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Title:

Surrogate species vs. landscape metric: Does presence of a raptor species explains
diversity of multiple taxa more than patch area?

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Abstract

Prioritizing conservation areas is a central theme in conservation biology. The use of surrogate species and landscape metrics to identify areas with high conservation value is common. However, few studies have examined the relative efficacy of these two surrogates. In this study, we compared the efficacy of the presence/absence (PA) of a top predator (Eastern Marsh Harrier, *Circus spilonotus*) and wetland patch area on species richness, total abundance, and community composition of birds, plants, and small mammals, but species richness and community composition only for plants, in a fragmented wetland landscape. Although harrier PA was an effective indicator of the distribution of birds, it had no significant efficacy on the distributions of plants and small mammals. Patch area was more effective indicator of the distributions of plants and small mammals. These results suggest that surrogate species can be more effective indicators than landscape surrogates when there are ecological linkages between surrogate species and the focal taxa (e.g., similarity of habitat requirements between surrogate species and focal taxa or hetero-specific attraction). On the other hand, landscape surrogates would be useful when ecological knowledge about the relationships is limited.

Keywords

Biodiversity conservation, Fragmented landscape, Multiple taxa, Patch area, Surrogate

45 species, Wetland.

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Introduction

Biodiversity has rapidly been declining in recent decades at a global scale (Cardinale et al. 2012) due to the worldwide loss of natural habitat and fragmentation of remaining habitats (Fahrig 2003). Prioritizing conservation areas is now a central theme in conservation biology. The use of surrogate species such as top predators, keystone species, and umbrella species to identify areas of high conservation value is a common practice in conservation prioritization because it is difficult to build conservation plans based on habitat requirements of all species in the target ecosystem (Wilcox 1984). This approach has attracted considerable attention (e.g., Di Minin and Moilanen 2014), as it can raise environmental awareness (Leader-Williams and Dublin 2000) and generate good financial support for conservation programs (Caro and O'Doherty 1999). However, the surrogate species approach tends to carry inconsistent outcomes and often lacks an ecological rationale (e.g., Cabeza et al. 2008). Nonetheless, some studies have suggested that there are species that promote the survival of many associated species in the community (e.g., Pakkala et al. 2006; Mönkkönen et al. 2007), and that some species/species groups can be used as indicators of community composition in fragmented landscapes because communities tend to be nested with progressive fragmentation (Sætersdal and Gjerde 2011; Larsen et al. 2012). Therefore, it may be possible to select useful surrogate species by considering their ecological roles and focal landscape type.

The use of landscape metrics (e.g., patch area, shape, and connectivity) to identify areas with high conservation value has also received considerable attention, along with remarkable technical improvements in remote sensing in recent years (e.g., Faith 2003; Hortal et al. 2009). Such an approach has several advantages for conservation prioritization. For example, landscape metrics can be relatively easily measured on a large scale for any places for which satellite or aerial images are available (Banks-Leite et al. 2011). However, the efficacy of the landscape surrogate approach has not been validated with biological data in the field (but see Banks-Leite et al. 2011; Barton et al. 2014) although several studies have looked at correlations (and causality) between landscape metrics and biodiversity metrics (e.g., Oja et al. 2005; Goetz et al. 2010). In addition, landscape surrogates may not be effective for raising financial support and environmental awareness.

Particular surrogate species/species groups are never associated with the species richness and community composition of all taxonomic groups present (Niemi and McDonald 2004; Sattler et al. 2014). Similarly, responses to landscape metrics vary among species/taxonomic groups (e.g., Davis 2004; Barbaro et al. 2005). Therefore, taxonomic groups expected to be protected based on species/landscape surrogate approaches would be limited. In other words, the efficacy of these approaches may differ among taxa. To evaluate the effectiveness of each approach for protecting biodiversity, a comparison between species and landscape surrogate approaches across

multiple taxa is needed. Nevertheless, only a few studies have examined the relative efficacy of these two approaches (but see Bräuniger et al. 2010; Banks-Leite et al. 2011; Lindenmayer et al. 2014).

In this study, we examined the relative efficacy of the presence/absence (PA) of surrogate species and landscape surrogates on the species richness, total abundance, and community composition of birds, plants, and small mammals, but species richness and community composition only for plants, in wetland fragments. We used the Eastern Marsh Harrier, *Circus spilonotus*, which is an avian top predator, as a surrogate species. This is because raptor species have been used as presumed indicator species of species richness and the abundance of some taxonomic groups such as birds and plants (e.g., Sergio et al. 2005; Burgas et al. 2014). We used wetland patch area as a landscape surrogate because patch area is the most basic landscape metric that affects species richness, abundance, and community composition of various taxa (e.g., Krauss et al. 2004; Yamaura et al. 2008; Hu et al. 2011). We used birds and plants as focal taxa. These are widely used for biodiversity assessments because of the rich body of knowledge on their ecology, and their species richness is positively correlated with that of other taxa in many cases (Gardner et al. 2008; Kessler et al. 2011). We also used small mammals as additional target taxon because of the likely existence of predator-prey interactions between the marsh harrier and small mammals (Morioka et al. 1995). Specifically, we tested the following two hypotheses. The first is that harrier PA

is an effective indicator of the distribution of other wetland birds and small mammals, but not of the distribution of wetland plants. This is because the harrier has similar habitat requirements to other wetland birds, the harrier can be an important cue in the habitat selection of other bird species (i.e., hetero-specific attraction) (e.g., Mönkkönen et al. 2007), and the harrier mainly preys on small mammals (Simmons 2000). The second hypothesis is that patch area is broadly associated with biodiversity metrics across three taxonomic groups. Wetland ecosystems are one of the most endangered ecosystems due to clearance for prime agricultural land and industrial areas (Dudgeon et al. 2006). However, the effectiveness of surrogate approaches for biodiversity conservation has not been demonstrated in wetland ecosystems (but see Brose 2008; Ormerod et al. 2010).

Materials and methods

Study area and its wetland

The study area is located in the Iburi region, central Hokkaido, northern Japan (Fig. 1). Although there were huge expanses of wetlands in this region in the early 1900s, more than 90% of those wetlands have been lost due to the development of agricultural lands and urbanization. Currently, the wetlands in this area consist of patches of various sizes (Fig. 1). All wetland patches in this region are dominated by common reed *Phragmites australis* that may include subdominant sedge (*Carex* spp.) and *Juncus* spp.,

Phynchospora spp., and *Eleocharis* spp communities.

Measuring wetland patch areas

We defined continuities of reed, sedge, and rush communities as “wetland patches.”

We treated these vegetation cover types, surrounded by other landscape features (e.g., forest, river, and road) of more than 50 meters, as separate wetland patches. Areas of all patches were calculated using ArcMap 10.0 (ESRI 2011) from aerial photographs taken in 2002. The study area had a total of 97 wetland patches.

Survey of surrogate species

We used the Eastern Marsh Harrier as a surrogate species for the following reasons.

First, the Marsh Harrier is easily detected because it is a medium-sized raptor that occurs in open habitats. Second, its ecology and natural history are well-known (e.g., Simmons 2000). Third, avian surrogate species are better associated with species richness and the abundance of co-occurring species than are mammalian surrogate species (Branton and Richardson 2011). Finally, the presence of breeding raptors is an important cue in the habitat selection of various bird species (e.g., Mönkkönen et al. 2007). These criteria are needed for effective use of the surrogate species approach (Caro and O’Doherty 1999). In the study region, the harriers prey on small- or medium-sized birds and mammals (Morioka et al. 1995), arrive in late March, which is

earlier than most migratory wetland bird species (M. Senzaki unpublished data), and breed from early April to early August on a reed-bed in wetland patches. This species is listed as Endangered by the 4th Red List of Threatened Birds of Japan (Japan Wildlife Research Center 2002).

We investigated whether each of the 97 patches in the study area was used by harriers as breeding patches from early April to early June in 2012. We established 46 observation points across the study area and conducted observation surveys, in which we stayed for 2 h to locate harriers at each observation point. We observed up to 10 wetland patches at an observation point. Each wetland patch was observed up to three times on different dates (i.e., totally up to 6 h), if we could not detect harriers during the first or second observation periods. Since we were not able to fully observe some wetland patches from the single observation points, we observed such patches from multiple observation points. When we observed any breeding behavior of marsh harriers (i.e., nest building, feeding of chicks), we treated those habitats as breeding patches. We identified 21 such patches from among the 97 wetland patches.

Surveys of birds, plants, and small mammals

We selected a total of 32 patches of various size (4.3–100.8 ha) to quantify the densities of birds, plants, and small mammals. We conducted surveys for birds, plants, and small mammals at 30, 32, and 20 patches, respectively. Marsh harriers bred at half

of the total number of sites for each taxonomic group (i.e., 15, 16, and 10 patches, respectively). There was no relationship between the PA of the harrier and the log-transformed patch areas for birds (ANOVA, $F_{(1, 28)} = 2.43$, $p = 0.13$), plants (ANOVA, $F_{(1, 30)} = 1.58$, $p = 0.22$), or small mammals (ANOVA, $F_{(1, 18)} = 1.48$, $p = 0.24$) (Fig. 5).

We conducted daytime and nighttime bird surveys from early June to early July in 2012 (25 patches) and 2013 (5 patches). For daytime surveys, we set up a 300 m census route on a reed-bed in each wetland patch. Then we walked slowly along the route, and recorded all birds seen or heard within 50 m of either side of each route. We completed the surveys between 0400 to 0900 h on clear days when diurnal birds were most active. For nighttime surveys, we conducted unlimited-radius point counts that consisted of a 30-min passive listening period at the center of a census route used in the diurnal surveys. We recorded the number of individuals of all birds heard simultaneously at each survey point. We completed the surveys between 2000 to 0200 h in fair weather conditions (no rain or strong wind). Both daytime and nighttime surveys in each patch were conducted two times on different dates in the same year. We conducted separate plant surveys for three dominant plant communities from late July to early September in 2012 (26 patches) and 2013 (6 patches). We defined vegetation cover dominated by the common reed as a “reed community.” We also defined vegetation cover dominated by sedges (*Carex* spp.) of approximately 1.0 m in

height as a “sedge community,” and that dominated by rushes (*Juncus* spp.,
Phynchospora spp., and *Eleocharis* spp.) of approximately 0.5 m in height as a “rush
community.” If there were any community groups in the wetland patches, we
established two 2 m × 2 m quadrats in each community and recorded all vascular plant
species in each quadrat. We also measured the cover of each species within each
quadrat. We did not conduct surveys in cases where the area of each community was
too small to survey (<8 m² in a patch). We examined whether each plant community
existed in each patch using aerial photographs and field surveys. As a result, we
conducted surveys in 32 patches for the reed community, 22 patches for the sedge
community (13 patches with harriers and 11 patches without harriers), and 14 patches
for the rush community (six patches with harriers and eight patches without harriers).
There were no relationships between the PA of the harrier and log-transformed patch
area in the reed community (ANOVA, $F_{(1, 30)} = 1.58$, $p = 0.22$), sedge community
(ANOVA, $F_{(1, 20)} = 0.73$, $p = 0.40$), or rush community (ANOVA, $F_{(1, 12)} = 2.67$,
 $p = 0.13$) (Fig. 5).

Small mammal surveys were conducted from late June to late July in 2013. We
used a live-trapping method, which is the most common method used to study small
mammals (Michel et al., 2006). We established two 90-m-long parallel trap-lines that
were placed 50 m apart in reed-beds in each wetland patch. Ten Sherman traps (7.6 cm
× 8.9 cm × 22.8 cm, H. B. Sherman Trap) were placed sequentially every 10 m along

each trap-line, hence 20 traps were placed in each patch. Traps were baited with oatmeal. Three visits were made at dawn, 24, 48, and 72 h after installation. Individuals captured on the first and second visits were temporarily marked (color mark on the tail or abdomen) and then released.

To avoid pseudoreplication, we spaced the sampling sites between patches at least 500 m apart. For birds and plants, we grouped all species recorded into wetland species (i.e., species that breed in wetland) and species that prefer other habitat types following the literature (Umezawa et al. 2009; The Ornithological Society of Japan 2012). For small mammals, this grouping was omitted because no species that prefer other habitats were recorded. Finally, we obtained a total number of species (i.e., species richness) for wetland birds, plants, and small mammals and total abundance for wetland birds and small mammals at each sampling site. We defined total abundances as the sum of the maximum number of individuals of each wetland species at each sampling site. Non-wetland species (i.e., species that breed in other habitats) were excluded from the above calculations for the following two reasons. First, we were interested in the conservation of wetland species because wetland species have a higher conservation profile than non-wetland species in our study area. Second, although wetlands often provide important resources for non-wetland species, they cannot be conserved by protecting the harrier or wetland because their breeding habitat is not protected.

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228 Statistical analysis

229 We used a generalized linear model (GLM) with a Poisson error and a log link function
230 to examine the effectiveness of the PA of the marsh harrier and patch area on the species
231 richness and abundance of the three target taxa. For wetland plants, abundance was not
232 calculated. Explanatory variables were PA of the marsh harrier and log-transformed
233 patch areas.

234 We conducted principal component analysis (PCA) to examine the community
235 composition of wetland patches for birds, small mammals, and each of the three plant
236 communities separately, using the abundance of each species for wetland birds and
237 small mammals and coverage of each species for wetland plants. We used the first two
238 principal axes as the indices of community composition. We used a generalized linear
239 model (GLM) with a Gaussian error with each of two axes as a response variable, and
240 the PA of the marsh harrier and log-transformed patch area as two explanatory variables.

241 We constructed regression models for combinations of all possible explanatory
242 variables and ranked them by Akaike's information criterion for small sample situations
243 (AICc). Models with a $\Delta AICc$ ($\Delta AICc_i = AICc_i - AICc_{min}$, where $AICc_i$ and $AICc_{min}$ is
244 the AICc value for model_i and the AICc value of the best model in the model subset,
245 respectively) smaller than 2 have substantial support (Burnham and Anderson 2002).
246 We performed model averaging when there were several models with a $\Delta AICc$ smaller

than 2. We interpreted parameters in averaged models at the 5% significance level and 10% marginal significance level. In addition, for all focal taxa, we performed Pearson correlation analysis between species richness and abundance (except for plants), between species richness and the first two axes of the PCA, and between abundance and the first two axes of the PCA (except for plants). All analyses were conducted using R software (ver. 2.15.3 R Core Team 2013).

Results

We recorded a total of 733 individuals of 13 wetland bird species, 117 wetland plant species (70 species in the reed community [$n = 32$], 77 species in the sedge community [$n = 22$], and 66 species in the rush community [$n = 14$]), and 102 individuals (excluding recaptures) of 6 wetland small mammal species.

For wetland birds, the PA of the harrier was significantly associated with species richness, total abundance, and the first two axes of the PCA (Fig. 2; Table 1). For wetland plants, patch area was significantly associated with the species richness of the reed and rush communities (Fig. 3; Table 1), and had marginally significant associations with the first axis of the rush community and the second axis of the reed community (Fig. 3). For small mammals, no covariate was associated with species richness (Figs. 2, 3; Table 1). Total abundance was significantly associated with patch

area (Fig. 3; Table 1). Both the PA of the harrier and patch area had little association with the first two axes of the PCA (Figs. 2, 3; Table 1).

For wetland birds, species richness was positively correlated with abundance and the first axis of PCA, and negatively correlated with the second axis of PCA (Table 2). Total abundance was positively correlated with the first axis of PCA (Table 2). For wetland plants and small mammals, there were no consistent correlations among species richness, total abundance (for small mammals only), and the first two axes of PCA (Table 2).

Discussion

As predicted, we found strong relationships between the PA of the harrier and species richness, total abundance, and community composition of wetland birds (Fig. 2; Table 1). These results imply that the habitat requirements of the marsh harrier are similar to those of many wetland bird species, in line with a previous study (Sattler et al. 2014). For example, the harrier often breeds in a reed-bed with a high groundwater level (Morioka et al. 1995; M. Senzaki unpublished data), which is also suitable breeding habitat for wetland specialists such as the Water Rail (*Rallus aquaticus*), Baillon's Crake (*Porzana pusilla*), and Eurasian Bittern (*Botaurus stellaris*); such habitat may be protected from terrestrial mammalian predators. However, another possible explanation of our results is that the presence of the harrier may be a cue for habitat selection of

other wetland birds (heterospecific attraction). The effects of predators on their potential prey species are not always only negative (i.e., predation risk) but may also be positive (i.e., protection benefits). In fact, several studies have shown that the abundances of various potential prey species decrease with distance from avian predator nests (e.g., Pakkala et al. 2006; Mönkkönen et al. 2007). In our study region, the marsh harrier arrives earlier at the breeding site than most migratory wetland bird species (M. Senzaki unpublished data). Therefore, wetland birds arriving later may select the breeding site depending on the presence of harriers as an important cue. In addition, for wetland birds, there were significant correlations among species richness, abundance, and the first two axes of PCA (Table 2). We also found strong relations between these variables and the PA of the harrier (Fig. 2; Table 1). These relationships indicate that wetland bird assemblages in the study area are determined by the ecological conditions and that the PA of the harrier reflects these communities/conditions (Niemi and McDonald 2004; Sætersdal and Gjerde 2011).

On the other hand, harrier PA was not a good indicator for wetland plants and especially for small mammals regardless of the likely existence of predator-prey interactions between the marsh harrier and small mammals (Fig. 2; Table 1). These results are likely because there are no or only weak ecological links between the harrier and these taxonomic groups, or because the factors that affect the habitat selection of each taxon differ. For example, in this study area, the Marsh Harrier rarely forages in

the breeding wetland patches (i.e., they have foraging habitats separate from nesting wetland patches) (M. Senzaki personal observation), and so the Marsh Harrier may select breeding wetland patches independently of the abundance of small mammals in the wetland patches. In addition, the amount of leaf litter and nitrogen content of the soil may affect the species richness, abundance, and community composition of wetland plants and small mammals (Foster and Gross 1998; Odachi et al. 2009; Loydi et al. 2013), while the Marsh Harrier selects breeding patches independently of these factors.

Studies have shown that patch area is a key factor that can explain the species richness, total abundance, and community composition of various taxa (e.g., Krauss et al. 2004; Hu et al. 2011). However, patch area was not a perfect indicator of these parameters in our study, although it was a relatively better indicator than harrier PA for plants and small mammals (Table 1; Fig. 3). These results indicate that it is difficult to extract critical landscape metrics related to species richness, abundance, and community composition of focal taxa (Holland et al. 2004). For example, the key factors affecting species richness, total abundance, and community composition within each plant community may not be related to the extent of wetland vegetation cover (i.e., wetland patch area), but rather the cover of each plant community. Moreover, there may be a difference between vegetation cover and actual available area for small mammals because it is difficult to quantitatively assess submerged area of vegetation cover using aerial photographs and/or satellite images.

Numerous studies have criticized the use of surrogate species to identify areas of high conservation value (e.g., Cabeza et al. 2008), however, our results suggest that this approach can be useful when habitat requirements of surrogate species are similar to those of the focal taxa and when there are ecological reasons for why the PA of surrogate species is an effective indicator of the focal taxa. Therefore, this approach would be more effective than landscape surrogate approaches when there is prior knowledge on the focal taxa, communities, and ecosystems of the area under consideration. On the other hand, several studies have indicated that landscape surrogate approaches are simpler, cheaper, and more useful than surrogate species approaches (e.g., Banks-Leite et al. 2011; Barton et al. 2014). Our results also show that the overall performance of patch area for multiple taxa is higher than that of the presence/absence of harrier. In addition, if more complicated landscape metrics other than patch area (e.g., connectivity, habitat shape, and habitat amounts) are incorporated, the performance of landscape surrogate approaches may be improved. A number of studies have successfully modeled species distribution over various taxonomic groups using multiple landscape metrics (e.g., Oja et al. 2005; Goetz et al. 2010). Therefore, landscape surrogates may be more effective when there is not enough knowledge on the relationships between surrogate species and focal taxa (Ferrier 2002). Alternatively, because species and landscape surrogates are not mutually exclusive, the combination of these two surrogates is a promising option that may deliver more effective conservation

output across multiple taxonomic groups rather than focusing on a single surrogate (Di
Minin and Moilanen 2014). For example, in our study area, although a single surrogate
approach (i.e., harrier PA or Patch area) was effective at protecting a particular
taxonomic group (Table 1; Figs 2 and 3), prioritizing larger wetland patches with
harriers was the most practical and effective strategy for conserving many wetland
species across multiple taxonomic groups. However, variation in such combination
approaches is rarely tested and needs further work.

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496 **Table**

497 **Table 1** Parameters (β) and unconditional SE in each averaged models. Unselected
 498 parameters in each averaged model are not shown. Single and double asterisks indicate
 499 marginal significance ($p < 0.10$) and significance ($p < 0.05$), respectively.

500

Response variable	Variables	β	SE	p
Birds				
Species richness	Intercept	1.78	0.11	< 0.001**
	Presence of raptor	0.32	0.14	0.02**
Abundance	Intercept	3.06	0.06	< 0.001**
	Presence of raptor	0.26	0.07	< 0.001**
Composition_PC1 ^a	Intercept	-0.66	0.36	0.08*
	Presence of raptor	1.31	0.51	0.02**
Composition_PC2 ^b	Intercept	0.56	0.36	0.13
	Presence of raptor	-1.12	0.51	0.04**
Plants				
Reed community				
Species richness	Intercept	1.83	0.18	< 0.001**
	Patch area	0.15	0.07	0.03**
Composition_PC1 ^a	Intercept	-0.29	0.81	0.72
	Presence of raptor	1.49	1.21	0.24
Composition_PC2 ^b	Intercept	-1.40	1.51	0.36
	Patch area	0.89	0.48	0.08*
Sedge community				
Species richness	Intercept	2.48	0.20	< 0.001**
	Presence of raptor	-0.21	0.12	0.11
	Patch area	0.10	0.07	0.21
Composition_PC1 ^a	Intercept	-0.71	1.07	0.52
	Presence of raptor	2.20	1.28	0.10
Composition_PC2 ^b	Intercept	-1.03	1.80	0.58
	Patch area	0.90	0.66	0.20
Rush community				
Species richness	Intercept	2.16	0.31	< 0.001**
	Patch area	0.18	0.08	0.047**
Composition_PC1 ^a	Intercept	2.90	3.28	0.40
	Patch area	-1.83	0.93	0.08*

Composition_PC2 ^b	Intercept	0.43	1.04	0.70
	Presence of raptor	-2.44	1.56	0.16
Small-mammals				
Species richness	Intercept	0.87	0.39	< 0.05**
	Patch area	-0.17	0.20	0.44
Abundance	Intercept	2.78	0.36	< 0.001**
	Patch area	-0.43	0.14	< 0.01**
Composition_PC1 ^a	Intercept	-0.23	0.68	0.75
	Patch area	0.30	0.34	0.41
Composition_PC2 ^b	Intercept	0.51	0.86	0.57
	Patch area	-0.44	0.32	0.19

^a Axis 1 by principal component analysis. ^b Axis 2 by principal component analysis.

Figure captions

Fig. 1

Map of wetland patches (*green*) in Hokkaido, northern Japan.

Fig. 2

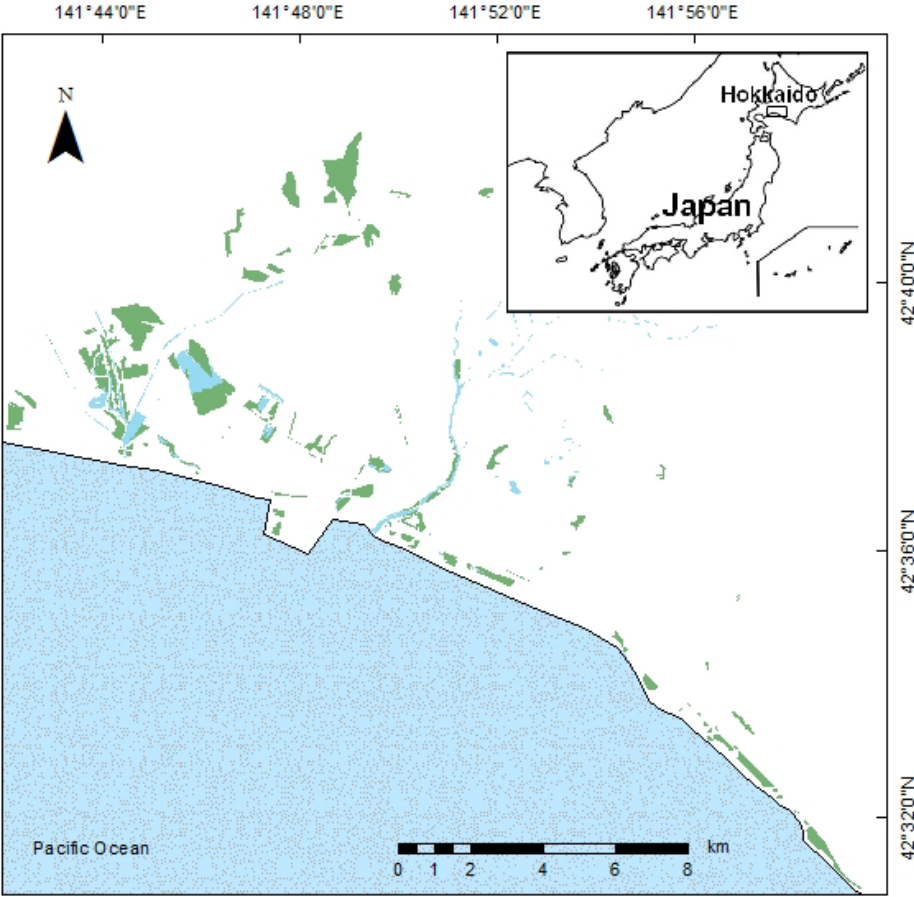
Association of harrier PA (presence/absence of the marsh harrier) with (a) species richness, total abundance, and the first two axes of the PCA of wetland birds, (b) species richness and the first two axes of the PCA of the wetland plants, and (c) species richness, total abundance, and the first two axes of the PCA of wetland small mammals. Asterisks indicate significance below 5%.

Fig. 3

Association of patch area with (a) species richness, total abundance, and the first two axes of the PCA of wetland birds, (b) species richness and the first two axes of the PCA of the wetland plants, and (c) species richness, total abundance, and the first two axes of the PCA of wetland small mammals. Solid and dashed lines indicate significance below 5 and 10%, respectively.

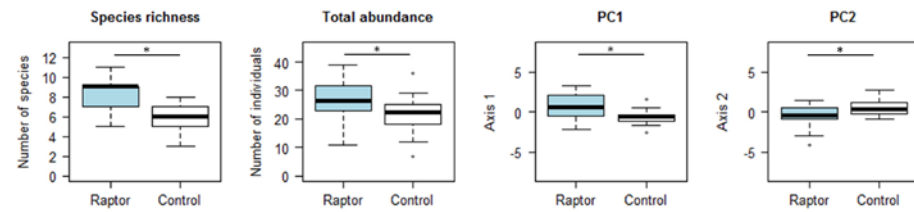
Figures

Figure. 1

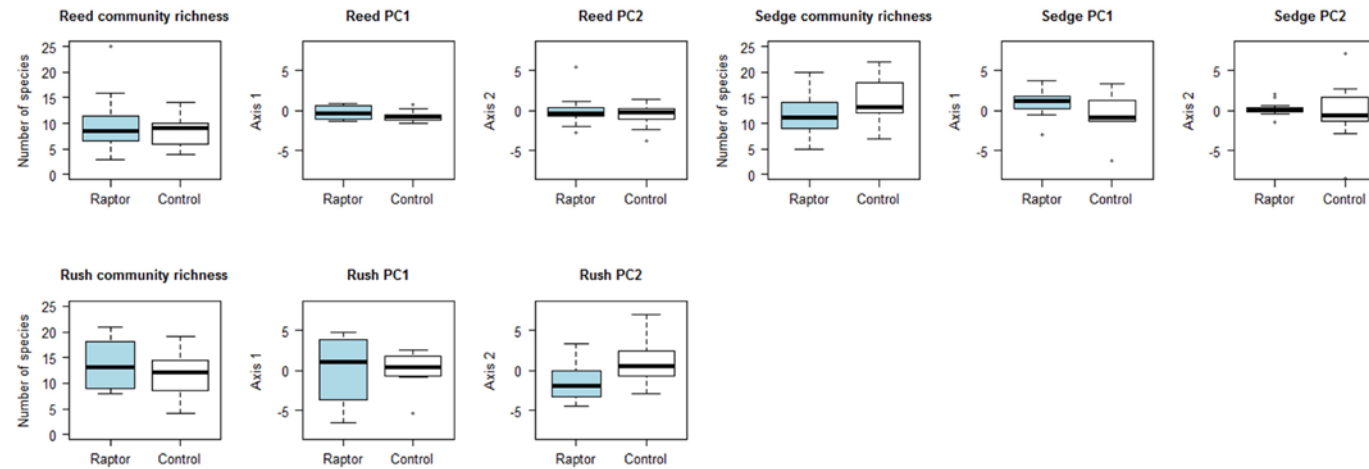


529 Figure 2

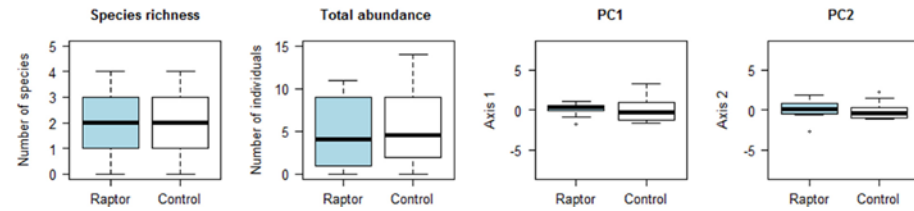
a) Wetland Birds



b) Wetland Plants



c) Wetland Small-mammals

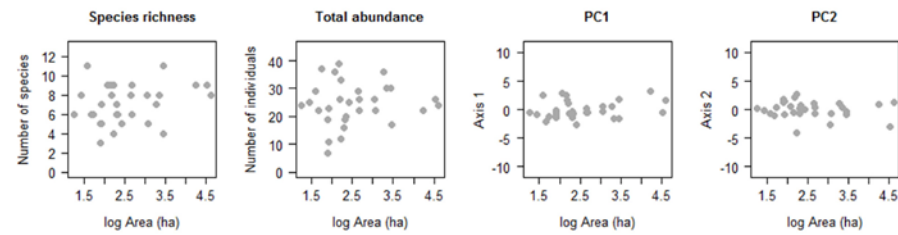


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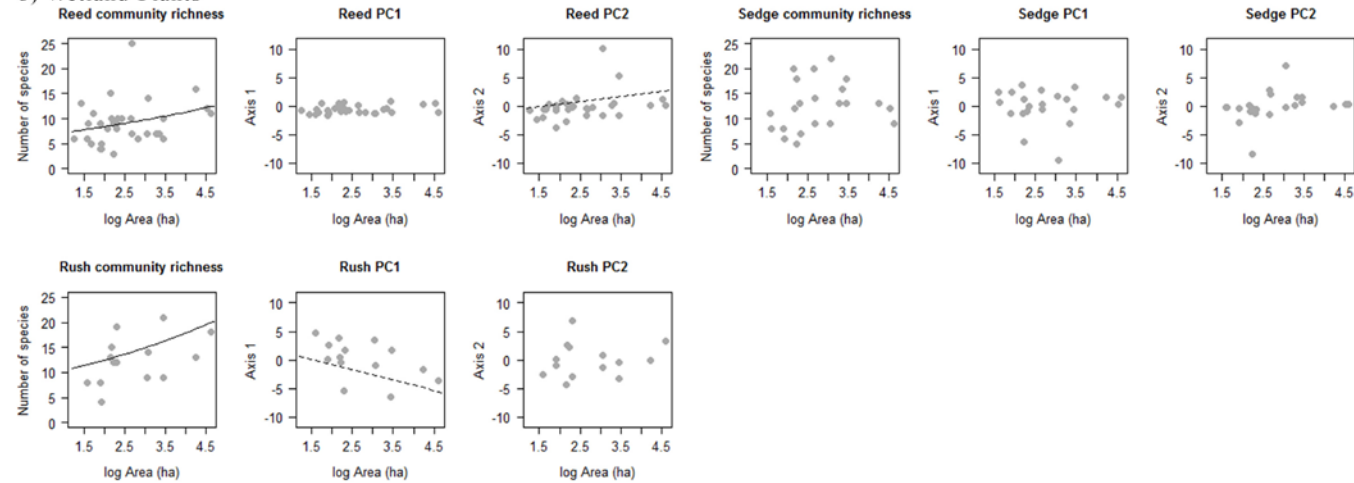
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532 Figure 3

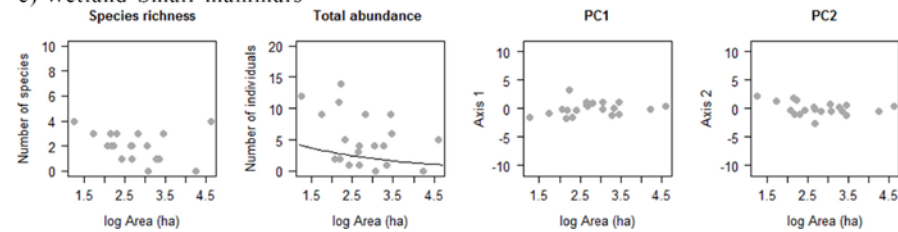
a) Wetland Birds



b) Wetland Plants



c) Wetland Small-mammals



Appendices

Table 2 Results of Pearson's correlation tests. Asterisks show significant correlations: * - $P\text{-value} < 0.05$; ** - $P\text{-value} < 0.01$.

a) Birds

	Bird_richness	Bird_abundance
Bird_abundance	0.64*	
Bird_PC1	0.67**	0.37*
Bird_PC2	-0.40*	-0.35

b) Plants

Reed		Sedge		Rush	
	Reed_richness		Sedge_richness		Rush_richness
Reed_PC1	0.72**	Sedge_PC1	-0.39	Rush_PC1	-0.82**
Reed_PC2	-0.17	Sedge_PC2	-0.23	Rush_PC2	-0.01

c) Small-mammals

	Mammal_richness	Mammal_abundance
Mammal_abundance	0.70**	
Mammal_PC1	-0.15	0.12
Mammal_PC2	0.36	0.64**

538 **Table 3** Results of model selection. "Weight" indicates "Akaike weight".

Response variable	Variablr	Rank	ΔAIC_c	Weight
Birds				
Species richness	Raptor	1	0.00	0.62
	Raptor + Patch	2	2.34	0.19
		3	3.17	0.13
	Patch	4	4.44	0.07
Abundance	Raptor	1	0.00	0.76
	Raptor + Patch	2	2.35	0.23
		3	9.53	0.01
	Patch	4	11.45	0.00
Composition_PC1a	Raptor	1	0	0.65
	Raptor + Patch	2	2.31	0.20
		3	3.91	0.09
	Patch	4	4.91	0.06
Composition_PC2b	Raptor	1	0	0.59
		2	2.31	0.19
	Raptor + Patch	3	2.64	0.16
	Patch	4	4.2	0.07
Plants				
Reed community				
Species richness	Patch	1	0.00	0.55
	Raptor + Patch	2	2.01	0.20
		3	2.54	0.15
	Raptor	4	3.45	0.10
Composition_PC1a		1	0	0.46
	Raptor	2	0.86	0.30
	Patch	3	2.24	0.15
	Raptor + Patch	4	3.45	0.08
Composition_PC2b	Patch	1	0	0.47
		2	1.01	0.29
	Raptor + Patch	3	2.22	0.16
	Raptor	4	3.42	0.09
Sedge community				
Species richness	Raptor	1	0.00	0.30

		2	0.11	0.29
	Raptor + Patch	3	0.44	0.24
	Patch	4	1.24	0.16
Composition_PC1a	Raptor	1	0	0.44
		2	0.36	0.37
	Raptor + Patch	3	2.97	0.10
	Patch	4	3.05	0.10
Composition_PC2b		1	0	0.47
	Patch	2	0.73	0.33
	Raptor	3	2.52	0.13
	Raptor + Patch	4	3.72	0.07
Rush community				
Species richness	Patch	1	0	0.58
		2	1.97	0.22
	Raptor + Patch	3	3.3	0.11
	Raptor	4	3.59	0.10
Composition_PC1a	Patch	1	0	0.47
		2	0.61	0.35
	Raptor + Patch	3	2.88	0.11
	Raptor	4	3.92	0.07
Composition_PC2b		1	0.00	0.45
	Raptor	2	0.69	0.32
	Raptor + Patch	3	2.42	0.13
	Patch	4	3.01	0.10
Small-mammals				
Species richness		1	0.00	0.56
	Patch	2	1.80	0.23
	Raptor	3	2.48	0.16
	Raptor + Patch	4	4.54	0.06
Abundance	Patch	1	0.00	0.78
	Raptor + Patch	2	2.75	0.20
		3	8.32	0.01
	Raptor	4	9.82	0.01
Composition_PC1a		1	0	0.58
	Patch	2	1.95	0.22

	Raptor	3	2.71	0.15
	Raptor + Patch	4	5.11	0.045
Composition_PC2b		1	0	0.47
	Patch	2	0.71	0.33
	Raptor	3	2.77	0.12
	Raptor + Patch	4	3.52	0.081

539 ^a Axis 1 by principal component analysis. ^b Axis 2 by principal component analysis.

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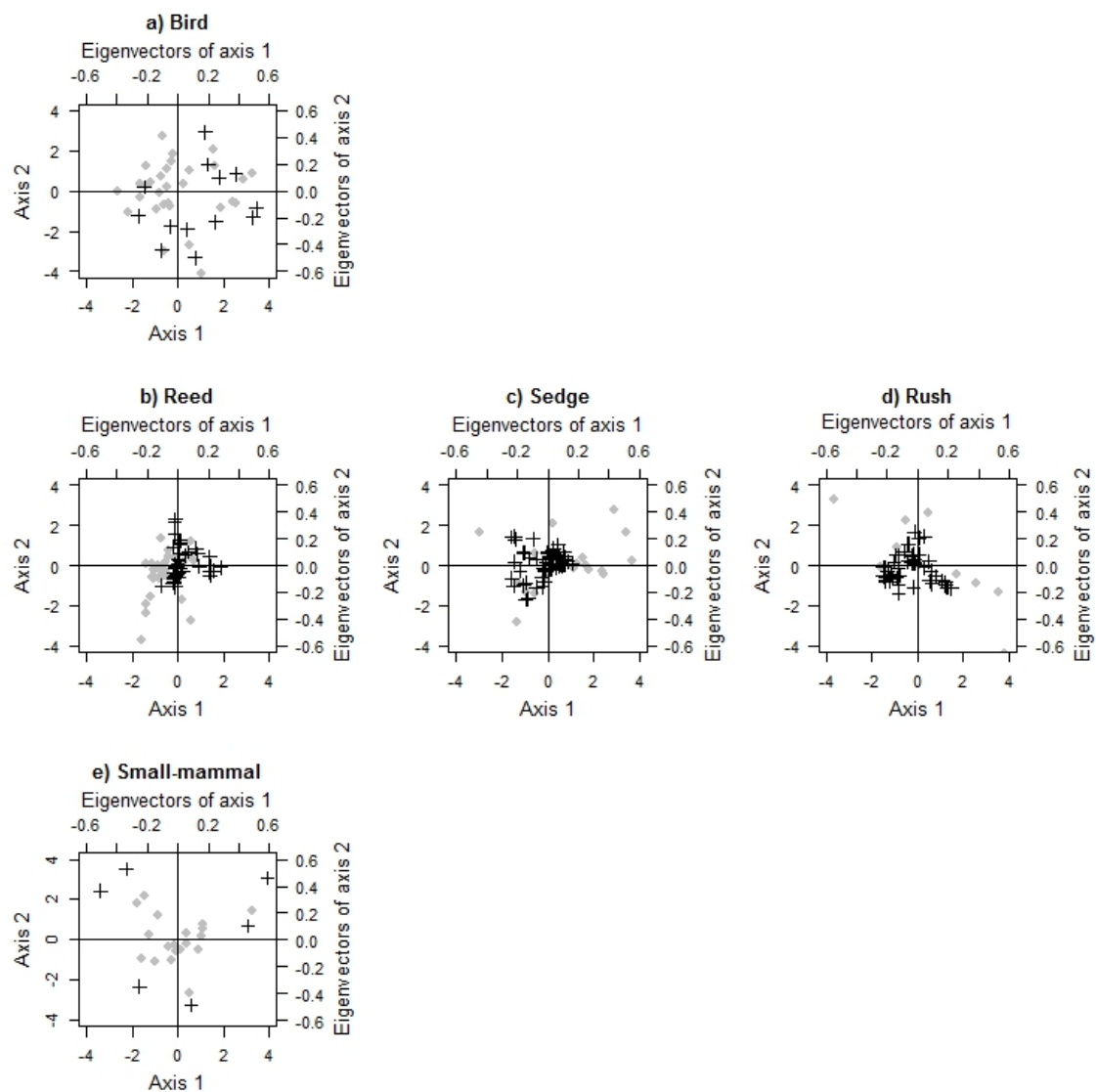


Fig. 4

Results of principal components analysis (PCA). The grey circles indicate site scores and plus signs the eigenvector of each species.

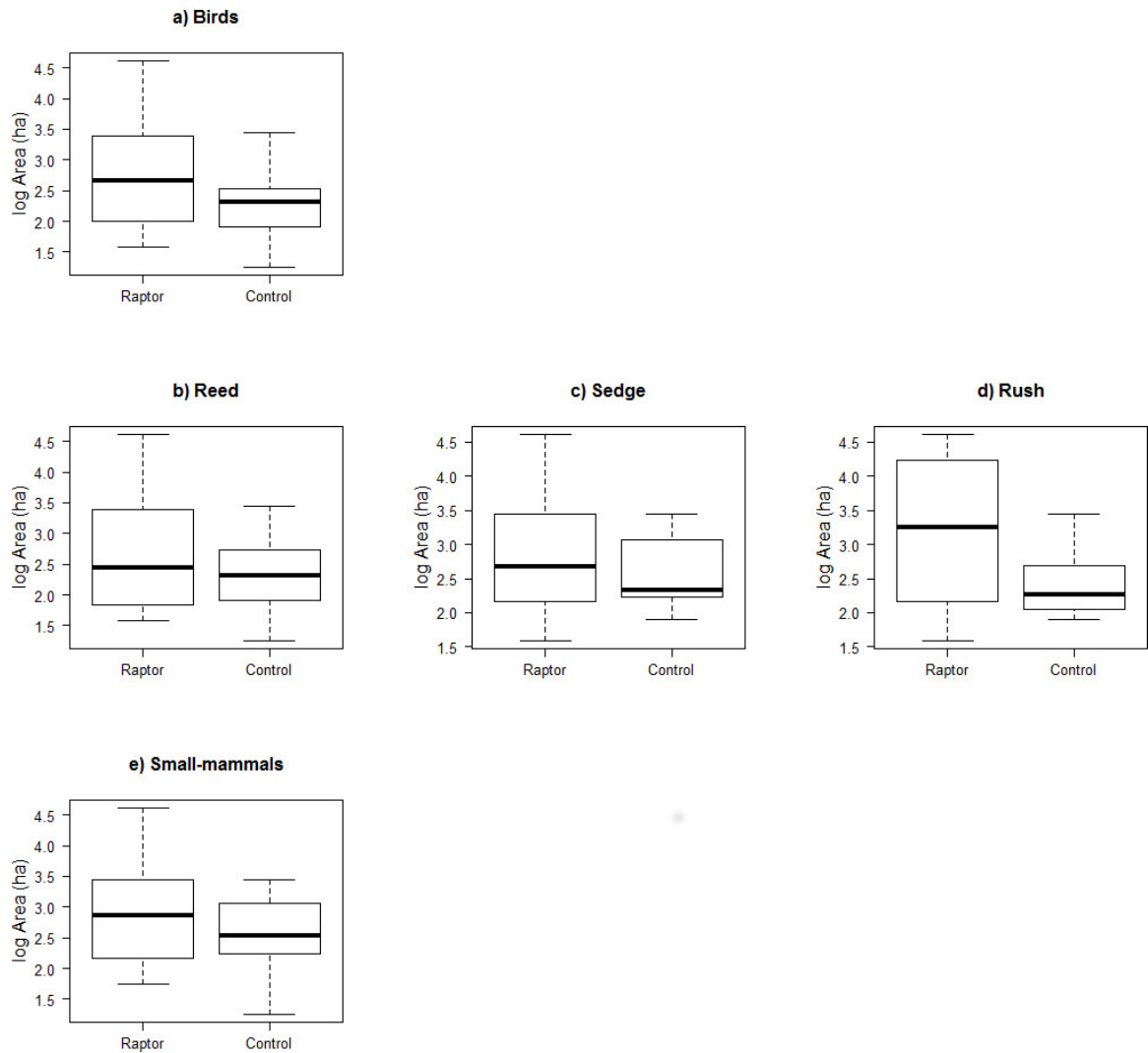


Fig. 5

Relationships between the harrier PA and the log-transformed patch area (ha) for birds, plants (reed, sedge, and rush communities), and small mammals.