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Vertebrates respond differently to human disturbance: implications for the use of a focal species approach

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ABSTRACT

Focal species are surrogates assuming that all species under consideration respond similarly to the threatening processes. Focusing management only on a small number of species would improve conditions for other species. However, the across-taxa congruency of the response to threatening processes, and the subsequent efficiency of focal species as surrogates, has seldom been tested. In this study, we evaluated the effects of recreational disturbance and wood structure on the communities of terrestrial vertebrates in the wood patches of a large urban park. We measured two effects of recreation: direct disturbance (people presence) and litter disturbance (effect of trampling). We used multiple techniques to assess the distribution of small mammals, birds, reptiles and amphibians in 44 wood patches. Disturbance and wood maturity influenced the distribution of some species and the species richness of amphibians and reptiles; however, the pattern was not consistent across species within classes or among classes. The performance of focal species as a multi species umbrella was poor. Our results suggest that species specific differences in the response to the same source of disturbance can be strong; these differences can hinder the usefulness of focal species as surrogates and as a management tool.

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1. Introduction

The planning of biodiversity conservation is a difficult task. Lambeck (1997) suggests that an ideal pathway would be as follows: first, the species occurring in the 'focal area' should be assessed; second, the threatening processes and the resources limiting the populations should be identified. The

identification of threats would then allow the planning of the management actions required for the conservation of the species present.

In practice, this approach is not feasible. Comprehensive studies on the status of biodiversity are time consuming and expensive. Lawton et al. (1998) estimated that the species inventory of a representative hectare of tropical forest would

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require 10–20% of the global workforce of systematists. The identification of threats may be a still more difficult task, since relationship between species and natural and anthropogenic processes are frequently hard to define. The difficulties associated with comprehensive studies have led to the use of ‘surrogates’, based on the assumption that a subset of species can be used as an indicator of the processes ongoing in the landscape, and that management actions aimed at their protection can be beneficial to a large proportion of the species (Caro and O’Doherty, 1999). The use of surrogate species (or taxa) relies on the assumptions that different components of the ecosystem respond similarly to the processes and threats. However, it is unlikely that the requirements of only one species may be able to capture those of the entire ecosystem (e.g., the ‘umbrella’ species): in response to this limitation multi-species or multi-taxa surrogates have been developed, such as the ‘focal species approach’ (Lambeck, 1997) or the ‘shopping basket approach’ (Sauberer et al., 2004 and references therein).

The ‘focal species approach’ assumes that all species under consideration respond similarly to the threatening processes. This is assumed because there are not enough data to demonstrate that it is the case, nor time to collect those data. The species that are most sensitive to each of the threatening processes (i.e., decline most rapidly as the intensity of the threat increases) are selected as the focal species. Management is focused on focal species, assuming that as conditions improve for the focal species they will also improve for other species (Lambeck, 1997). Focal species are an extension of the more classical ‘umbrella’ species, and are supposed to perform better than other surrogates, yet this approach has been only partially validated (reviewed by Roberge and Angelstam, 2004). Actually, very few studies tested a crucial assumption of focal species as surrogates, that is whether species respond similarly to the threatening processes (Roberge and Angelstam, 2004; but see Blair, 1999; Posa and Sodhi, 2006). It is thus critical to understand how different species or taxa respond to the threatening processes affecting the landscape, in order to evaluate whether the monitoring and the protection of a limited subsample of the biodiversity can be effective for understanding and managing the processes threatening the overall biota.

In recent decades, the demand by European and North American citizens for natural environments in which to spend free time has been rapidly increasing, and recreational activities become a major cause of ecosystem alteration and threat biodiversity (Cole and Landres, 1995; Christ et al., 2003). Recreational disturbance can have strong effects on animals, leading to behavioural modifications, a different use of habitats, and a reduction in survival or reproductive success of individuals (Liddle, 1997; Fernandez-Juricic and Telleria, 2000; Parent and Weatherhead, 2000; Rodgers and Cox, 2003; Rodriguez-Prieto and Fernandez-Juricic, 2005; Whittington et al., 2005). The recreational disturbance on natural environments can be particularly strong in human dominated landscapes, where only a few, small natural patches (such as woodlands) still persist. Unfortunately, these residual patches attract people living in urban areas, being therefore affected by multiple stressors, including small size and isolation, human exploitation, and the direct disturbance caused by large numbers of people (Liddle, 1997; Whittington et al., 2005). In the most exploited areas, there is therefore an urgency to protect the

biodiversity of residual patches, since for many species they represent the only available habitat. This urgency can be particularly strong in areas inhabited by rare or endemic species.

In this study, we compared the responses of different terrestrial vertebrates (small mammals, birds, reptiles and amphibians) to recreational disturbance and wood features in a large urban park, in order to investigate whether the abundance of a group of species might act as surrogate for the whole community. Vertebrates include attractive species and species requiring a large amount of habitats, thus they have frequently been used as flagship or umbrella species (see Roberge and Angelstam, 2004). In order to avoid the confounding effects of synanthropic opportunistic species living in open habitats (Watson, 1979; Cole and Landres, 1995), we focused our analyses on the communities living in woods. In detail, we investigated (1) how the distribution of terrestrial vertebrates within the park is related to the human disturbance; (2) how much the response to disturbance is consistent across taxa, and (3) whether a set of focal species can be used as a measure of the response of all vertebrates to the threatening processes. A positive answer to this latter question would mean that the monitoring of a limited number of species could be enough to trace the effects of different management action to sustain the biodiversity at local scale.

2. Study area

The study was carried out from 1999 to 2004 in the Monza Park (45.35N, 9.16E), a 750 ha urban park north of Milan (Lombardy, Northern Italy) within the Lambro Valley Natural Park (Ronconi, 1998). The altitude was 162–200 a.s.l. Woods were highly fragmented and covered 50% of the park, while open grasslands accounted for 32%. The remaining 18% was represented by the Lambro river, by historical buildings and farmhouses and by the facilities of the National Motordrome of Monza and the Milano Golf Club. The composition of woods included species typical of the River Po Plain belonging to the hornbeam *Carpinus betulus* and pedunculate oak *Quercus robur* woods, but many ornamental and domestic species have been introduced in successive stages for reforestation. Mean wood age was 70–80 years. Underwood was dominated by elder *Sambucus nigra*, hazel *Corylus avellana*, hawthorn *Crataegus monogyna*, bramble *Rubus* spp. and North American blackthorn *Prunus serotina*, which recently colonized northern Italy.

3. Methods

We collected data about human disturbance, environmental features, and vertebrate distribution within 44 wood patches, as defined by the forestry management plan of the park (Cereda, 1998).

3.1. Measure of disturbance and environmental features

Throughout the year, many people frequent the Monza Park for recreation, principally for walking, jogging, playing sports or riding. The network of pathways allows visitors to reach all the areas of the park and people usually stay very close

to the pathways. Two main kinds of disturbance to animals arise from the human recreational activities: the direct disturbance due to the simple presence of people, and the habitat alteration due to both trampling and damages to the understorey. We refer to the first source of disturbance as ‘direct disturbance’ and to the second as ‘litter disturbance’. For each wood patch, we measured the direct disturbance by counting the number of pedestrians transiting during 15 min point counts along the pathways of the patch. All point counts were performed in early June, on sunny afternoons (0200–0500 pm), during workdays.

Preliminary observations suggest that, in our study area, people walk out of pathways mainly during sport events. International sport events (e.g., the Italian Formula 1 Grand Prix, the Superbike World Championship and golf competitions) attract thousands of people (more than 150,000 during Formula 1 Grand Prix) that invade the park and concentrate close to the sport structures and facilities. Litter disturbance is maximum after the sport events; however, the effects of disturbance on soil and leaf litter persist throughout the year (Ficetola, 2001). For each wood patch, we measured litter disturbance the day after the Italian Grand Prix (September), using a rank scale, in an area with a 30 m radius in the centre of each wood patch. The ranks of this scale were: 0, no footprints or signs of human disturbance; 1, footprints or isolated tracks on the ground; 2, litter partially turned over, several tracks on the ground; 3, trampling all over the sampling area, small areas with bare ground; 4, prevalence of bare ground all over the sampling area. Direct disturbance and litter disturbance were not intercorrelated (Table 1). Lack of correlation between these variables probably reflected different behaviours of habitual recreationists, who do not usually leave pathways crossing the woods, and sports fans, who also frequent areas far from the pathways.

We obtained data about the structure of wood patches from the forestry management plan of the Monza Park (Cereda, 1998), which described in detail all the wood patches included in the park. In this plan, tree features were assessed by measuring all of the trees inside each wood patch. Available data for each of the 44 patches were the average tree diameter, the tree density (N/ha) and the patch surface area. The tree species composition was quite homogeneous across patches, and was therefore not considered in our analyses.

Average tree diameter and tree density were strongly intercorrelated (Table 1), with trees in lower density patches tending to have a higher mean diameter. The presence of strongly correlated variables may bias the results of multiple regression models (Berry and Feldman, 1985), thus these variables cannot be included together in the models. Therefore, we used principal component analysis (PCA) to reduce tree diameter and tree density to a single factor. PCA extracted only one component explaining 86.1% of the variance of the two factors. The factor was positively correlated with the average tree diameter and negatively with the tree density; we therefore assumed the scores of this factor to be an estimate of wood maturity. Wood maturity was not correlated with direct disturbance or litter disturbance (Table 1).

3.2. Sampling of vertebrates

We trapped small mammals in each patch using 10 snap traps (5 × 10 cm), arranged in linear transects at 10-m intervals. Three additional large snap traps (15 × 10 cm) were collocated near the second, the fifth and the ninth small traps. Traps were baited with chocolate cream and sunflower seeds, and were checked twice every day (3 h after dawn and 3 h before dusk). Each trapping session lasted four nights: traps were not sprung during the first night, and afterwards they were armed and rebaited at each occasion, if necessary (Galeotti et al., 2005). Three trapping sessions were carried out for each wood patch during 1999, corresponding to the following three periods of population dynamics: (a) the winter decline phase (1st session, February), (b) the increasing phase (2nd session, June), and (c) the autumn peak density phase (3rd session, November). Overall, a total of 132 transects was employed for a total of 396 days of trapping.

We used point counts (Blondel et al., 1981) to assess bird abundance in 32 wood patches out of the 44. In the remaining 12 patches the environmental noise (such as cars) did not allow us to hear bird calls efficiently. We therefore did not census birds in these patches, in order to avoid biases in analyses of bird abundance. However, wood patch features and human disturbance did not differ significantly between patches that were monitored for birds and those that were not (direct disturbance and wood maturity: ANOVA, all $P > 0.7$; litter disturbance: Mann–Whitney test, $P = 0.948$). We performed

Table 1 – Pearson’s correlation between environmental features in 44 wood patches

		Litter disturbance	Average tree diameter	Tree density	Wood maturity	Patch area
Direct disturbance	<i>r</i>	–0.066	0.063	–0.149	0.114	–0.075
	<i>P</i>	0.672	0.683	0.334	0.459	0.629
Litter disturbance	<i>r</i>		0.204	–0.215	0.225	0.185
	<i>P</i>		0.185	0.162	0.141	0.229
Average tree diameter	<i>r</i>			–0.723	0.928	–0.107
	<i>P</i>			< 0.0001	< 0.0001	0.491
Tree density	<i>r</i>				–0.928	0.122
	<i>P</i>				< 0.0001	0.432
Wood maturity	<i>r</i>					–0.123
	<i>P</i>					0.427

Wood maturity is a factor extracted by a principal component analysis (see Section 3 for details).

censuses during the breeding season of 1999 (April to July), recording all birds heard or seen during a 10-min sampling period at each point.

Following Massa et al. (1998) and Bani et al. (2002), for Lombardy, we considered the following species as ‘forest birds’: wood pigeon *Columba palumbus*; cuckoo *Cuculus canorus*; green woodpecker *Picus viridis*; great spotted woodpecker *Dendrocops major*; lesser spotted woodpecker *D. minor*; wren *Troglodytes troglodytes*; robin *Erithacus rubecula*; nightingale *Luscinia megarhynchos*; blackcap *Sylvia atricapilla*; chiffchaff *Phylloscopus collybita*; long-tailed tit *Aegithalos caudatus*; great tit *Parus major*; blue tit *P. caeruleus*; marsh tit *P. palustris*; nuthatch *Sitta europaea*; short-toed treecreeper *Certhia brachidactyla*; chaffinch *Fringilla coelebs*.

We searched for reptiles in all the 44 patches along the ecotones, covering standard transects. We performed 87 transects under sunlight (Donà et al., 1991), 3 days a week, between March and October 2000 and 2002, in late morning (spring and autumn) or in early morning (summer). Each transect was completed on average in 4 h and crossed more than one of the 44 patches (on average: 8.8 patches, range 6–10). The sampling effort was therefore nearly 4 h per patch per year. In order to avoid multiple recaptures of the same individuals, all snakes were individually marked by scale clipping (Blanchard and Finster, 1933), and snake abundance in each patch was expressed as the total number of individuals captured over the 2-year study.

In order to detect amphibians during their terrestrial activity phases, we performed visual encounter surveys from April to July 2000 and 2001, using a randomised walk design (Crump and Scott, 1994). During these surveys we crossed repeatedly all 44 wood patches, using headlamps to light up the ground; we performed these surveys after dusk, mainly during or immediately after rainfall to maximize the likelihood of detecting amphibians. Overall, 69 surveys were performed; the average sampling effort was 1.3 h per patch per year.

We preferred to not permanently mark amphibians and lizards, because of the concern about the risks associated with the commonly used toe-clipping (McCarthy and Parris, 2004). Therefore, only presence/absence within patches was recorded.

3.3. Data analysis

We investigated the effects of human disturbance and environmental features on the vertebrate community using a two-step procedure: first, we analysed each species independently from

others (species level analysis), then we analysed groups of species belonging to the same class (class level analysis). Forest specialist birds were also considered as a group in these analyses in order to avoid the possible confounding effect of generalist species. Therefore, at class level analysis we classified species as belonging to the following groups: mammals, all birds, forest birds, reptiles and amphibians (Table 2).

At species level, we used generalized linear models (GLMs) to relate the abundance of species (number of individuals within patches or point count abundance) to direct disturbance, litter disturbance, wood maturity, and patch size, assuming a Poisson error distribution. For species with only presence/absence within patches available, we performed logistic regressions using presence–absence within wood patches as dependent variable. We assessed the significance of independent variables using a likelihood ratio test. Only species detected in at least 10 of the monitored patches were considered, and, for birds, we restricted the species-level analysis to the woodland species.

At the class level, we also used GLMs to relate the species richness of each taxon to direct disturbance, litter disturbance, wood maturity and patch size, assuming a Poisson error distribution.

A lower number of patches was sampled for birds than for other vertebrates, leading to the possibility that differences among classes would arise simply because of differences in the identity of the analysed patches rather than from true differences among communities. Thus, all models performed for mammals, reptiles and amphibians were repeated by analysing only the 32 patches sampled for birds. Since all but one of the models performed on the subset of 32 patches were almost identical to those performed on the overall data set, we concluded that differences between the two data sets were negligible. Therefore, to increase the power of analyses we used the largest sample available. In preliminary analyses, we also evaluated if different processes of model selection (such as forward stepwise and backward elimination of the least significant variables) produce different results. The variables identified as significant were always the same, independently from the method used.

Focal species were selected by ranking the species according to threatening processes (direct disturbance, litter disturbance, and wood maturity) on the basis of the effect sizes obtained from GLMs (see Table 3). The top one of the list for each threat was chosen as a focal species. We then analysed the value of focal species to protect the whole

Table 2 – Number of vertebrate species and number of protected species found in the study area

Classes	No. of species	Species per plot	No. of species of community interest for the European Union ^a	No. of species of regional conservation concern ^b
Mammals	9	0–6	0	3
Birds (all species)	45	5–15	0	11
Birds (forest species)	17	2–9	0	7
Reptiles	4	0–4	4	3
Amphibians	5	0–2	4	4

a Species included in the Habitat Directive (1992/42/EEC, annexes II or IV) or in the Bird Directive (1979/409/EEC, annex I) of the European Union as species requiring rigorous protection and/or the designation of special areas for their conservation.

b Species having a priority score of 8–14 in the Regional Law 7/4345/2001 of Lombardy.

vertebrate community by computing the Pearson's correlation between the number of focal species of each patch and their biodiversity value, i.e. the total number of species found in a patch minus the number of focal species (Kati et al., 2004).

When multiple tests were performed, we applied the sequential Bonferroni's correction (Rice, 1989). However, debate is ongoing about the application of Bonferroni's correction to conservation studies, because not performing management when a potential threat exists can have negative consequences, and therefore type II errors (i.e., incorrectly accepting the null hypothesis), can be much more costly than type I (Moran, 2003; Field et al., 2004). Results close to the

significance thresholds should therefore be carefully considered during the decision making process.

In all analyses, residual plots were screened to evaluate violations of assumptions of models; we did not observe strong violations of assumptions (normality, homoscedasticity or non-autocorrelation) (Bowerman and O'Connell, 1990). Statistical analyses were run using R 2.1 (R Development Core Team, 2005).

4. Results

We found 63 vertebrate species in the study area, 71% of them being birds (Table 2). All reptiles and all amphibians but one

Table 3 – General linear models relating species abundance (mammals, birds and *Hierophis viridiflavus*) and presence/absence (*Podarcis muralis* and *Bufo viridis*) to human disturbance and wood maturity

Species	Variable	B	Z	χ^2_1	P
Mammals					
<i>Apodemus sylvaticus</i>	Direct disturbance	+0.001	0.071	0.005	0.942
	Litter disturbance	–0.251	–3.188	10.285	0.001
	Wood maturity	–0.022	–0.275	0.079	0.779
	Patch area	–0.009	–0.395	0.133	0.716
<i>Clethrionomys glareolus</i> ^a	Direct disturbance	+0.034	+3.375	11.999	0.0005
	Litter disturbance	–0.315	–4.000	16.207	<0.0001
	Wood maturity	+0.199	+2.482	6.172	0.013
	Patch area	–0.025	–1.174	1.159	0.282
Birds					
<i>Dendrocops major</i>	Direct disturbance	–0.002	–0.063	0.04	0.949
	Litter disturbance	–1.023	–2.903	11.814	0.0006
	Wood maturity	+0.434	+1.726	3.349	0.067
	Patch area	–0.007	–0.082	0.007	0.935
<i>Sitta europaea</i>	Direct disturbance	+0.028	1.290	1.547	0.214
	Litter disturbance	+0.511	+2.829	7.745	0.005
	Wood maturity	–0.237	–1.322	1.732	0.188
	Patch area	–0.071	–1.439	2.174	0.140
<i>Parus caeruleus</i> ^a	Direct disturbance	–0.134	–0.459	0.215	0.643
	Litter disturbance	+0.162	+0.738	0.536	0.464
	Wood maturity	+1.432	+3.376	20.472	<0.0001
	Patch area	+0.819	+2.801	9.346	0.002
Reptiles					
<i>Hierophis viridiflavus</i>	Direct disturbance	–0.084	–1.738	3.959	0.047
	Litter disturbance	–0.905	–2.346	7.399	0.007
	Wood maturity	–0.124	–0.451	0.204	0.651
	Patch area	–0.270	–0.330	0.111	0.739
<i>Podarcis muralis</i> ^a	Direct disturbance	–0.143	–2.484	8.357	0.004
	Litter disturbance	–0.430	–1.191	1.456	0.228
	Wood maturity	+0.718	1.757	3.497	0.062
	Patch area	+0.101	0.932	0.904	0.342
Amphibians					
<i>Bufo viridis</i>	Direct disturbance	–0.067	–1.069	0.253	0.253
	Litter disturbance	–1.548	–2.283	8.396	0.004
	Wood maturity	+0.786	+1.663	3.162	0.075
	Patch area	–0.150	–0.907	0.921	0.337

B, multiple regression coefficients; Z, effect size (B/SE). In bold, results significant after Bonferroni's correction.

a Species selected as 'focal species'.

were protected by the European Union (i.e., they are listed within the annexes II or IV of the Habitat Directive –1992/42/EEC), while all birds and mammals were not (Table 2). Three to eleven species per classes were under protection of regional laws (Regional Law 7/4345/2001 of Lombardy), birds being the classes with the larger number of regionally protected species ($N = 11$). Two species were included in the IUCN red list: the harvest mouse *Mycromis minutus* (near threatened) and the Italian agile frog *Rana latastei* (vulnerable).

Eight species of vertebrates were observed in at least 10 patches: two mammals (the wood mouse *Apodemus sylvaticus*, occurrence $O = 84\%$ of patches; and the bank vole *Clethrionomys glareolus*, $O = 75\%$), three forest birds (the great spotted woodpecker *Dendrocops major*, $O = 44\%$; the nuthatch *Sitta europaea*, $O = 50\%$, the blue tit *Parus caeruleus*, $O = 34\%$), two reptiles (the western whip snake *Hierophis viridiflavus*, $O = 25\%$ and the wall lizard *Podarcis muralis*, $O = 61.4\%$) and one amphibian (the green toad *Bufo viridis*, $O = 23\%$). Therefore, only these species were included in the species level analysis.

4.1. Species level analysis

Direct disturbance negatively affected the presence of two species, the wall lizard and the western whip snake, but the effect of the whip snake was not significant after Bonferroni's correction. By contrast, the abundance of the bank vole significantly increased according to direct disturbance (Table 3).

Litter disturbance significantly affected the distribution of most species of mammals, birds, reptiles and amphibians considered in this study (Table 3). Mammals, reptiles and amphibians were less abundant in woods having higher levels of

litter disturbance, while the sign of this relationship varied among birds. The abundance of nuthatch increased, while that of great spotted woodpecker decreased as litter disturbance increased (Table 3).

We observed a significant, positive relationship between the distribution of blue tit and wood maturity. Positive relationships, but marginally non-significant or not significant after Bonferroni's correction were also observed for bank vole, great spotted woodpecker, wall lizard and green toad (Table 3). Patch area positively influenced the abundance of only one species, the blue tit (Table 3).

The bank vole was the species most negatively affected by litter disturbance, the blue tit was the most positively affected by wood maturity and patch area, and the wall lizard the most negatively affected by direct disturbance (see Table 3). Therefore, these three species constituted our set of focal species.

4.2. Classes level analysis and effectiveness of focal species

The species richness of amphibians was negatively related to litter disturbance; litter disturbance also negatively affected species richness of reptiles but this effect was not significant after Bonferroni's correction. The species richness of reptiles was negatively related to direct disturbance (Table 4). The species richness of small mammals, birds or forest birds was not related to the recorded habitat features (Table 4).

The correlation between the number of focal species and their biodiversity value was positive, but weak and not significant ($r = 0.299$, $N = 32$, $P = 0.1$). That is, patches hosting more focal species did not host the richest communities of vertebrates.

Table 4 – General linear models relating species richness in small mammals, birds, reptiles and amphibians to human disturbance and wood maturity

Classes	Variable	B	Z	χ^2_1	P
Mammals	Direct disturbance	+0.001	+0.040	0.002	0.968
	Litter disturbance	-0.097	-1.231	1.530	0.216
	Wood maturity	+0.029	+0.360	0.134	0.714
	Patch area	-0.002	-0.072	0.005	0.945
Birds (all species)	Direct disturbance	+0.007	+0.623	0.377	0.539
	Litter disturbance	+0.040	+0.407	0.163	0.687
	Wood maturity	+0.076	+0.818	0.677	0.411
	Patch area	-0.003	-0.177	0.014	0.906
Birds (forest species)	Direct disturbance	-0.010	-0.831	0.675	0.412
	Litter disturbance	+0.127	+1.310	1.692	0.193
	Wood maturity	-0.015	-0.162	0.027	0.870
	Patch area	-0.006	-0.248	0.062	0.803
Reptiles	Direct disturbance	-0.034	-3.400	8.449	0.004
	Litter disturbance	-0.171	-2.177	4.145	0.042
	Wood maturity	+0.104	+1.300	1.590	0.207
	Patch area	+0.003	+0.127	0.013	0.908
Amphibians	Direct disturbance	-0.073	-1.413	2.364	0.124
	Litter disturbance	-1.162	-2.345	8.382	0.004
	Wood maturity	+0.781	+2.224	5.714	0.017
	Patch area	-0.194	+0.152	2.614	0.106

B, multiple regression coefficients; Z, effect size (B/SE). In bold, significant results after Bonferroni's correction.

5. Discussion

Our results suggest that human disturbance and wood features are important factors influencing the distribution and abundance of vertebrates, and that the effects of disturbance may be very different for different species. For example, we found that the same factor can affect the distribution of some species negatively, while other species within the same class may be affected positively (Table 3). Environmental features also seemed to differently affect vertebrate distribution at class level: species richness of reptiles and amphibians was negatively related to the litter disturbance, while for small mammals and birds we did not observe any relationship (Table 4). Finally, the set of three focal species selected on the basis of threatening processes was able to predict only a small proportion of the biodiversity in our study area. Thus, managing for the species most negatively affected by litter disturbance, the bank vole in our study case, will not improve conditions for all forest mammals or for all vertebrates in the area.

A possible criticism to our study relies in the sampling protocol. Not all vertebrates were sampled during the same year: birds and mammals were sampled during 1999, amphibians during 2000 and 2001, reptiles during 2001 and 2003. Thus, it is possible that the distribution of different taxa were not intercorrelated not because the lack of relationships among taxa, but simply because the variations of species abundances among years might have masked all relationships among taxa. However the human exploitation of the park did not vary across years: the areas used for sport events were the same (cf., Ficetola, 2001), and no major changes occurred in woodland structure during these study years. Similarly, the spatial pattern of habitual frequentation did not seem to be changed across years (G.F. Ficetola and R. Sacchi, personal observation). Moreover, we did not observe any congruence even for the pattern of classes surveyed during the same year (e.g., mammals and birds or amphibians and reptiles; Table 4), and we observed opposite responses to the same source of disturbance for species belonging to the same class, despite the fact that they were monitored simultaneously (Table 3). Altogether, these considerations suggest that differences among years did not strongly bias our results.

5.1. Effects of threatening processes: human disturbance and wood maturity

Litter disturbance negatively affected the distribution of several species of small mammals, reptiles and amphibians surveyed in this study. Litter disturbance also negatively affected the pattern of species richness of reptiles and amphibians at class level (Tables 3 and 4). These results confirmed that trampling negatively affects the species distribution of ground dwelling animals.

In our study area litter disturbance was mainly caused by people that trampled outside the pathways, mainly during sport events. Trampling compacts soil, reduces or modifies litter amount and structure, and reduces invertebrate abundances (Chappel et al., 1971; Duffey, 1975; Bayfield, 1979). Therefore, terrestrial animals living in trampled areas find a modified, unfavourable habitat. For example, the reduction

of the leaf litter layer can provide lesser amount of shelter and lower food availability; moreover, burrowing could be more difficult in the compacted soil. Several studies showed strong relationships between leaf litter and the distribution of many terrestrial vertebrates, including the bank vole (e.g., Gurnell, 1985; Canova, 1993; Block and Morrison, 1998; Ecker et al., 2002). Our study confirms the generality of the negative effects of litter disturbance on ground dwelling vertebrates.

Litter disturbance was also significantly related to the distribution of two bird species. This relationship was negative for the great spotted woodpecker but positive for the nuthatch. This relationship is quite puzzling. A possible explanation might be the different ability of the species to manipulate dead wood due to their different cranial structure. The great spotted woodpecker is able to excavate dead and rotting tree in order to find insects, while nuthatch need broken wood for collecting insects (Cramp, 1985). Therefore, the positive relationship between litter disturbance and the abundance of nuthatch might reflect the increased availability or affordability of prey following the damage to the understorey and plants. A second possible explanation might be the different response of the species to wood closure and density. Both species are forest birds, but nuthatch is more tolerant of open and scattered woodlands, with low developed understorey than the great spotted woodpecker (Cramp, 1985). The negative response of the great spotted woodpecker might therefore reflect a reduction of wood cover due to the direct damage to the understorey. Finally, it is possible that there are fewer downed logs in areas heavily traversed by people, either because people avoid areas with lots of downed logs or destroy them through repeated trampling. This might explain the negative response of the great spotted woodpecker.

A further puzzling relationship is between the abundance of bank vole and the direct disturbance. Apparently, bank vole *C. glareolus* was more abundant in the areas where the disturbance is stronger. Is it possible that this positive relationship arises from a common correlation with a third unknown factor. For example, human disturbance could reduce the abundance of predators (such as reptiles (Table 4), or carnivores, not investigated by this study). In turn, bank vole might be more abundant in the areas where predators are less abundant. It should also be noted that this species is a strictly nocturnal species (Wojcik and Wolk, 1985; Canova, 1993). Habitual disturbance in the Monza Park is exclusively diurnal because people are forbidden to enter the park during the night. Therefore, the negative consequences of disturbance on this species are unlikely to have a direct biological effect, while indirect effects, including positive, are possible.

By contrast, the species richness of reptiles and the abundance of wall lizard and western whip snake was negatively related to the direct disturbance. Reptiles are expected to be strongly influenced by this kind of human disturbance. First, the species living in the park are strictly diurnal, therefore they share the same activity patterns of visitors. Moreover, snakes are frequently considered 'harmful' or 'dangerous', and can be killed or displaced by recreationalists (Parent and Weatherhead, 2000).

Finally, wood maturity, a factor positively related to woods having large diameter trees, was positively related to the presence of the blue tit. The association of blue tit with high

quality woodlands has also been observed in other studies performed in northern Italy (Massa et al., 1998).

5.2. Efficiency of focal species

There is little consensus about the efficiency of surrogate taxa for the conservation of biodiversity. Several studies showed strong relationships of species richness across taxa, suggesting that some groups (such as vascular plants or birds) could be used as an efficient surrogate for the conservation of overall biodiversity (Saetersdal et al., 2003; Kati et al., 2004; Sauberer et al., 2004; Warman et al., 2004); however, other studies found little or no consensus across taxa (Prendergast et al., 1993; Prendergast and Eversham, 1997; Lawton et al., 1998; Ricketts et al., 2002; Saetersdal et al., 2005).

By analysing the species specific response to disturbance, our study provides further insights on the conditions that can reduce the efficiency of surrogates. We observed very different responses to human disturbance across species and these differences are likely to play an important role in the scarce performance of our focal species as a surrogate. In landscapes highly affected by human activities, such as our study area, species-specific responses to environmental features are frequently different (e.g., Lindenmayer et al., 1999; Ficetola and De Bernardi, 2004; Anand et al., 2005; Fisher et al., 2005; Denoël and Ficetola, in press). In these cases, no single conservation measure will benefit all species, since the response of some species is directly opposed to others, and the efficiency of surrogates for conservation can be expected to be low (Lindenmayer and Fisher, 2003; Fisher et al., 2005).

Multi species umbrellas have been proposed as surrogates in complex landscapes where multiple threatening processes are ongoing (Lambeck, 1997). However, our focal species failed to capture a significant portion of the variation in the diversity of vertebrate community. Therefore, it is unlikely that management plans solely based on our three focal species can allow correct management of the overall landscape.

We underline that several studies showing a poor performance of potential surrogates have been carried out in areas suffering intense human activities and multiple stressors (e.g., Prendergast et al., 1993; Lawton et al., 1998; Anand et al., 2005); many studies showing a good performance of surrogates have been carried out in more pristine environments and/or in large protected areas (e.g., Saetersdal et al., 2003; Kati et al., 2004; Warman et al., 2004; but see also Sauberer et al., 2004). If the response to human disturbance was totally consistent among taxa, the biodiversity of a community would decrease in response to increasing intensities of disturbance. But this is not the case, since the highest values of biodiversity are not found in most pristine communities, but in communities suffering intermediate levels of disturbance, probably because some species are favoured and other species are negatively affected by disturbance (Connell, 1978). This leads us to suppose that the relationship between biodiversity and human disturbance can be very complex, reducing the effectiveness of surrogates to predict the response of indirectly sampled species to an increase of the disturbance intensity.

Finally, the use of surrogates is sometimes advocated to reduce the number of monitored taxa within a given area, since monitoring all taxa consumes a great deal of time and money

and involves completely different census techniques. However, our three focal species belong to three different classes (mammals, birds and reptiles) and require completely different monitoring techniques, making the possibility of reducing the sampling effort small.

Some authors underline that scientific evidence of the effectiveness of surrogate species (such as focal species) is scarce, and thus other strategies should be used to overcome the impossibility of comprehensive studies: surrogates can be useful only as 'social hooks', using the attractiveness of some species to fund the protection of the whole ecosystem (Andelman and Fagan, 2000; Lindenmayer and Fisher, 2003, but see also Lambeck, 2002; Roberge and Angelstam, 2004). Our results show that, in a community highly affected by human activities, species sharing similar habitat requirements (e.g., mammalian and avian forest specialists) might have different responses to the same source of stress (Lawton et al., 1998; Lindenmayer and Fisher, 2003), reducing the performance of our set of focal species. The possibility that surrogates could be less effective in the most disturbed areas (Anand et al., 2005), encourages the development of alternative approaches that are as attractive and practical as the use of surrogates.

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