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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-

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