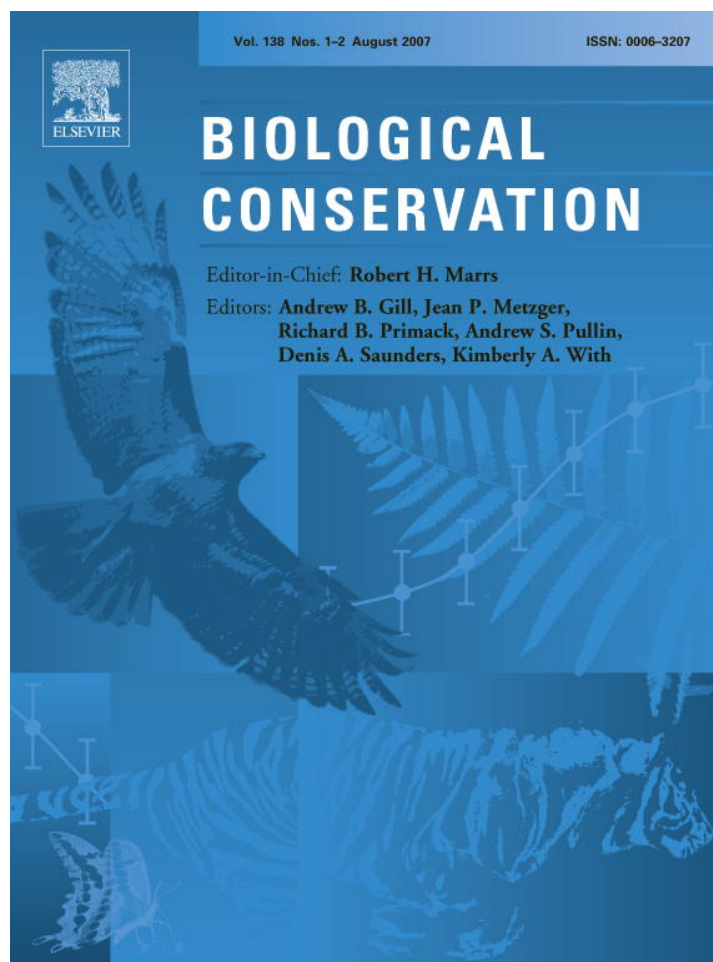


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Common species determine richness patterns in biodiversity indicator taxa

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ABSTRACT

Identification of spatial patterns of species diversity is a central problem in conservation biology, with the patterns having implications for the design of biodiversity monitoring programs. Nonetheless, there are few field data with which to examine whether variation in species richness represents consistent correlations among taxa in the richness of rare or common species, or the relative importance of common and rare species in establishing trends in species richness within taxa. We used field data on three higher taxa (birds, butterflies, vascular plants) to examine the correlation of species richness among taxa and the contribution of rare and common species to these correlations. We used graphical analysis to compare the contributions to spatial variation in species richness by widely-distributed ('common') and sparsely-distributed ('rare') species. The data came from the Swiss Biodiversity Monitoring Program, which is national in scope and based on a randomly located, regular sampling grid of 1 km² cells, a scale relevant to real-world monitoring and management. We found that the correlation of species richness between groups of rare and common species varies among higher taxa, with butterflies exhibiting the highest levels of correlation. Species richness of common species is consistently positively correlated among these three taxa, but in no case exceeded 0.69. Spatial patterns of species richness are determined mainly by common species, in agreement with coarse resolution studies, but the contribution of rare species to variation in species richness varies within the study area in accordance with elevation. Our analyses suggest that spatial patterns in species richness can be described by sampling widely distributed species alone. Butterflies differ from the other two taxa in that the richness of red-listed species and other rare species is correlated with overall butterfly species richness. Monitoring of butterfly species richness may provide information on rare butterflies and on species richness of other taxa as well.

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1. Introduction

The identification of spatial patterns of species occurrence and richness is an essential component of design of reserve networks (Pressey et al., 1993; Williams et al., 1999; Cabeza et al., 2004), of adaptive management for biodiversity conser-

vation (Kremen, 1992; Kremen et al., 1994; Carroll et al., 1999), and of national monitoring programs for meeting obligations of international biodiversity treaties (Plattner et al., 2004). Describing these patterns using comprehensive sampling of all taxa would be expensive and time consuming (Raven and Wilson, 1992). This recognition has led conservation

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biologists to study surrogate species and species richness relationships among supra-specific taxa ('higher taxa') to monitor variability in biodiversity (Noss, 1990), detect patterns of ecological degradation and/or responses to management (Elzinga et al., 2001; Noon, 2003), and accommodate divergent requirements of members of natural communities (Lambeck, 1997). Nonetheless, while evaluation of patterns in indicator groups could simplify and facilitate management and monitoring, the degree to which specific indicators satisfy multiple roles and fulfill diverse criteria remains unclear (Hilty and Merenlender, 2000; Lindenmayer et al., 2000).

Uncertainty concerning the utility of indicator groups in conservation and management results from several recurring issues. Questions surround the use of species richness in indicator taxa as a criterion for planning for biodiversity conservation and monitoring because the location of diversity hotspots may differ among taxa (van Jaarsveld et al., 1998; Prendergast et al., 1999). Also, diversity within proposed indicator taxa may inadequately represent geographic patterns of the species with greatest conservation need (Panzer and Schwartz, 1998). Further, conflicting results arise upon examination of the indicator properties of species at risk themselves. Some studies suggest that species at risk may be associated with patterns of total species richness (Mikusinski et al., 2001; Lawler et al., 2003; Warman et al., 2004) and have useful indicator properties for monitoring ecosystem integrity (Pearman, 2002). Other studies suggest that rare and threatened species have special habitat requirements that limit their coincidence with areas of high total species richness (Prendergast et al., 1999; Chase et al., 2000; Aubry et al., 2005; Orme et al., 2005), which is determined on continental scales by spatial occurrence patterns of common species (Jetz and Rahbek, 2002; Vazquez and Aizen, 2003; Lennon et al., 2004). It remains unclear whether common species also determine spatial patterns of species richness at subcontinental or national scales, which would be more relevant for optimizing nationally mandated programs of biodiversity monitoring.

Many studies that have addressed the concurrence between patterns of species richness and the distribution of rare (or red-listed) species have been conducted using species range maps or atlas data. These data may consist of observational units of 100–10,000 km² or more (e.g., Prendergast et al., 1999; Warman et al., 2004; Orme et al., 2005). This approach seeks to identify large areas for establishing reserves, but the resolution is too coarse-grained to assist with the assessment of natural trends or impacts of management within an actual management area. Further, variation in species richness at coarse resolution may be related to atlas units containing large topographical relief and habitat diversity (Heikkinen et al., 1998) or crossing latitudinal gradients of spatially correlated climatic variation at continental scales (Warman et al., 2004). In contrast, restricting analyses to areas of similar vegetation, abiotic environment, or to a subcontinental region may alter indicator relationships (Villasenor et al., 2005). This suggests that studies of limited geographic extent may not confirm results from studies conducted at a continental scale (Hess et al., 2006). Finally, we know of no fine-scale field studies that identify the distribution of the species most responsible for geographic variation in species richness in multiple higher taxa and examine the coincidence

of species richness among these groups. This suggests that study is needed of the among-taxon correlation of species richness of both widely and sparsely distributed species, because planning and management based on occurrence patterns of rare species may be inadequate to conserve biological diversity and the ecological services it provides (Higgins et al., 2004; Molnar et al., 2004; Hooper et al., 2005).

This study contributes to understanding the relationship between species distribution and spatial variation in species richness. We address these relationships at 1 km² scale and at a spatial extent relevant to monitoring regional and national species richness and rare species trends in Switzerland. We examine occurrence data from a comprehensive, national monitoring program, Biodiversity Monitoring Switzerland, BDM (Hintermann et al., 2002; Plattner et al., 2004). Because of our use of occurrence data exclusively, we subsequently use 'rare' and 'common' synonymously for sparsely- and widely-distributed species, respectively, while recognizing that many types of rarity have been proposed (Rabinowitz, 1981).

We examine the relative contributions of rare and common species to spatial variability in species richness of birds, butterflies and vascular plants. These groups are proposed indicators for planning and monitoring biodiversity conservation and reserve management (Kremen, 1992; Ryti, 1992; Balmford and Long, 1995). We also include analysis of species in three classes of commonness/rarity and additionally the species on the national Red Lists of Switzerland, so as to address broadly used definitions of rarity. We determine for each higher taxon whether the contributions to total species richness by rare and common species are qualitatively similar for physiographically distinct parts of Switzerland, distinguishing between areas of low and high elevation. Finally, we estimate the correlation of richness of common species with richness of nationally red-listed species and other sparsely distributed species.

2. Methods

2.1. Data source

Data on species occurrences come from an existing database of samples taken on Switzerland's landscape diversity sampling grid (Fig. 1). This nearly regular grid of 520 square cells forms the basis for landscape-level biodiversity monitoring nationally in Switzerland, constituting one of several steps taken to meet Switzerland's commitments resulting from the Rio de Janeiro Convention on Biological Diversity (www.biodiv.org, Hintermann et al., 2002; Weber et al., 2004). Unlike many atlas-based datasets, these Swiss data were collected with a documented sampling protocol. A sampling grid was established to align with an existing national coordinate system of 41,285 rectangular cells of 1 km². The number of regularly-distributed grid cells to be sampled was based on (1) the need for sufficient coverage of sub-national regions, and (2) a simple t-test power analysis of a set of preliminary samples of each taxon (see Hintermann et al. (2002) for details, www.biodiversitymonitoring.ch). The data collection methods are described below). The preliminary analysis determined the number of sites neces-

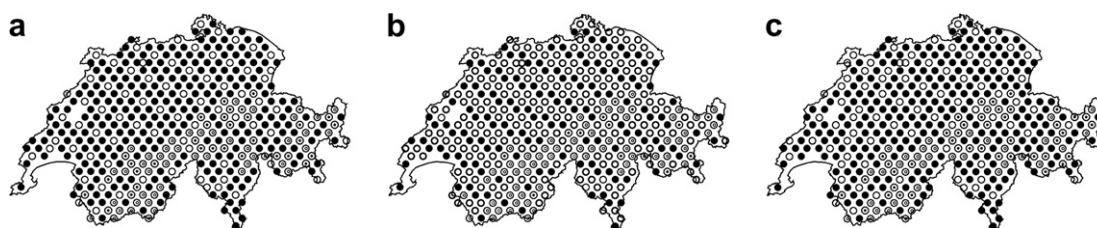


Fig. 1 – Sampling grid. Location of cells and samples along the Swiss national Biodiversity Monitoring Program grid, for birds (a), butterflies (b), and plants (c). The grid was established based on a randomly chosen reference cell and an a priori determined grid density. Symbols represent: unsampled grid cells (open circles), unsampled grid cells in areas above tree line (double open circles), and sampled grid cells, either entirely filled circles (below tree line) or double circles in which only the inner circle is filled (above tree line).

sary to detect a 10 % difference between two samples, using a single preliminary estimate of spatial variability present in the preliminary data as a surrogate for variability that may occur over time. While this may underestimate variability over time, no other estimate was available at the time of program establishment. Once the density (and thus, number) of regularly spaced samples was established, the sampling grid's location was fixed to a randomly chosen reference cell on the national coordinate system. We use data from 3 years of sampling, 1992–1994. A regular block of one-fifth of the 520 sites was sampled in each of the 3 years, except for butterflies for which samples were available from only 2 years (Fig. 1). Because of this, some sites were not sampled for all three taxa. Yearly samples were, nonetheless, country-wide in scope. Where necessary we focus the analysis on a reduced set of sites for which there are data on all three taxa. The current system of regularly distributed sites on a randomly located grid provided stratified samples across all sub-national jurisdictions and regional topography (although a detailed analysis of bias in the dataset has just begun and likely rare habitats would be unsampled). The authors' role in this research was to analyze the available data and report results coming from the first 3 years of sampling. We present detailed description of field methodology because (1) they are documented and (2) data collection details have been absent from similar studies.

2.2. Data collection

2.2.1. Plants

For each of 3 years and within each sample site, surveyors walked transects to record the presence of vascular plant species. The 29 botanists involved in this work received special training to reduce among-observer variation. Two transects in each site were continuous, 2.5 km in length and along each diagonal of the square cells. Surveyors electronically registered the presence of each vascular plant species growing in swaths 2.5 m wide on either side of transects, walking the transect in both directions. Sampling transects once in spring and again in late summer assured that data collection maximally spanned variation in flowering phenologies that likely influence species detection. The sampling characteristics of this methodology are well-characterized in a previous analysis (Plattner et al., 2004). In that work, two botanists independently assessed 23 transects. The mean of the absolute value

of the differences between two assessments was 7.9% (19.7 species \pm 4.88, mean \pm SE, 250 total species encountered).

2.2.2. Birds

For each of 3 years the presence of breeding birds was sampled in one-fifth of the sample sites three times during the breeding season (15 April–15 July). High elevation sites with less than 10% forest cover were only visited twice because of the shorter breeding season compared to low elevation sites. Sampling was done by haphazardly assigned, qualified volunteer ornithologists who used a territory mapping method to assess species richness (Bibby et al., 1992). Volunteers followed an irregular transect route aiming to cover fully each site and detect all breeding bird species regardless of terrain. This resulted in forested areas having greater transect length than open sites. Transect lengths averaged 5.1 km (range 1.2–9.4 km). The sampling characteristics for the avian sampling portion of the program have been studied in detail (Kéry and Schmid, 2004; Kéry and Schmid, 2006). Two to three visits during the breeding period produced mean species detection probabilities of 89% (range 72–100%) across sites, with detectability being somewhat higher at high elevation sites, in spite of receiving fewer visits (Kéry and Schmid, 2006). This compares favorably with a mean detectability of approximately 76% estimated for the North American Breeding Bird Survey (Boulinier et al., 1998).

Avian detectability also does not vary with the proportion of species that have not arrived at sites by the time of the first sample. Detectability decreases with increasing community size (Muller et al., 2003), meaning that species richness at diverse low elevation sites may be underestimated compared to high elevation sites. Because of these characteristics and considering that sampling was done to span the breeding season, we did not expect differences in number of visits or species detectability among sites to create a consistent trend among high- versus low-elevation sites. Further, species detectability does not vary strongly among species, among years, or with observer experience. Overall, species detectability varies little with other recognized sources of variation and no strong biases are present in the sample of bird occurrence data that has been examined (Kéry and Schmid, 2006).

2.2.3. Butterflies

Sampling butterflies was based on the British Butterfly Monitoring scheme (Pollard and Yates, 1993). In each of 2 years

(butterfly sampling started one year later than the other taxa), seven surveys were conducted between 21 April and 21 September in the lowlands, and four surveys were distributed between July and August above approximately 2000 m elevation. High and low elevation sites received approximately equal sampling effort per week of flight season and, thus, differences in the number of visits should not bias the results on this taxon. The difference in numbers of visits corresponds to the shorter flying season at higher elevations. Surveys were conducted within time windows of 14 or 21 days, depending on a seasonal schedule, following a standardized protocol. Experienced and specially trained observers walked transects of 2.5 km (the same as for the plants, see above) in both directions during favorable weather conditions ($\geq 80\%$ sunshine, $>13\text{ }^{\circ}\text{C}$, $\leq 19\text{ km/h}$ wind (Beaufort level 3)). Species were identified based on excellent knowledge of physical characteristics, flight periods, behavior, habitat preferences, and existing information on ecoregional distribution. All detected day-flying butterfly species (including Hesperidae and Zygaenidae) $\leq 5\text{ m}$ from observers were recorded on hand-held computers. Mean detectability of butterflies across sites is likely somewhat less than that of birds (Kéry and Schmid, 2006) and some (unquantified) differences among species likely exist (Dennis et al., 2006).

2.3. Within-taxon correspondence: common and rare species contributions to species richness patterns

The contribution of common and rare species to among-site variation in species richness was determined by correlating overall species richness to richness in subsets of species that were constructed by grouping species with regard to their rarity/commonness (Vazquez and Aizen, 2003; Lennon et al., 2004). We defined commonness in terms of species' distribution (i.e. the number of occupied sites) and ranked species in order of decreasing number of sites occupied. Next, we formed a number of subsets of species, equal in total to the number of species, by including species successively in rank order one by one into subsets. The first subset included only the single most-widely distributed species and each subsequent subset included additionally the next most common species until all species were included in the last subset (common to rare subset assembly, CtoR). We then examined over sites the correlation of overall species richness with richness in each subset in succession. Similarly, the contribution of rare species to overall variability in richness was determined by correlating total species richness with richness in subsets that were formed starting with the rarest species and including successively more common species one by one into subsequent subsets (rare to common assembly, RtoC). The logic here is that although the correlation coefficient between overall richness and richness in successive groups approaches 1.0 with increasing subset size, the size (i.e., number of included species) a subset must be before the correlation between richness in the subset and total richness approximates one (1.0) may differ between CtoR and RtoC assembly. For example, the richness of a group of the 10 most-common species may be across sites highly correlated with total species richness, but that the richness of the 10 rarest species may be only weakly correlated with total richness, if at all.

We then plotted the correlation between overall richness and richness in successive subsets of species, for each subset in succession and for the two subset assembly methods. We did this for three groups of sites: all sites together, high-elevation sites only (distinguished by being at or above tree line, approximately 2000 m, an unambiguous ecological ecotone), and sites below tree line only. For each of these groups we analyzed only the species occurring in at least one site within the group of sites. We evaluated by inspection the differences in the contributions of rare and common species to variation in overall species richness across the sampling grid.

2.4. Within-taxon correspondence: correlations among subsets of common and rare species

We used correlation analysis to examine whether within each higher taxon the richness of common species was correlated with the richness of either rare or red-listed species. For each higher taxon, we defined listed species as those with Swiss red list designations falling within the highest three classes of listing. For birds and plants, these categories corresponded to species listed as critically endangered (CR), endangered (EN), and vulnerable (VU) in Switzerland and are the product of evaluations following World Conservation Union (IUCN) criteria (Keller et al., 2001; Sauberer et al., 2004). For butterflies, which in contrast to the other higher taxa have not yet been evaluated along current IUCN red list criteria, we analyzed all species listed nationally at levels 1, 2 or 3 (Duelli and Obrist, 1998).

Because red list status of species may differ among European countries, we also identified rare and common species independent of IUCN listing status by ranking all species in order of area of occupancy and selecting the least common and most common 25% of species, i.e., lower (1st) and upper (4th) quartiles, respectively. This second definition of rarity is simple to apply to other flora and fauna, and is not dependent on consistent assignment of species to country red lists. We also identified one additional group of 'very common' species by beginning with most common species and adding additional common species in order of decreasing commonness until together they contributed 25% of the total number of occurrences of all species within the taxon. This amounted to 8.0%, 6.7%, and 4.8% of species of birds, butterflies and plants, respectively. This definition for commonness is useful because it identifies groups based on species relative distributions within taxa, placing equal weight on each occurrence of each species. This criterion may also facilitate comparisons with studies from other areas because these common species are equally important to the occurrence of all species within each taxon in each dataset.

For all three taxa we calculated correlations between the number of red listed species and all other species using data on all observed species. For butterflies and plants, we calculated the correlations between 1st quartile and 4th quartile species using only unambiguously identified species. This was because morphospecies that might be consistent from site to site were not available. Unidentified species of plants and butterflies were few (3.15% and 1.04%, respectively) and their inclusion would unlikely alter the patterns we found or our conclusions.

Butterflies (151 sites sampled) were sampled at approximately half as many sites as either birds (301 sites) or plants (305 sites). Any differences among species in terms of within-taxon correlations might result from the use of different sites in the analysis of each taxon, or from differences among taxa in the number of sites. To examine this possibility, we conducted a second analysis using data from only the 134 sites for which there was at least one observation of a species from each of the three higher taxa.

2.5. Among-taxon correspondence: total species richness and subsets of rare species

To examine the correspondence of species richness patterns among the three indicator taxa, we calculated correlations among taxa for total species richness, as well as for 1st quartile species, red-listed species, 4th quartile species, and very common species. These correlations were calculated with data from the 134 sites for which data on all three taxa were available.

2.6. Statistical considerations

Data on rare and red-listed species constituted relatively few occurrences and were clearly non-normally distributed. Thus, for purposes of statistical inference, we calculated Spear-

man's rank correlation coefficient (Sokal and Rohlf, 1981). Significance levels were calculated using Dutilleul's degrees of freedom (a correction for spatial autocorrelation), as implemented in the program 'Modttest' (Legendre et al., 2002). This correction was necessary because spatial autocorrelation in both of the variables under consideration can greatly inflate Type-I statistical error rates (Lennon, 2000; Legendre et al., 2002). The correction of the degrees of freedom was made by calculating a first-order approximation of the effective sample size, which is related to the variance of the correlation coefficient, r (Dutilleul, 1993). Corrected percentile tables for the t -distribution, incorporating the effective sample size, were then generated by Modttest and the observed correlation coefficient was tested for difference from zero (Clifford et al., 1989). Performance of the test is only slightly conservative in the absence of spatial autocorrelation (Clifford et al., 1989; Legendre et al., 2002).

3. Results

3.1. Within taxon species richness pattern analysis

There were 137 identified bird species, 178 identified butterfly species, and 1652 identified plant species in the dataset. Of these, occurrence of species on Swiss national lists of critically endangered, endangered, and vulnerable species

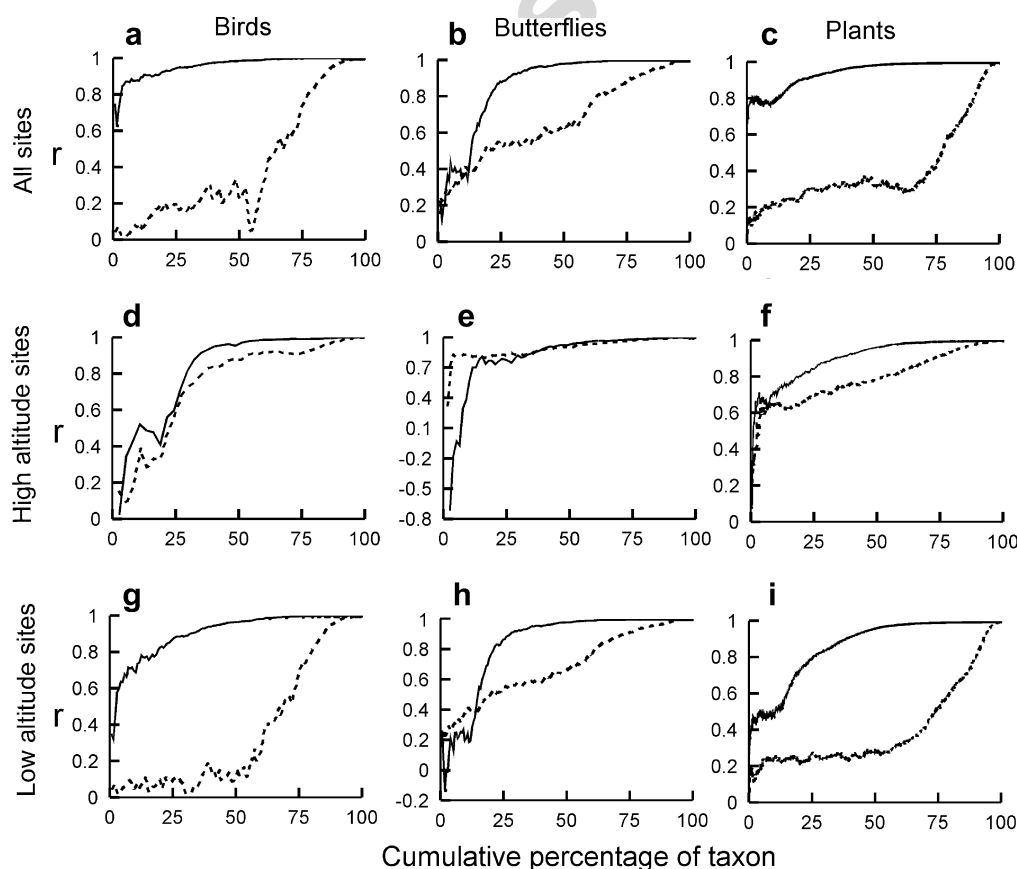


Fig. 2 – Contribution of rare and common species to overall pattern in species richness. Subsets of species were assembled by ranking species by number of sites occupied (area of occupancy), starting with either the most common species (solid line) or the rarest species (dashed line). Successively rarer (or more common) species were added one by one to form nested subsets, until all species within a taxon were included in the last subset.

included 22 bird species, 81 butterfly species and 131 plant species. The richness of a small proportion of common species approximated the spatial pattern of among-site variation in total species richness. When all sites were considered, subsets formed by common to rare assembly (CtoR) were highly correlated with overall species richness when as little as 10–25% of the entire taxon was included (Fig. 2a–c; solid line). In contrast, when subsets were formed by rare to common assembly (RtoC), approximately 50–80% of all species needed to be considered before correlation between species richness overall and species richness in the subset reached 0.60 (Fig. 2a–c; dashed line).

Common and rare species differed in their contribution to total variation in species richness depending on whether high or low elevation sites were considered. In data from high elevation sites (Fig. 2d–f), CtoR and RtoC assembly showed no substantive difference in terms of the number of species necessary to approximate the overall spatial pattern of species richness. In fact, a few rare butterfly species, selected by RtoC assembly, approximated the overall pattern of butterfly species richness (Fig. 2e). The dataset included samples from fewer high elevation sites than lowland sites, as a conse-

quence of the regular sampling design. There were also fewer species at high elevation (Table 1). To examine whether evaluating patterns among taxa was susceptible to the choice of high elevation sites, we conducted CtoR and RtoC assembly and correlation to total site richness for birds and plants using only the high elevation sites where butterflies had been surveyed. These graphical analyses showed that patterns for birds and plants were qualitatively similar to the original analyses for these taxa, with the exception of additional fluctuation on the left side of the RtoC curve (see 4, analyses not presented). Finally, and in contrast to data from high elevation sites, correlation of overall species richness and richness in subsets formed by CtoR and RtoC assembly at low elevation sites (Fig. 2g–i) displayed patterns similar to those resulting from plotting data from all sites (Fig. 2a–c).

3.2. Within-taxon correspondence: common species versus rare and red listed species

In birds, we found no evidence of correlation in species richness between red list species and other species, or between 1st (rare) and 4th (common) quartile species (Table 2). The richness of red list plants and 'other' plants was significantly positively correlated, but we found no evidence for correlation between species richness of red list plants and additional groups of plants (Table 2). Marginally significant correlations (for butterflies and plants, Table 2) became non-significant after correcting for spatial autocorrelation. In contrast to the situation with birds and plants, the species richness of red listed butterflies was highly correlated with the richness of other butterflies and with the richness of common butterflies (Table 2). Further, we found that richness of butterfly species in the 1st (rare) quartile correlated significantly with richness in the 4th quartile (Table 2). Our analysis of a restricted set of 134 sites that provided data for all three taxa did not alter

Table 1 – Species richness summary

(Sites/species number)	Birds	Butterflies	Vascular plants
All sites	301/137	151/178	305/1652
High elevation	33/37	13/78	41/612
Low elevation	268/136	138/177	264/1626

The recorded species richness of three higher taxa, birds, butterflies, and vascular plants at all sampled sites, sites at or above tree line, and at sites below tree line are shown.

Table 2 – Within-taxon species richness correlations

Taxon	Spearman correlation	Modified degrees freedom	P	Corrected P ^b
<i>Birds (n = 301)^a</i>				
Red list birds versus other birds	0.07	228.2	0.25	0.31
Red list birds versus 4th quartile (common)	–0.04	213.2	0.54	0.60
Red list birds versus 25% total occurrences (11 ^c)	0.0	251.0	0.96	1.0
1st quartile (rare) versus 4th quartile	0.03	174.7	0.59	0.68
<i>Butterflies (n = 151)^a</i>				
Red list butterflies versus other butterflies	0.82	55.3	<0.0001	<0.0001
Red list butterflies versus 4th quartile	0.83	67.0	<0.0001	<0.0001
Red list butterflies versus 25% total occurrences (12 ^c)	0.17	63.0	0.04	0.18
1st quartile (rare) versus 4th quartile	0.51	112.0	<0.0001	<0.0001
<i>Plants (n = 305)^a</i>				
Red list plants versus other plants	0.30	239.5	<0.0001	<0.0001
Red list plants versus 4th quartile	0.12	176.8	0.04	0.11
Red list plants versus 25% total occurrences (80 ^c)	0.06	134.6	0.29	0.49
1st quartile (rare) versus 4th quartile	0.05	155.0	0.4	0.53

Spearman correlations between species richness of rare and commons species are provided for birds, butterflies and plants. Data are from the Swiss Biodiversity Monitoring Program. The Bonferroni critical value for 12 tests is 0.0042. *n* is number of sites included in an analysis.

a Number of sites included in an analysis.

b Degrees of freedom corrected for spatial autocorrelation, following Dutilleul (Legendre et al., 2002) and a corresponding t-test.

c Number of ranked common species that comprise approximately 25% of all species occurrences in a given taxon.

Table 3 – Among-taxon species richness correlations

		Spearman correlations	Modified degrees of freedom ^a	P	Corrected P ^a
All species	Birds versus butterflies	−0.19	36.2	0.03	0.25
	Birds versus plants	0.23	86.7	0.006	0.03
	Butterflies versus plants	0.57	94.5	<0.0001	<0.0001
First quartile	Birds versus butterflies	−0.01	112.5	0.9	0.9
	Birds versus plants	0.06	131.8	0.5	0.5
	Butterflies versus plants	0.45	87.5	<0.0001	<0.0001
Red listed	Birds versus butterflies	0.07	85.6	0.5	0.5
	Birds versus plants	0.22	126.2	0.10	0.12
	Butterflies versus plants	0.06	81.4	0.5	0.6
Fourth quartile	Birds versus butterflies	−0.05	46.6	0.5	0.7
	Birds versus plants	0.51	38.8	<0.0001	0.0007
	Butterflies versus plants	0.50	66.6	<0.0001	<0.0001
Most common	Birds versus butterflies	0.52	58.1	<0.0001	<0.0001
	Birds versus plants	0.69	39.9	<0.0001	<0.0001
	Butterflies versus plants	0.65	48.9	<0.0001	<0.0001

Spearman correlations are between species richness in groups of rare and common species of birds, butterflies and plants. The strength of the correlations vary both among taxonomic groups and with the portion of the taxon that is analyzed, but are usually low. The Bonferroni critical value for 15 tests is 0.0033.

a Degrees of freedom and P for Spearman correlations corrected for spatial autocorrelation, following Dutilleul (Legendre et al., 2002) and a corresponding t-test; n = 134.

these patterns or conclusions on statistical significance (results not shown).

3.3. Among-taxon correspondence of rarity and species richness

We found correlations among taxa when we examined richness in each of the five categories of distribution/commonness of species. Over all species, the pattern of species richness of butterflies correlated with the richness of plant species. In comparison, bird species richness correlated weakly with species richness of plants and butterflies (Table 3). Similarly, we observed significant correlation between butterflies and plants in the richness of 1st quartile (rare) species, but not between birds and either plants or butterflies. However, we found no evidence of correlation among the three taxa in terms of richness of red list species. In contrast, all three taxa demonstrated significant correlation in terms of richness of very common species (Table 3). Further, the richness of 4th quartile plants and richness of 4th quartile species in the other two taxa were correlated (Table 3).

4. Discussion

4.1. Patterns of commonness and rarity: implications for indicator taxa

Our analysis shows that for two of the three higher taxa we studied (birds and plants), strategies aiming to conserve and monitor sites for rare species would not intersect sites with high species richness for these taxa, except in high elevation sites. Previous work suggests that widely-distributed species are primarily responsible for spatial variability in levels of species richness (Vazquez and Aizen, 2003; Lennon et al., 2004). Similarly, the spatial pattern of species richness of

widely-distributed species in our study was correlated to a greater degree with overall richness than was the spatial pattern of species with few occurrences (Fig. 2a–c). The conservation significance of these patterns is that efforts directed at sampling and monitoring levels of species richness will detect spatial variation primarily among areas that vary in the number of widely-distributed species. This is not true, in contrast, when only high elevation sites are considered. In this case, the spatial patterns of rare and common species were similar in their relationship to overall species richness (Fig. 2d–f). These differences between groups of sites suggest that in some areas, in this case a high elevation subset of study sites, rare species will be ‘captured’ in efforts to monitor and conserve sites with high species richness. This is consistent with another study which found that scale and extent of study affected observed indicator relationships (Hess et al., 2006).

The large-scale patterns of the coincidence of hotspots for rare species and areas of high species richness can be low or differ among taxa (McGeoch and Chown, 1997; Panzer and Schwartz, 1998; Prendergast et al., 1999; Chase et al., 2000). In our data on birds and plants, for example, the spatial pattern of richness of relatively rare species is not strongly correlated with the spatial pattern of species richness of widely distributed species (Table 2). However, the richness of rare (first quartile) butterfly species is significantly correlated with the richness of broadly distributed (fourth quartile) butterfly species. Further, the richness of red-listed butterfly species in our data generally follows the same spatial pattern as the richness of common butterfly species, specifically, and of un-listed butterflies in general (Table 2). These observations suggest that the way in which rare and common species contribute to overall species richness patterns differs between butterflies and the other higher taxa. Regional monitoring programs will need to adapt strategies to the taxon under consideration and a single strategy will unlikely serve for

monitoring both rare species and within-taxon species richness in general. Consideration of regional variation in the size of populations and species composition may further influence conservation priorities in Switzerland and elsewhere (Pearman, 2002). Finally, correlations of species richness that demonstrate marginal significance should be interpreted with skepticism because of the potential effects of autocorrelation and multiple comparisons on actual rates of Type-I statistical errors.

4.2. Similarity of diversity patterns among taxa

Some studies have suggested that patterns of species richness vary among taxa, and thus that identification of indicator relationships among higher taxa is complicated and, in some cases, may be impossible (Flather et al., 1997; Lawton et al., 1998; Kerr et al., 2000; Vessby et al., 2002; Perfecto et al., 2003). Other studies have demonstrated correlation in species richness among taxonomic groups, especially across particular habitat gradients and within restricted regions (Blair, 1999; Swengel and Swengel, 1999; Mikusinski et al., 2001; Garson et al., 2002). Our analyses suggest that regional environmental heterogeneity may influence the magnitude of species richness correlations.

First, differences in the degree of correlation of spatial patterns of rare and common species in our analyses depended on whether only high elevation sites were considered or a much broader range of sites. Studies that seek indicator relationships across gradients that terminate in very unfavorable environments (e.g., dense urbanization (Blair, 1999), intensive agriculture landscapes (Gregory et al., 2005), broad habitat variation (Howard et al., 1998; Pearson and Carroll, 1998), or alpine habitat (this study)) may find correlations in diversity among taxonomic groups or other patterns that are useful to conservation because many species lack suitable habitat near one end of the gradient (Fleishman et al., 1998). This may lead some sites to have low species richness across all taxa, strengthening among-taxon correlations.

Second, biological relationships among the species of some higher taxa may favor correlated distributions and the existence of indicator relationships. For example, vascular plants and some other plants and animals are expected to show correlated patterns of diversity because of influence of habitat structure provided by woody plants on animal community complexity, host-plant specificity of some animals, mutualisms, and other symbioses, although these expectations are not always confirmed (Kati et al., 2004; Anand et al., 2005; Chiarucci et al., 2005).

Third, richness of widely distributed species in one taxon may be more likely than the richness of narrowly distributed species to correlate with species richness (of widely distributed species) in another taxon. This is because common species determine geographic patterns in higher taxon species richness both in this study and at larger scales (our Table 3, Lennon et al., 2004), and the correlation of richness among taxa is stronger when widely distributed species are considered. Further confirmation of such regularities as described here, through investment in similar studies, could inform efforts to define indicator species/groups for monitoring effectiveness of biodiversity management. Our findings could

support the conservation and management of levels of species richness in other study areas that may vary in size, topography, level of environmental degradation or that may present strong natural environmental gradients.

4.3. Limitations and potential biases

One potential bias that may affect our results is variation in the mean detectability of avian species. Earlier studies show a negative relationship between the average detectability of avian species and the overall number of avian species that actually are detected. Correspondingly, sites at higher elevation (and few species) have higher average detectability of species than lower elevation sites (Kéry and Schmid, 2006). Nonetheless, this source of variation among sites unlikely influences the patterns of rare and common avian species relative to one another. This is because previous analysis of the sampling methods used here reveals exceptionally high detectability of species overall and little variation detectability among avian species per se or among years (Kéry and Schmid, 2006). Systematic variability in detectability of additional indicator groups requires more detailed study, so that appropriate measures can be implemented if necessary. This suggests that caution should be used when the results of the present analysis of data on plants and butterflies are used in making policy decisions. Additionally, high variability in correlation levels for birds and other taxa near the origin in Fig. 2 likely results because of the inclusion of few species occurrences in the first few sets of species, especially in RtoC assembly. More high-altitude sites need to be sampled in the future to avoid potential biases caused by small sample size.

Another potential concern is the impact that application of different standards among taxa in the designation of red list species may have had on our results. Red list designation for bird and plants in Switzerland has incorporated IUCN criteria, which include trends in populations, extent of occurrence and area of occupancy. Criteria for designation of butterflies was developed using ad hoc criteria specific to Switzerland (Duelli and Obrist, 1998). One reason that the richness of red-listed butterflies parallels the richness of common species might be that red-listed butterflies in Switzerland form a substantial proportion of all observed butterfly species. Nevertheless, it is unlikely that the correlations between the distributions of red-listed butterfly species and un-listed butterflies is due to red-listed species constituting a larger proportion of all butterfly species, in comparison to the contribution of red listed species to richness in the other two taxa. This is because the positive correlation between the distribution of butterflies in the first (rare) and fourth (common) quartiles (Table 2) exhibits the same phenomenon but does not depend on the proportion of red-listed butterflies and other taxa. This suggests that site conditions that are adequate to support common butterfly species also support rare butterflies. Monitoring programs that focus on a subset of widely distributed butterfly species should produce data relevant to describing the distribution of species richness of relatively rare species. In contrast, similar comparisons in the other taxa (Table 2) produced low correlations, even if highly significant.

Finally, this analysis addressed three taxa that are frequently considered as indicators for monitoring and management. Further study will be necessary to determine the degree to which richness in these taxa correlates with that of other taxa. Some variation among additional taxa is likely inevitable, suggesting that some useful indicator relationships may exist. The study sites here span substantial gradients in elevation, and both north and south slopes of the Alps and the Jura mountain ranges. Nonetheless, numerous gradients in temperature and moisture exist at smaller scales, potentially within some of the study sites. Clearly we were able to analyze species richness over only a small fraction of Swiss territory and biases created by the sample size and regular distribution of sites is currently under study. The study area does not include areas of northern and central Europe and the results should not be used for monitoring or conservation planning at the continental scale. However, none of the species studied here were endemic to Switzerland and many areas of central and Eastern Europe present substantial elevation gradients. This suggests that similar patterns may be found in other countries (e.g., Germany, France, Austria) and in other areas with mountains and associated lowlands (e.g., the Carpathian range).

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