

# Top predators as indicators for species richness? Prey species are just as useful

Tobias Roth<sup>1,2,3\*</sup> and Darius Weber<sup>1</sup>

<sup>1</sup>Biodiversity Monitoring Switzerland, c/o Hintermann & Weber AG, Austrasse 2a, 4153 Reinach BL, Switzerland;

<sup>2</sup>Research Station Petite Camargue Alsacienne, Rue de la Pisciculture, 68300 Saint-Louis, France; and <sup>3</sup>Zoological Institute, University of Basel, Vesalgasse 1, 4051 Basel, Switzerland

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## Summary

1. The use of surrogates to identify protected areas is a common practice in conservation biology. The use of top predators as surrogates has been criticized but recently a strong positive relationship was found between the presence of top predators and species diversity of several taxa. As mentioned by the authors, these striking results need to be assessed on a larger scale.

2. We used data from the Swiss Biodiversity Monitoring Programme and the Swiss breeding bird survey to analyse the use of raptor species as a surrogate for plant, butterfly and bird species richness. For each raptor species, we compared species richness in sites where a raptor species was recorded and compared these sites with the remaining sites in which the raptor species was not recorded. For comparison we conducted the same analyses using tits *Parus* spp. Tits are common prey species of some raptor species and were the most species-rich generalist genus in our data.

3. We found little justification for a focus on top predators when identifying conservation areas. For bird and plant species richness, raptors were reasonable surrogates for high species richness but no raptor species predicted sites with above-average butterfly species richness.

4. The presence of tit species performed equally as well as the presence of raptor species to predict sites with high species richness of birds and plants, and performed even better for predicting high butterfly species richness.

5. *Synthesis and applications.* Conservation planners using indicator species should be aware that relationships among higher taxa are complex and depend on the species group and the scale of analysis. As shown with the case of raptors, the usefulness of a biodiversity indicator can vary between adjacent areas even if the same species groups are analysed. We recommend the use of more than one indicator species from different taxonomic groups when identifying areas of high biodiversity.

**Key-words:** biodiversity, indicator species, *Parus*, predictor, raptor, surrogate, Switzerland, tit

## Introduction

A key interest in applied ecology is the identification of areas with high native species richness, partly because it has been argued that these areas have high conservation importance. In fact, few conservation practitioners select areas based on species richness alone (Pressey 1994; Margules & Pressey 2000; Jackson, Kershaw & Gaston 2004). In particular, some impoverished places, such as semi-arid areas and mountain tops, host a specific fauna and/or flora not found elsewhere. In these cases, complementarity and not species richness might be the goal for conservation (Cabeza & Moilanen 2001;

Williams *et al.* 2006). Nevertheless, there is continued interest in whether a single or few species groups should be used as indicators of high species richness (Noss 1990; Simberloff 1998; Thomson *et al.* 2007).

Top predators have considerable publicity value but their use as indicator species in conservation is controversial (Kerr 1997; Andelman & Fagan 2000; Roberge & Angelstam 2004; Ozaki *et al.* 2006). Recently, Sergio and colleagues (Sergio, Newton & Marchesi 2005; Sergio *et al.* 2006) emphasized the benefits to biodiversity conservation of the preservation of top predators. In the Italian Trentino region, Sergio, Newton & Marchesi (2005) and Sergio *et al.* (2006) recorded more bird, tree and butterfly species in 1-km squares inhabited by raptor species compared with paired controls. They

\*Correspondence author. E-mail: roth@hintermannweber.ch

concluded that there is a tight association between the occurrence of top predators and high biodiversity value, at least in the Trentino region, and suggested that the generality of these findings should be assessed further. We have performed one such assessment.

In a comprehensive national biodiversity monitoring programme (Biodiversity Monitoring Switzerland), bird, butterfly and plant species richness were estimated based on repeated visits to about 500 grid cells of 1 km width (Hintermann, Weber & Zangger 2000; Weber, Hintermann & Zangger 2004; www.biodiversitymonitoring.ch, accessed 1 June 2007). We tested whether grid cells where a raptor species was observed had higher species counts of birds, butterflies and plants than grid cells where the same raptor species had not been observed. This approach is similar to the one used by Sergio, Newton & Marchesi (2005) and Sergio *et al.* (2006) but we aimed to assess the generality of their findings at a larger spatial scale. Sergio, Newton & Marchesi (2005) and Sergio *et al.* (2006) suggested that predators are more useful as an indicator than species from a lower trophic level. We tested that assertion by performing the same analyses on both raptors and the most species-rich generalist genus, selected a priori, the tits *Parus* spp.

## Methods

Switzerland is a small country (41 285 km<sup>2</sup>) in western Europe. A country-wide biodiversity monitoring programme was begun in 2001 (Hintermann, Weber & Zangger 2000). We selected 509 out of the 41 285 possible 1-km grid cells (hereafter called cells) by taking a systematic sampling grid fixed to a randomly selected reference cell. This sampling scheme was designed to produce factual information on the dynamics of biodiversity within the country for government agencies, politicians and the general public (Weber, Hintermann & Zangger 2004). Eight cells were covered entirely by lakes or glaciers and 26 others were too dangerous to survey. Those cells were excluded, hence the data set represents Switzerland excluding the area of lake surfaces, glaciers and steep cliffs. The altitudes of the cells excluded because of steep cliffs were too high to provide potential breeding habitat for raptors or tits (Schmid *et al.* 1998) and we did not expect the exclusion of these cells to bias our analyses systematically. Average forest cover ( $\pm$  SD) was 31.5% ( $\pm$  27.8) and 18% of cells were attributed to the Jura mountains, 23% to the Swiss plateau and the remaining 59% to the Alps.

Fieldwork lasted from 2001 (2003 for butterflies) to 2005, with one-fifth of the cells surveyed each year. The subsample of cells surveyed each year was regularly spaced over the whole of Switzerland. Therefore the shorter monitoring period for butterflies resulted in a smaller sample size but not in a systematic bias in the results. Species richness of birds, butterflies and plants was estimated based on repeated visits by specialists to each cell. Each cell was visited twice for plants, up to three times for birds [three visits in cells  $\leq$  2000 meters above sea level (m a.s.l.) and two in cells  $>$  2000 m a.s.l.] and up to seven times for butterflies (seven visits in colline and montane cells, six in subalpine cells and four in alpine cells). Plants and butterflies were counted along the same 2.5-km long transect within cells. The transect was selected using fixed rules that aimed to cover as much as possible of the cell area. Bird data originated from the Swiss breeding bird survey Monitoring Häufige Brutvögel (Schmid, Zbinden & Keller 2004; Kéry & Schmid 2006). A few surveys of cells not fulfilling the strict sampling protocol (e.g. restrictions on date, time or weather conditions) were excluded from the analyses. Studies of biodiversity patterns are sometimes criticized because of detectability problems (Boulinier *et al.* 1998) but we were confident that species detectability in this study was high for the following reasons: (i) species detectability of birds has been assessed and has been proven to be high and vary little with sources of variation such as species observer and sites (Kéry & Schmid 2006); (ii) species detectability of plants and butterflies was enhanced by repeated visits. For more details about data collection see Pearman & Weber (2007) and Schmid, Zbinden & Keller (2004).

For the main analyses we used the entire data set, which contained the species lists of 464 (for birds), 283 (for butterflies) and 459 (for plants) 1-km grid cells. The canton of Tessin in the southern part of Switzerland and the Trentino mountains (the study area of Sergio, Newton & Marchesi 2005; Sergio *et al.* 2006) are adjacent areas with, presumably, much the same species pool (Table 1). To compare better our results with those reported by Sergio, Newton & Marchesi *et al.* (2005) and Sergio *et al.* (2006) we also analysed a subset of the data that included the cells from the canton of Tessin only. For each analysis, the 1-km cells from the Swiss Biodiversity Monitoring Programme were divided into two groups: one group of cells where a raptor species was recorded (raptor cells) and a second group with all the remaining cells (control cells). All raptor species recorded in at least 20 cells were analysed: red kite *Milvus milvus* L. (103 cells), black kite *Milvus migrans* Bodd. (117), goshawk *Accipiter gentilis* L. (26), sparrowhawk *Accipiter nisus* L. (47), common buzzard *Buteo buteo* L. (260), kestrel *Falco tinnunculus* L. (138) and tawny owl *Strix aluco* L. (38). We assessed the differences in species richness of birds (excluding the raptor species analysed), butterflies and plants between raptor and control cells. As count

	Switzerland	Tessin	Trentino
Total area (km <sup>2</sup> )	41 285	2812	6206
Number of 1-km grid cells	402*	47*	64†‡
Minimum altitude (m a.s.l.)	192	192	67
Maximum altitude (m a.s.l.)	4634	3400	3769
Number of regular breeding raptors	15–17§	7–8§	8–9§
Number of regular breeding bird species	174¶	148¶	145**

\*Mean number of grid cells among the three species groups.

†Mean number of sample sites (raptor territories and controls).

‡Sergio *et al.* (2006); §Hagenmeijer & Blair (1997); ¶Schmid *et al.* (1998); \*\*Pedrini, Caldonazzi & Zanghellini (2005).

**Table 1.** Features of the study sites, throughout Switzerland (this study), the canton Tessin (this study) and the Trentino mountains (study site of Sergio, Newton & Marchesi 2005 and Sergio *et al.* 2006)

**Table 2.** Results of the Mann–Whitney *U*-test. The Bonferroni critical value for 36 tests is 0.0014; *w*, test statistic; *n*, number of grid cells with presence of the raptor or *Parus* species

	Birds			Butterflies			Vascular plants		
	<i>w</i>	<i>n</i>	<i>P</i> -value	<i>w</i>	<i>n</i>	<i>P</i> -value	<i>w</i>	<i>n</i>	<i>P</i> -value
<b>Raptors</b>									
<i>Milvus milvus</i>	5 885	103	< 0.001***	10 418	67	< 0.001***	18 104	102	0.931
<i>Milvus migrans</i>	7 440	117	< 0.001***	11 770	78	< 0.001***	18 947	116	0.443
<i>Accipiter gentilis</i>	2 661	26	< 0.001***	2 485	17	0.392	3 996	26	0.013*
<i>Accipiter nisus</i>	6 451	47	< 0.001***	3 275	27	0.800	7 420	47	0.009**
<i>Buteo buteo</i>	7 438	260	< 0.001***	10 781	161	0.028*	16 551	257	< 0.001***
<i>Falco tinnunculus</i>	18 695	138	0.004**	7 784	87	0.437	20 764	136	0.355
<i>Strix aluco</i>	4 417	33	< 0.001***	2 789	21	0.779	5 089	32	0.016*
<b>Tits</b>									
<i>Parus ater</i>	3 418	368	< 0.001***	2 936	226	< 0.001***	4 952	363	< 0.001***
<i>Parus caeruleus</i>	8 285	257	< 0.001***	13 070	157	< 0.001***	17 372	252	< 0.001***
<i>Parus cristatus</i>	14 549	264	< 0.001***	5 911	161	< 0.001***	14 323	262	< 0.001***
<i>Parus major</i>	2 584	330	< 0.001***	8 900	202	0.025*	9 059	325	< 0.001***
<i>Parus montanus</i>	24 243	145	0.405	2 878	91	< 0.001***	16 027	144	< 0.001***
<i>Parus palustris</i>	7 708	236	< 0.001***	11 695	143	0.002**	16 012	231	< 0.001***

\**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001.

data often deviate from a normal distribution, we used the non-parametric Mann–Whitney *U*-test to assess differences among raptor and control cells.

The genus *Parus* (tits) represents species that are more generalist in their diets and have smaller per-pair area requirements than raptors. They were the most species-rich generalist genus recorded. All *Parus* species recorded in at least 20 cells were analysed in the same way as the raptors. The following *Parus* species were included in the analysis: coal tit *Parus ater* L. (368 cells), blue tit *Parus caeruleus* L. (257), crested tit *Parus cristatus* L. (264), great tit *Parus major* L. (330), willow tit *Parus montanus* Conrad (145) and marsh tit *Parus palustris* L. (236). All calculations and graphs were carried out using the software R (R Development Core Team 2006).

## Results

The mean  $\pm$  SD number of observed species for all cells in the Swiss Biodiversity Monitoring Programme was  $32.1 \pm 12.6$  bird species,  $34.0 \pm 17.3$  butterfly species and  $230.1 \pm 64.9$  plant species. The mean number of cells only from the canton of Tessin was  $23.8 \pm 9.7$  bird species,  $42.7 \pm 14.3$  butterfly species and  $230.5 \pm 91.0$  plant species.

For each of the seven raptor species, bird species richness per cell was higher in cells where the raptor was observed than in cells where it was not observed (Table 2 and Fig. 1). Four raptor species indicated cells with high plant species richness but none of the raptor species indicated high butterfly species richness. In contrast, the mean number of butterfly species in cells with records of black kite, red kite and common buzzard was significantly lower compared with control cells.

Five out of six tit species indicated high bird species richness, and all tit species indicated high plant species richness per cell (Table 2 and Fig. 1). The occurrence of coal tit, crested tit and willow tit also indicated cells with high butterfly species richness, but the mean of butterfly species richness of cells

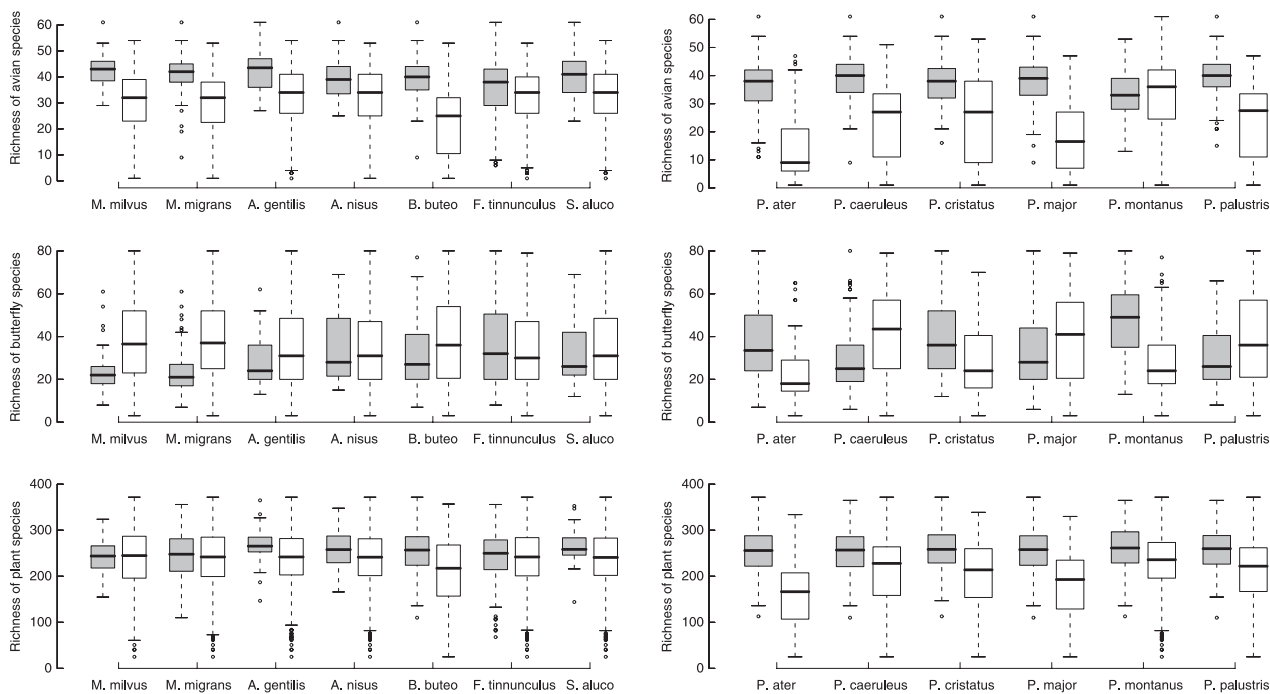
with blue tit, great tit and marsh tit was significantly lower compared with control cells.

All analyses were repeated using the grid cells from the canton of Tessin only. The results of these analyses were comparable with the above results (see Table S1 in the Supplementary material).

## Discussion

We used data from the national Swiss Biodiversity Monitoring Programme to show that the observed presence of a raptor species indicated cells with high species richness of birds and plants. We did not find that the presence of a raptor indicated high butterfly species richness. Moreover, *Parus* species performed equally well compared with raptor species as predictors for cells with high bird and plant species richness, and even better as predictors for cells with high butterfly species richness.

Sergio, Newton & Marchesi (2005) and Sergio *et al.* (2006) provided evidence of the usefulness of raptor species as an indicator of high species richness. The authors also claimed that bird species of lower trophic level, such as insectivorous and herbivorous species, are not good predictors of high species diversity. However, our results suggest that the performance of raptor species as indicators of high species richness largely depends on the species group analysed; raptors predicted cells with high bird species richness, to a lesser extent cells with high plant species richness, but not cells with high butterfly species richness. Furthermore, the species of tit, representing a lower trophic level, performed equally well in indicating cells with high species richness. Our results support other studies that show indicator relationships among higher taxa to be complex and to depend on the species group (Vessby *et al.* 2002; Thomson *et al.* 2007).



**Fig. 1.** Performance of raptor species (graphs to the left) and *Parus* species (graphs to the right) as species richness indicators. The box plots show species richness per 1-km grid cells occupied by a raptor or *Parus* species (dark boxes) and grid cells not occupied by the species (light boxes). Boxes represent median and 25th and 75th percentiles, whiskers are non-outlier ranges and dots are outliers of avian (first row), butterfly (second row) and plant (third row) species richness.

In this study we assessed the value of top predators as indicators of high species richness at a larger scale than the study of Sergio, Newton & Marchesi (2005) and Sergio *et al.* (2006). In biodiversity indicator studies, variation in scale may lead to different results because of the inclusion of more or fewer biogeographical regions or habitat types (Bohning-Gaese 1997; Favreau *et al.* 2006). For example *Parus* species that are more common in the Alps than in other parts of Switzerland, such as the coal tit, crested tit and willow tit (Schmid *et al.* 1998), were good predictors of high butterfly species richness in this study. These results may simply reflect the fact that the numbers of butterfly species are higher in the Alps than in other parts of Switzerland (Koordinationsstelle Biodiversitätsmonitoring Schweiz 2006). These particular *Parus* species might be of less value in predicting species richness in a study on a smaller scale that only included the Alps. However, we also analysed data from the canton of Tessin, adjacent to the study area of Sergio, Newton & Marchesi (2005) and Sergio *et al.* (2006) and at a comparable scale. Our conclusions remained the same as from our analyses of data from the whole of Switzerland: *Parus* species predict species richness at least equally as well as raptor species.

Sergio, Newton & Marchesi (2005) and Sergio *et al.* (2006) stated that each of their bird species assessments reflected the biodiversity of an area of approximately 1 km<sup>2</sup> (Sergio *et al.* 2006). However, these authors detected only around 6.5 avian species on average, which is about four times less than the number of species detected per 1-km cell in this study. The canton of Tessin in the southern part of Switzerland and the Trentino mountains are adjacent areas with, presumably,

much the same species pool. If we considered cells from the canton of Tessin only, the average avian species richness of the Sergio, Newton & Marchesi (2005) and Sergio *et al.* (2006) study was 3.5 times lower than ours. The species detectability of birds in the Swiss Biodiversity Monitoring Programme used for this study was estimated to be 89% (Kéry & Schmid 2006). In contrast, we assume that a large number of birds remained undetected in Sergio, Newton & Marchesi (2005) and Sergio *et al.* (2006) study. Imperfect detection of species is a fundamental problem in ecological studies (Boulinier *et al.* 1998): measures of species richness may be confounded by the detectability of species and the problem is pronounced for very low species detection probabilities.

Sergio, Newton & Marchesi (2005) and Sergio *et al.* (2006) concentrated on regions where the target raptor species occurred. For each raptor species the regions differed in size and location. Therefore the results may be biased towards the representation of these species and interpretation of the results may be difficult. More importantly, conservation priorities are usually drawn up within administrative regions or biogeographically meaningful regions: a method based on the presence of a raptor species as a surrogate for species richness cannot judge if some of the most important places for conservation are outside the range of the raptor species. Our study used sites throughout Switzerland, therefore our assessment was based on a given region, which is a rational unit within which conservation priority decisions can be made.

We also noted that, while some studies have suggested that species with few occurrences are better indicators of species richness (Lawler *et al.* 2003) and others have found the

opposite pattern (particularly for Switzerland; Pearman & Weber 2007), the spatial pattern of species richness of widely distributed species is correlated to a greater degree with overall richness than the spatial pattern of species with few occurrences. Our study provides no evidence that single species with few occurrences (e.g. goshawk and sparrowhawk in this study) differed in their potential to indicate cells with high species richness from widely distributed species (e.g. *Parus* spp. and common buzzard).

Sergio, Newton & Marchesi (2005) and Sergio *et al.* (2006) reframed an old debate in conservation biology by suggesting that top predators are valuable as biodiversity surrogates. However, from an ecological perspective, based on the database of the Swiss Biodiversity Monitoring Programme and the Swiss breeding bird survey, we have found little evidence to justify conservation focusing on top predators. Raptor presence indicated areas with high species richness reasonably well, at least for avian and plant species richness. However, other species groups, such as tit species, are of equal value in identifying areas of high species richness. We conclude that the usefulness of a biodiversity indicator can vary between adjacent areas even if the same species groups are analysed. This should be considered when using surrogate species for conservation planning. We recommend the use of complementary indicator species from different trophic groups to assess biodiversity.

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## References

- Andelman, S.J. & Fagan, W.F. (2000) Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 5954–5959.
- Bohning-Gaese, K. (1997) Determinants of avian species richness at different spatial scales. *Journal of Biogeography*, **24**, 49.
- Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E. & Pollock, K.H. (1998) Estimating species richness: the importance of heterogeneity in species detectability. *Ecology*, **79**, 1018–1028.
- Cabeza, M. & Moilanen, A. (2001) Design of reserve networks and the persistence of biodiversity. *Trends in Ecology and Evolution*, **16**, 242–248.
- Favreau, J.M., Drew, C.A., Hess, G.R., Rubino, M.J., Koch, F.H. & Eschelbach, K.A. (2006) Recommendations for assessing the effectiveness of surrogate species approaches. *Biodiversity and Conservation*, **15**, 3949–3969.
- Hagenmeier, E.J.M. & Blair, M.J. (1997) *The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance*. T. & A. D. Poyser, London, UK.
- Hintermann, U., Weber, D. & Zangger, A. (2000) Biodiversity monitoring in Switzerland. *Schriftenreihe für Landschaftspflege und Naturschutz*, **62**, 47–58.
- Jackson, S.F., Kershaw, M. & Gaston, K.J. (2004) The performance of procedures for selecting conservation areas: waterbirds in the UK. *Biological Conservation*, **118**, 261–270.
- Kerr, J.T. (1997) Species richness, endemism, and the choice of areas for conservation. *Conservation Biology*, **11**, 1094–1100.
- Kéry, M. & Schmid, H. (2006) Estimating species richness: calibrating a large avian monitoring programme. *Journal of Applied Ecology*, **43**, 101–110.
- Koordinationsstelle Biodiversitätsmonitoring Schweiz (2006) *Zustand der Biodiversität in der Schweiz*. Bundesamt für Umwelt, Bern, Switzerland.
- Lawler, J.J., White, D., Sifneos, J.C. & Master, L.L. (2003) Rare species and the use of indicator groups for conservation planning. *Conservation Biology*, **17**, 875–882.
- Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.
- Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, **4**, 355–364.
- Ozaki, K., Isono, M., Kawahara, T., Iida, S., Kudo, T. & Fukuyama, K. (2006) A mechanistic approach to evaluation of umbrella species as conservation surrogates. *Conservation Biology*, **20**, 1507–1515.
- Pearman, P.B. & Weber, D. (2007) Common species determine richness patterns in biodiversity indicator taxa. *Biological Conservation*, **138**, 109–119.
- Pedrini, P., Caldonazzi, M. & Zanghellini, S. (2005) Atlante degli Uccelli nidificanti e svernanti in provincia di Trento. Museo Tridentino di Scienza Naturali, Trento. *Studi Trentini di Scienze Naturali, Acta Biologica*, **80** (Supplement 2), 1–662.
- Pressey, R.L. (1994) Ad hoc reservations: forward or backward steps in developing representative reserve systems. *Conservation Biology*, **8**, 662–668.
- R. Development Core Team (2006) *R: A language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Roberge, J.M. & Angelstam, P. (2004) Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology*, **18**, 76–85.
- Schmid, H., Luder, R., Naef-Daenzer, B., Graf, R. & Zbinden, N. (1998) *Schweizer Brutvogelatlas. Verbreitung der Brutvögel in der Schweiz und Im Fürstentum Liechtenstein 1993–96*. Swiss Ornithological Institute, Sempach, Switzerland.
- Schmid, H., Zbinden, N. & Keller, V. (2004) *Überwachung der Bestandentwicklung Häufiger Brutvögel in der Schweiz*. Swiss Ornithological Institute, Sempach, Switzerland.
- Sergio, F., Newton, I. & Marchesi, L. (2005) Top predators and biodiversity. *Nature*, **436**, 192–192.
- Sergio, F., Newton, I., Marchesi, L. & Pedrini, P. (2006) Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology*, **43**, 1049–1055.
- Simberloff, D. (1998) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation*, **83**, 247–257.
- Thomson, J.R., Fleishman, E., MacNally, R. & Dobkin, D.S. (2007) Comparison of predictor sets for species richness and the number of rare species of butterflies and birds. *Journal of Biogeography*, **34**, 90–101.
- Vessby, K., Soderstrom, B., Glimskar, A. & Svensson, B. (2002) Species richness correlations of six different taxa in Swedish seminatural grasslands. *Conservation Biology*, **16**, 430–439.
- Weber, D., Hintermann, U. & Zangger, A. (2004) Scale and trends in species richness: considerations for monitoring biological diversity for political purposes. *Global Ecology and Biogeography*, **13**, 97–104.
- Williams, P., Faith, D., Manne, L., Sechrest, W. & Preston, C. (2006) Complementarity analysis: mapping the performance of surrogates for biodiversity. *Biological Conservation*, **128**, 253–264.

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## Supplementary material

The following supplementary material is available for this article.

**Table S1.** Table with results of Tessin grid cells only.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01435.x>  
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