hypotheses as alternatives is also applicable to SER.

However, bird species richness was not totally determined by random sampling. Energy density and its spatial dispersion further limited the species richness of birds (II). This was not due to the metabolic constraints of birds but most likely resulted from increased habitat heterogeneity benefiting specialist species. Together with random sampling, the main mechanism underlying the species-energy relationship in this system, energy density and its spatial dispersion explained over 82 % of variation in species richness. These results strongly corroborate the importance of energy in shaping species richness, and that multiple mechanisms may account for species richness patterns simultaneously.

Aquatic macrophyte species richness was determined by multiple factors: shoreline length, potential productivity, and non-nutrient related water quality. As predicted the relative importance of the variables depended on the specific life-form group studied. While the effect of potential productivity on macrophyte species richness was positive, species turnover showed a unimodal relationship with potential productivity. Thus, although the level of potential productivity may increase local species richness (i.e. within a lake), it may also decrease the regional species diversity as species turnover between the lakes

may be reduced. This result contradicts with the predictions of the random sampling and the more individuals hypotheses and indicates that most likely several mechanisms are involved in shaping productivity-compositional turnover patterns.

Dragonfly species richness had a positive correlation with habitat heterogeneity measured as aquatic macrophyte species density, rather than area or energy (IV). The six species showing the strongest relationship with aquatic plant density shaped the entire relationship between species richness and aquatic plant species density. Although these species were all relatively common, the commonness alone was not a sufficient factor for a species to shape the species richness pattern. By contrast rare species did not have an effect on species richness patterns.

5.2 Increasing energy, increasing species richness?

One major challenge of our times is the global climate change. In addition to land-use change it is the most important threat to biodiversity (Sala *et al.* 2000). Over the past 100 years, the global average temperature has increased by approximately 0.74°C, and is predicted to continue to rise (IPCC 2007). Despite this global pattern of increasing temperature the regional effects of climate change are likely to differ. For instance, precipitation is diminishing in some areas whilst elevating in others (IPCC 2007). Moreover, the frequency of extreme events such as hurricanes, floods and droughts is likely to increase (IPCC 2007). This makes the prediction of the regional effects difficult.

Human-induced climate change is already affecting natural systems all over the globe. Species are responding to increasing temperatures, for instance, by experiencing phenological shifts, such as changing their breeding and migration patterns (Parmesan and Yohe 2003, Root *et al.* 2003). As species are also changing their distributions with increasing temperatures (Parmesan and Yohe 2003, Root *et al.* 2003) species richness patterns are likely to be affected. According to SER species richness should increase with increasing temperatures.

In order for species richness to increase as SER predicts, species must find suitable habitats. Given the great speed of land use change and degradation of habitats, the increasing levels of temperature may be irrelevant if the amount and/or quality of habitats diminish drastically, as is the case all over the world. Although temperature matters, the habitat area available is the first prerequisite for species persistence. Moreover, species should be able to disperse along rapidly changing climate gradient. It seems that even for birds, a group with great dispersal ability, changes in distribution are too slow to keep up with the rate of climate change (Devictor *et al.* 2008). On the other hand, species distributions may not solely be determined by climate.

Species richness has been observed to increase with increasing temperatures due to climate change (see e.g. La Sorte and Jetz 2010). As the

magnitude of temperature change will be greatest at northern latitudes and precipitation is likely to increase simultaneously (IPCC 2007), the amount of productive energy may increase. This should benefit bird species richness in boreal forests that is according to my results heavily determined by the productive energy of the forest (I, II). Current protected areas are often situated in unproductive regions with low economic value (Pressey 1994), particularly in Fennoscandia (Nilsson and Götmark 1992, Virkkala 1996, Stokland 1997). Thus the need to protect more highly productive sites is obvious (Virkkala *et al.* 1994, Angelstam and Andersson 2001) which unfortunately contradicts with the demands of the forest industries. So, at a first glance it would seem that climate change would solve the problem by increasing amount of productive energy in the reserves which should enhance species richness.

However, the future is not necessarily as bright as suggested above. Although total forest growth may increase in Finland due to climate change, the south forest growth may be reduced and only the north may increase (Kellomäki *et al.* 2008). Consequently the special features of northern forests may be diminished (Kellomäki *et al.* 2008). Overall, this suggests that the Finnish forest environment is likely to be homogenized at the national scale. Variation in energy levels within an area increases species richness but (most likely) benefiting specialized species (II). Some of these species were specialized on low-energy conditions (II). Such species may face serious habitat loss in future climate regimes and are susceptible to major range contractions due to climate change, (e.g. Virkkala *et al.* 2008). Even if these low-energy specialists are replaced by other species preferring higher energy levels resulting in no change in local species richness the outcome could be homogenized regional species pools. Moreover, global scale climate change is likely to lead to a considerable amount of species extinction (Thomas *et al.* 2004, but see Lewis 2006) further shrinking regional species pool.

Climate change may affect SER due to its effects on temperature and precipitation patterns and consequently on solar and productive energy regimes. As precipitation may either increase or decrease as temperature increases, knowing whether a primary determinant of species richness is solar or productive energy is of great importance. However, if we define energy as potential productive energy, namely nutrient availability (III, IV) also other anthropogenic processes may affect energy and consequently species richness patterns. Despite that aquatic macrophyte species richness increased with increased nutrient availability, the excessive nutrient loading resulted in higher similarity within lakes in terms of species composition i.e. reduced β-diversity (III). Thus, human induced eutrophication can lead to regional homogenization of the species pool (Donohue *et al.* 2009). This may further lead to cascading effects, for instance dragonfly species richness being highly dependent on aquatic macrophyte species richness (IV). If different species mixtures of aquatic macrophytes sustain different dragonfly species assemblages, it may be that regional homogenization of macrophyte species composition may homogenize also the dragonfly species composition. Indeed, nitrogen deposit is recognized as one of the major threats to biodiversity (Sala *et al.* 2000) and its effects may

interact with the effects of climate change on freshwater diversity (Heino *et al.* 2009). To conclude, revealing the mechanistic basis of SER could help to predict the consequences of climate change and other anthropogenic disturbance.

5.3 Species richness and conservation

Species richness is an intuitive measure of biodiversity and protecting maximal species richness is a common conservation target. Consequently, sites with higher number of species are often considered more valuable than species poor sites. The fact that common species have a greater effect on observed species richness patterns than rare ones (I, IV, Jetz and Rahbek 2002, Lennon *et al.* 2004, Šizling *et al.* 2009) have thus interesting practical implications. In the regions where accurate data on species distributions are not available, more accurate prediction of the species richness patterns could be made on the basis of distributions of common rather than that of rare species (Lennon *et al.* 2004). Further, if only a handful of the common species drive the spatial variation in species richness (IV), the variation could be predicted based on data of a few species. However, if common species drive species richness patterns selecting sites for protection based on their species richness does not necessarily provide a network of sites that would effectively cover the rare species that often are the ones considered to be in need of special conservation attention. Hence, there may be a trade-off between selecting sites in the basis of occurrence of rare species or species richness (Arthur *et al.* 2004, Juutinen and Mönkkönen 2007; but see Berg and Tjernberg 1996). This poses a rather value-laden problem whether to protect species richness (i.e. common species and compositional integrity) or rare species?

Although common species have received considerably less attention compared to rare ones they form an essential part of ecosystems: by definition they build up much of the structure and biomass. Moreover, the importance of common species for ecosystem functioning is likely to be large, although few experiments have explicitly tested that (Gaston 2010). Recently, also common species have been experiencing marked declines (Gaston 2010). Thus, it may be both logically invalid and unethical to state that common species do not need conservation. On the other hand, some common species are exotic invaders that may have destructive effects on the rest of biodiversity. In addition, some generalist species may increase in numbers whilst replacing more specialized species, as exemplified by the homogenizing effects of climate change on biodiversity.

Although being intuitive and simple measure of biodiversity species richness has several problems (Magurran 2004), especially when used for conservation purposes (Fleishman *et al.* 2006). Species richness as such does not provide any information on species identity or the functional roles of individual species in ecosystem processes. It may be best used in combination with other information on, for example, composition, function and endemism of species

(Fleishman *et al.* 2006). Then, selecting reserves for biodiversity maintenance could be done by considering multiple goals, such as conserving species richness and rare species, simultaneously (Arthur *et al.* 2004, Juutinen and Mönkkönen 2007). Such practice may reveal that these two goals may be fulfilled at the same time in some cases (Arthur *et al.* 2004).

Acknowledgements

First, I would like to express my gratitude to my three high-class supervisors: Mikko Mönkkönen, Janne Kotiaho and Jean-Michel Roberge. Mikko, you have been my main guide during these 5 years. The conversations with you have taught me a lot. Throughout these years your door has remained open and despite of your ever increasing work load you have managed to find time to for me. Moreover, you have let me to do the things in my own way, although it has not always proven to be the most successful way. However, those experiences have been perhaps the most instructive. Thank you for your enthusiasm and guidance.

Janne, you are perhaps one of the most hilarious people I know. I think the few times we have been really working together have been very fruitful. But most importantly, I feel that you have always believed in me (also in times when I myself have not). Thank you for that.

Jean-Michel, you have had an enormous impact in my scientific thinking. When discussing face-to-face over the scientific issues you have showed me what deep thinking is, and just how fun science can be! Although you were not my official supervisor from the beginning you have always behaved as one. I admire your passion to your work, and I sincerely hope that we are able to continue working together in one way or another.

I want also thank the co-authors who have put their effort in the manuscripts: Kristian Meissner, Antti Kanninen, Janne Alahuhta, Ari Rajasärkkä and Katri Liljeroos. It has been a pleasure to work with you. I am extremely thankful to Aili-Maria Sorjanen: without you I would have never been able to conduct the dragonfly study. Looking back, it seems a little miracle that we managed to survive that summer, just the three of us: you, me and the rubber-boat. I also want to thank Miska Luoto and David J. Currie whose constructive criticism improved my thesis. Finally, I am thankful for Jari Haimi for his help and never-ending patience during the publication process and Heather Mariash for correcting the language used in the thesis. Moreover, this work would not have been possible without Academy of Finland and Rector of University of Jyväskylä who kindly funded my work.

There are two persons who are highly responsible for me being in this situation: Katja and Erna. Thank you for your encouragement to take this path, and your friendship during it! I have been lucky to work in such a relaxed and nice atmosphere. As it is by no means self-evident, I am thankful for the personnel in the Section of Ecology, as well as the whole Department of Biological and Environmental Science. Particularly, I want to thank the current and past members of Sauna & Support as well as Monday Coffee Club. Moreover, the lunch and coffee breaks have been exceptionally hilarious moments: thank you Anne, Mikael, Elisa, Aapo, Inka and Atte for the conversations loaded with laugh and also your sympathy when things have not gone just like they should have had. It has meant the world to me.

YHTEENVETO (RÉSUMÉ IN FINNISH)

Pinta-alan, energian ja elinympäristöjen monimuotoisuuden suhde lajimäärään

On ilmeistä, että maapallolla elävät lajit eivät ole jakautuneet tasaisesti: toisilla alueilla on enemmän lajeja kuin toisilla. Tutkijat ovat 1800-luvun alkupuolelta lähtien pohtineet syitä tähän ilmiöön. Laajassa maantieteellisessä mittakaavassa tarkasteltuna lajimäärän on havaittu pääasiallisesti olevan yhteydessä kolmeen eri tekijään: pinta-alaan, energiaan ja elinympäristöjen monimuotoisuuteen. Kaikki nämä tekijät vaikuttavat useimmiten lajimäärään positiivisesti: mitä suuremmasta alueesta on kyse, mitä enemmän se sisältää energiaa tai mitä monimuotoisempi alue on, sitä enemmän siellä on lajeja. Vaikka lajimäärän suhdetta niin pinta-alaan, energiaan kuin elinympäristöjen monimuotoisuuteenkin on tutkittu paljon, on kuitenkin epäselvää, mistä esimerkiksi energian ja lajimäärän välinen positiivinen suhde johtuu. Tämän sekä muiden lajimäärään vaikuttavien mekanismien ymmärtäminen on kuitenkin tärkeää luonnonsuojelullisten tavoitteiden asettamisessa sekä toteuttamisessa. Väitöskirjatyössäni tutkin lajimäärän vaihtelun yhteyttä edellä mainittuihin kolmeen tekijään sekä mekanismeja tämän yhteyden takana. Tutkimuskohteenani olivat Suomen metsäisten suojelualueiden linnut, vesikasvit Itä-Suomen järvissä sekä Keski-Suomen pienten metsälampien sudenkorennot.

Suojelualueiden lintujen lajimäärää parhaiten selittävä tekijä oli pinta-alan tai elinympäristöjen monimuotoisuuden sijasta alueen sisältämä energia, toisin sanoen tuottavuus. Suurempi lajimäärä hyvin tuottavilla alueilla johtui suuremmasta lintuyksilöiden määrästä, ja perustui suurelta osin satunnaisuuteen: mitä suurempi joukko yksilöitä poimitaan satunnaisesti, sitä suurempi on todennäköisyys, että nämä valitut yksilöt edustavat eri lajeja. Tämä satunnaisuusmekanismi ei kuitenkaan selittänyt lintujen lajimäärää täydellisesti. Alueen sisältämän kokonaistuottavuuden lisäksi myös alueen keskimääräinen tuottavuus ja sen vaihtelu alueen sisällä lisäsivät lajimäärää. On todennäköistä, että keskimääräisen tuottavuuden kasvaessa myös elinympäristöjen monimuotoisuus lisääntyy. Lisäksi jotkin lintulajit suosivat hyvin matalatuottoisia ja jotkin korkeatuottoisia alueita. Näin yhä useammalla eri lintulajilla on mahdollisuus esiintyä alueella, jossa on korkea keskimääräinen tuottavuus ja sen vaihtelu. Siten sekä energia että sen vaihtelu lisäsivät lintujen lajimäärää suojelualueilla. Tutkimuksestani kävi myös ilmi, että yhden ainoan lajimäärään vaikuttavan mekanismin sijasta tällaisia mekanismeja on useita, ja ne voivat toimia samanaikaisesti.

Myös vesikasvien lajimäärään vaikuttivat useat eri tekijät: sekä suuremmilla että tuottavammilla järvillä oli enemmän vesikasvilajeja kuin pienemmillä tai vähätuottoisemmilla. Lisäksi myös veden kemialliset ominaisuudet, kuten pH, alkaliniteetti ja sähkönjohtavuus, vaikuttivat suuresti järven vesikasvien lajimäärään. Vaikka tuottavuus lisäsi lajimäärää, sen suhde

lajiston koostumukseen ei ollut yhtä yksinkertainen: matalan tuottavuuden järvet olivat toisiinsa verrattuna hyvin samankaltaisia kuten myös korkean tuottavuuden järvet. Sen sijaan keskimääräisillä tuottavuuksilla eri järvet olivat lajistoltaan hyvinkin erilaisia. Tästä seuraa, että vaikka ravinteiden päätyminen vesistöihin voi lisätä yksittäisten järvien tuottavuutta ja siten lajimäärää, lisääntynyt tuottavuus voi köyhdyttää lajiston monimuotoisuutta suuremmassa maantieteellisessä mittakaavassa. Tällä saattaa taas olla vaikutuksia vesikasveista riippuvaisiin eliöihin, kuten sudenkorentoihin.

Tutkimukseni mukaan sudenkorentojen lajimäärä riippuikin lammella esiintyvien vesikasvien lajitiheydestä, ei niinkään lammen koosta tai tuottavuudesta. Vaikka sudenkorennot ovat kaikissa elinkierron vaiheissaan petoja eivätkä siis syö kasveja, ne käyttävät vesikasvillisuutta moniin eri tarkoituksiin. Vesikasvien lajimäärää voidaankin pitää sudenkorennoille elinympäristöjen monimuotoisuutena. Havaitsin myös, että vain muutaman lajin positiivinen vaste vesikasveihin aiheutti lajimäärän ja vesikasvien lajitiheyden välisen positiivisen korrelaation. Nämä lajit olivat kohtuullisen yleisiä, kun taas harvinaisten lajien esiintyminen oli hyvin satunnaista. Siten lammella havaittava sudenkorentojen kokonaislajimäärä ei välttämättä kerro luotettavasti harvinaisten lajien määrästä, kuten usein oletetaan.

Yhteenvetona voidaan todeta, että useat eri tekijät ja mekanismit voivat samanaikaisesti vaikuttaa tietyllä alueella havaittavaan lajimäärään. Väitöskirjani tulokset valottavat erilaisia lähestymistapoja tutkia lajimäärää tuottavia mekanismeja, ja ne myös osaltaan auttavat muodostamaan yhä realistisempaa kuvaa niistä tekijöistä ja mekanismeista, jotka vaikuttavat lajimäärään. Ihmisen toiminta on vaikuttanut ja tulee lähitulevaisuudessa yhä voimakkaammin vaikuttamaan maankäytön muutosten ja ilmastonmuutoksen myötä niin lajien käytettävissä olevaan pinta-alaan, energiaan kuin elinympäristöjen monimuotoisuuteenkin. On siis erittäin todennäköistä, että näiden muutosten seurauksena myös lajimäärässä tapahtuu muutoksia. Tuloksillani on siten erityisesti myös luonnonsuojelubiologisia sovelluksia.

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