LINKING RAPTORS AND BIODIVERSITY;

ecological rationale and conservation relevance

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I Byholm, P., Burgas, D., Virtanen, T., & Valkama, J. (2012). ***Competitive exclusion within the predator community influences the distribution of a threatened prey species.*** *Ecology*, 93: 1802–1808.

II Burgas, D., Blanchet, G., Ovaskainen, O., & Byholm, P. (Manuscript). ***The fading ghost of the vanishing hawk: raptors shaping bird communities in space and time.***

III Burgas, D., Byholm, P. & Parkkima, T. (2014). ***Raptors as surrogates of biodiversity along a landscape gradient***. *Journal of Applied Ecology*, 51: 786–794

IV Burgas, D., Juutinen, A., Byholm, P. (Manuscript). **Cost-efficiency of protecting raptor nest sites to preserve further biodiversity.**

Table of contributions

	I	II	III	IV
Original idea	PB	PB	PB	PB
Study design	PB, DB	PB	PB, DB	PB, DB
Empirical data	DB, PB, JV	PB	DB, TP, PB	DB, PB
Analyses	PB, DB, TV	DB, GB, OO	DB	DB, AJ, PB
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AJ = Artti Juutinen, DB = Daniel Burgas, GB = F. Guillaume Blanchet, JV = Jari Valkama, OO = Otso Ovaskainen, PB = Patrik Byholm, TP = Tiina Parkkima, TV = Tarmo Virtanen

ABSTRACT

Under the current biodiversity crisis, there is the need to improve the conservation action. More areas need to be protected to curb biodiversity loss. Also, the methods for selection of both protected areas and management practices have to be well-informed in order to maximise the benefits from the limited resources allocated for conservation. However, because of limited information, decision making procedures are forced to use environmental variables and different species as surrogates of general biodiversity. Moreover, there is a bias towards charismatic and better known species like top predators. It is therefore important to forecast the consequences that favouring certain species might have on other organisms and to evaluate the effectiveness of preserving a subset of species.

In this thesis I use empirical data to investigate how avian predators (the Northern Goshawk *Accipiter gentilis* and the Ural Owl *Strix uralensis*) associate to biodiversity. The focus is two-fold; First, I investigate the role of species interactions in dictating biodiversity patterns. I show that interactions within the predator assembly can have stronger effect on prey distribution (the Siberian Flying Squirrel *Pteromys volans*) than landscape attributes. This finding points out that individuals may be able to respond to changes in the structure of the predator assemblage. Additionally, I examine the impact of the Goshawk altering the structure of the forest bird community. I found that not only the raptor conditioned species distribution across space, but that this effect persisted over the years after the Goshawk abandoned the breeding site.

Second, I evaluate the potential use of raptors as surrogates to indicate areas of relevant conservation value. On the one hand, I address how the two focal raptor species associate to different biodiversity metrics for birds and polypores (i.e. wood decaying fungi) over a landscape gradient. I found that, while both predator species indicated high biodiversity levels as compared to reference sites, the dominant Goshawk was superior to the Ural Owl. Interestingly, the surrogacy properties remained the same even if the environmental setting changed. On the other hand, I assess the value of preserving raptor nest sites in the context of the existing network of protected areas in the study region. I show that using goshawk nest sites is the most cost-efficient approach if considering only single species. However, combining both predator species further enhanced the conservation output.

Concluding, this thesis highlights the idea that avian top predators have a key role on species distributions and shaping community heterogeneity in space and time. Given this disproportionate influence in ecosystems, apex predators might also merit extra conservation commitment. Furthermore, information on the spatial distribution of raptors can indicate, over large areas, locations of disproportional biodiversity value.

I show that setting aside raptor nest sites is more cost-effective than other conservation approaches. Additionally, one has to consider that national-wide monitoring schemes already provide raptor nest locations at no extra cost. In the light of these results it is advisable to consider the use of raptors to complement existing and future reserve selection methods.

1. INTRODUCTION

Spatial patterns in biodiversity have long fascinated ecologists that, accordingly, have put remarkable effort in explaining the reasons behind them. Under the global biodiversity crisis there is nowadays stronger pressure than ever to understand the mechanisms that shape patterns in taxonomic diversity (Westman 1990). This knowledge is critical in order to answer two key questions for conservation endeavours; how to foresee changes in biodiversity and where the species are distributed. For instance, we must be able to better forecast the consequences of global change on the persistence of species —like the increase in novel species interactions after human facilitated dispersal or global warming (Mack and Simberloff 2000) — and to better identify the most relevant areas where the scant conservation resources should be allocated (Cowling et al. 1999, Margules and Pressey 2000).

1.1. Biodiversity surrogates

Conservation practitioners are confronted with the arduous task to decide where to direct conservation efforts and, consequently, also what to give up (Pressey et al. 1993, Margules and Pressey 2000, Moilanen et al. 2011). A major shortcoming in this endeavour is the vast lack of knowledge on species distributions even for the most common species, not to mention the more unknown taxa (Jetz et al. 2012). Conservation scientists are thus compelled to take shortcuts and try to make the best from the available information. These comprise, for instance, remote imagery, expert range maps, modelling population responses to anthropogenic changes and monitoring subsets of species (Lindenmayer et al. 2000, Jetz et al. 2012). The subsets of species that are used by scientists and practitioners to achieve further conservation reach are called surrogate species. Surrogate taxa can be roughly classified in three categories according to their main goal (Caro 2010): (i) those that are used to monitor environmental change (e.g. sentinel species), (ii) those used to raise public awareness (e.g. flagship species) and (iii) those used to locate spots to concentrate conservation (e.g. umbrella species).

Top predators awake admiration and respect. It is therefore not surprising that they are heavily represented within the surrogate species concept. There are several reasons that can justify the use of predators in the task to improve conservation action (see extensive reviews by Sergio et al. 2008, Caro 2010). This can be split in two main questions: whether predators can affect biodiversity (e.g. **I**, **II**) and whether predators are associated in space and time to biodiversity (e.g. **III**, **IV**).

1.2. Predators affecting species distributions

Beyond the obvious fact that food availability is of ultimate necessity for the individual to survive, ecologists started to realize early that interactions between individuals were strong drivers limiting local populations (Lotka 1925). This gradually evolved into the notion that species interactions were actually key mechanisms promoting diversity not only at local but also at regional scales (Gause 1934, Lack 1954, MacArthur 1965, MacArthur and Levins 1967, Ricklefs 1987, Cornell and Lawton 1992, Travis et al. 2005).

Strongly interacting species are expected to have large and disproportionate influence on the distribution and abundance of several other species, with the potential to alter entire ecosystems (Soulé and Estes 2005). With this notion, the keystone species concept (Paine 1966, 1969, Power et al. 1996) has had an enormous impact in ecology. Understandingly, predators have had a central role in this context, primarily because of the negative pressure they impose on prey that, in turn, it allows other organisms to proliferate in the absence of the displaced species (Ripple et al. 2014).

It is commonly accepted that individuals benefit from having the capability to asses habitat quality and therefore species are expected to select the locations that maximize their fitness (Fretwell and Lucas 1969, Rosenzweig 1981, Morris 2003). Because predation has direct implications on an individual's chance to reproduce (Magnhagen 1991), it is not surprising to find an impressive range of anti-predator behaviours among species predated upon (Lima and Dill 1990, Lima and Bednekoff 1999, Caro 2005, Lind 2005). Among those, predator avoidance can be expressed as a cost-efficient anti-predator behaviour where prey species are displaced to patches of often lower relative quality but with lower predation risks (Lind 2005). This requires that individuals recognize the risk of predation something for which we see a wide range of adaptations in the animal realm (Caro 2005). Direct predator recognition (Robinson 1980, Curio 1993, Coss and Ramakrishnan 2000) is most often coupled with awareness of indirect clues left by the predator like scent or predation remains (e.g. Thorson et al. 1998, Forsman et al. 2012) and, maybe most remarkably, by social information obtained from con- and heterospecifics (Conover 1987, Seppänen et al. 2007, Goodale et al. 2010). Several studies have showed the concept of heterospecific attraction (Mönkkönen et al. 1999) as applied to prey seeking shelter under protector species (see reviews by Caro 2005, Quinn and Ueta 2008, Lima 2009). For instance, Bogliani et al. (1999) found that Wood Pigeons *Columba palumbus* L. cluster their nests around active Hobby *Falco subbuteo* L. nests while gaining protection from nest predators. Or Ueta (2001) showed that Azure-winged Magpies *Cyanopica cyana* Pall. aggregate and synchronize their nests with breeding Japanese Sparrowhawks *Accipiter gularis* Temm. Nevertheless, the vast majority of studies investigating heterospecific attraction focus on only pairs of protective-protected species while not accounting for general consequences on the communities (but see e.g. Forsman et al. 2001, **II**).

Given that a species can have a disproportionate role in the community, such species might merit more conservation effort in order to retain its function. There are, however, still several open questions in the concept of keystone species. For instance, the vast majority of studies disregard that keystone species not only facilitate occupancy and proliferation of species protected by the apex predator, but that they can also attract them according to the heterospecific attraction concept. Additionally, avian predators seem to be partially neglected from the concept of keystone species as most of the studies on terrestrial keystone species focus on mammalian carnivores (Sergio et al. 2008a, Caro 2010)

1.3. Use of predators to locate spots of high biodiversity

Historically, conservation planning (i.e. deciding what, where, how and when you protect and manage) has been an arbitrary process performed with limited information and subjectivity and, therefore, preserving less biodiversity than otherwise desired. That can be the case, for instance, when implementing weakly grounded policies (e.g. Svancara et al. 2005, Santangeli et al. 2013), or making decisions based on one or a few, often publicly appealing species (Entwistle and Dunstone 2000, Andelman and Fagan 2000). Nevertheless, a big leap forward has been made with the generalization of systematic conservation were scientifically backed decisions are made in a methodological manner with the help of available objective information (Pressey et al. 1993, Margules and Pressey 2000, Sarkar et al. 2006). As a consequence, algorithms designed to prioritize conservation action nowadays often incorporate several biodiversity aspects with emphasis on environmental features (Margules and Pressey 2000). Nevertheless, it is evident that charismatic surrogate species may have positive implications for preserving biodiversity. For instance, they can divert funds towards conservation (Richardson and Loomis 2009, Smith et al. 2012), make decisions more publicly acceptable (Fischer and Vanderwal 2007) or even render the conservation action more affordable (Santangeli et al. 2012). This is especially true with predators, which gather a remarkable portion of the conservation attention (Sergio et al. 2008a, Smith et al. 2012). On the other hand, it bears no sense to apply equal weight to all species as (i) some species are more threatened than others, (ii) the function they deliver in the ecosystem varies, or (iii) they may be positively correlated with ecosystem properties promoting high biodiversity (e.g. species settling in spots of high productivity). Those notions fit the general attributes of top predators that are (i) often threatened (Ripple et al. 2014), (ii) they may act as keystone species in the ecosystem, and (iii) they benefit from high diversity and abundance of prey (Sinclair et al. 1998) and are usually sensitive to ecosystem dysfunctions (Newton 1979, Crooks 2002, Duffy 2002).

Despite this and the evidence from several empirical studies, the use of surrogate species in conservation is controversial and several open questions remain unanswered (Favreau et al. 2006). As to predators, the evidence both in favour and against their utility to prioritize what to protect is meagre (Sergio et al. 2008a, 2008b). For instance, the northern spotted Owls *Strix occidentalis* Xantus in California were found to co-occur with the high diversity of molluscs and salamanders (Dunk, Zielinski & Welsh 2006). But, while Sergio *et al.* (2006) found that the Northern Goshawk *Accipiter gentilis* L. was a good indicator of local biodiversity in the Italian Alps, Ozaki *et al.* (2006) found no such association among Goshawks studied in Hokkaido, Japan. Or Roth & Weber (2007) in Switzerland and Jenkins *et al.* (2012) in South Africa reported little or no association between raptor presence and biodiversity. Moreover, it is largely unknown what is the surrogacy consistence across space, neither is it well-known to what degree, if any, the surrogate efficiency of dominant species differ from that of subordinate ones in cases when the habitat preference is shared. Also it is disturbingly rare to find studies that effectively assess the efficiency of surrogates from an economical perspective (Roberge and Angelstam 2004, Juutinen and Mönkkönen 2004, Gardner et al. 2008). This clearly sets limitations to practical wider application of the surrogate species concept and can lead to undesired misuse of the scarce resources for conservation.

1.4. Aims and outline of the thesis

The original idea of this thesis was born after witnessing the concerning rate of habitat loss in boreal forests. Given that raptors are widely monitored in Finland as well as in several other countries and against the background discussed above, the general aim was to evaluate the role that avian top predators can tentatively have for conservation action. The aims of this thesis can be organised in three main points:

Firstly, we focused on underlying ecological mechanisms by which avian top predators may alter biodiversity (**I**, **II**). Specifically, we want to shed light on how predators induce changes in species distributions by both displacing their prey (i.e. predator-prey interactions) and by attracting other species that get protection from the predator (i.e. heterospecific attraction). We start by investigating the interplay between predator interactions in shaping prey distribution (**I**). Given that predators can modify other species distributions (both positively and negatively), it is as yet unclear to which extent these links remain when the environmental setting changes. To amend this shortcoming, **Chapter I** addresses how changes in the predator assemblage can alter the distribution of a threatened prey species. Next, we investigate the broader role of raptors at the community level (**II**). While there are several studies addressing predator effects on population dynamics and distribution, those are often based on species-specific cases and mostly concentrate on the predator-prey effect (but see Norrdahl and Korpimäki 1998, Forsman et al. 2001). Also, predatory species are especially sensitive to environmental change and suffer higher levels of extinction threat and, therefore, it is necessary to better understand what the consequences are of losing a top predator from an ecosystem. With this in mind, we set to widen the perspective on how a raptor species can create heterogeneity in the bird community across the space and time.

Secondly, we aim to contribute to the notion of top predators as surrogates of biodiversity (**III, IV**). We analyzed to what extent forest dwelling raptors in the boreal biome associate to areas with prominent biodiversity levels. Additionally, we compared the biodiversity levels in sites occupied by a dominant predator against a subordinated one. In the light of habitat selection (e.g. Rosenzweig 1981; Martin 1998; Clark & Shutler 1999) and species interaction theory (Sutherland 1996) one could expect that the dominant species pre-emptively displaces inferior competitors to suboptimal sites. Furthermore, in order to better generalize the findings, we investigated whether the surrogacy properties remain even when the broader environmental conditions change.

Finally, because the ultimate conservation action is most often budget-constrained, it is needed to assess the cost-efficiency of reserve networks delivered by surrogate taxa (Roberge and Angelstam 2004). In **Chapter IV**, we evaluated the economic value of preserving raptors in conjunction with the existing protected areas and compared it with different conservation strategies. Additionally, we revisited the idea of the dominant and subordinate species to see if the locations to where the subordinate species might be relegated can actually complement the areas protected with the dominant predator.

2. MATERIAL AND METHODS

2.1. Raptor species

We use two forest dwelling raptor species with distinct ecological attributes; the diurnal Northern Goshawk *Accipiter gentilis* L. (**I-IV,** Goshawk hereafter) and the nocturnal Ural Owl *Strix uralensis* Pall. (**II-IV**). Both species are among the most common forest raptor species in Finland and are reasonably well distributed, albeit the Ural Owl is absent in the south-western corner of the country (Valkama et al. 2011). While both species prefer to nest in mature mixed spruce forest, the Goshawk builds its own stick nests whereas the Ural Owl nests in existing tree cavities, nowadays predominantly manmade nest-boxes, or on stick nests build by diurnal raptors (Mikkola 1983, Tornberg et al. 2006). Adults of both species tend to be present nearby their nesting areas around the year, although outside of the breeding season, particularly the Goshawks, expand their range or disperse to areas with more food resources (Mikkola 1983, Tornberg and Colpaert 2001, Kenward 2006, Tornberg et al. 2006). While the Goshawk mainly preys upon middle sized birds, the Ural Owl's diet is chiefly composed of small mammals (Mikkola 1983, Tornberg et al. 2006). The Goshawk is a dominant predator in the Finnish forests shown to kill and displace other predators with smaller body mass (Mikkola 1983, Solonen 1993).

2.2. Study sites

The majority of empirical data for this thesis (**I-IV**) were collected in the region of Suupohja in the west coast of Finland (Figure 1) associated with a long-term monitoring of forest raptors in the region (Byholm et al. 2007, 2011, Byholm and Nikula 2007, Byholm and Kekkonen 2008). The area lies at the border between the southern boreal (in the west, due to sea influence) and the middle-boreal (to the east, inland) vegetation zones. As a result, there is a decrease in the vegetation complexity (and diversity) along the west-east axis (Ahti et al. 1968, Lahti et al. 1988). About 75% of the land is covered by forest, but only c. 0.5% of the study area is covered by forest nature reserves. Field data for **Chapter I** was complemented with Goshawk nests found in the South-West Finland (i.e. Varsinais-Suomi) where the Goshawk, but not the Ural Owl, occurs.

2.3. Sampling design and empirical data

To investigate the effect of the raptor assemblage on local prey distribution (**I**), we focussed on the spatial association of the nationally threatened Siberian Flying Squirrel *Pteromys volans* L. (Rassi et al. 2010; hereafter, Flying Squirrel) to both raptors. We

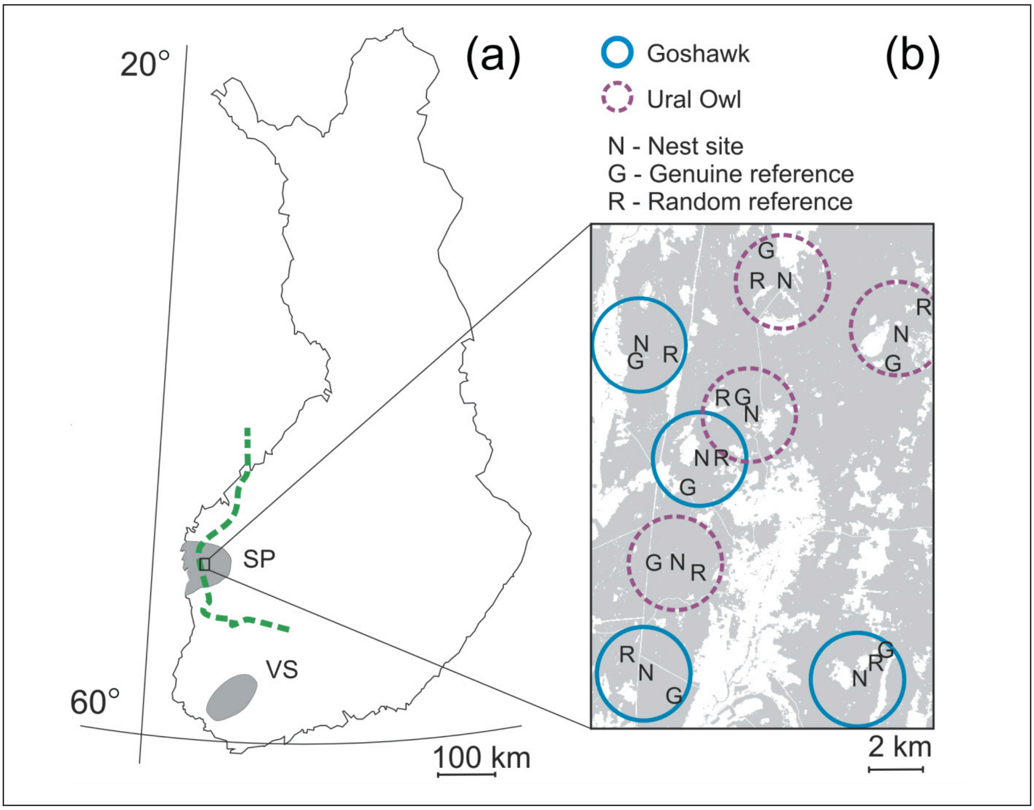

Figure 1. (a) Map of Finland with the study areas Suupohja (SP) and Varsinais-Suomi (VS) in grey and the border between the south- and midboreal vegetation zones (dashed line) indicated, and **(b)** detailed view of a part of the SP-study area showing Goshawk (solid blue circles) and Ural Owl (dashed purple circles) territory-clusters (r = 2 km) containing the tree different types of sampling plots; nest site (N), genuine reference (G) and random reference (R). Grey shade stands for forest habitats, white shade for open habitats (se methods for further details).

systematically surveyed for occurrence of Flying Squirrel within 150 m from 30 Goshawk and 35 Ural Owl nests in the Suupohja region. Flying Squirrel droppings were used as a proxy for its presence (e.g. Reunanen et al. 2002). Every nest had two distinct reference plots assigned to it: a genuine reference and a random reference. Both types of reference plots were always located on mineral soil characterized by forest vegetation, but, while the random references were scattered in any kind of forest habitat of any age and type, including clear-cuts and plantations, the genuine references were subjectively located to forest stands of the same size and with the same stand structure (tree age, tree species composition, percent canopy cover) as the nest sites. To account for the absence of a key predator on local distribution of the Flying Squirrel we further sampled Flying Squirrel occurrence in the Varsinais-Suomi region, where the Ural Owl is absent. Additionally, we include remotely obtained data to further investigate the effect of habitat attributes on Flying Squirrel distribution besides the predator influence.

In order to study the effect that the Goshawk has in shaping the bird assemblage (**II**), birds were recorded at 50, 250 and 500 m from Goshawk nests at the four cardinal directions making a total of 12 sampling locations clustered around each nest. To account for habitat effects, information on habitat cover at each sample plot was recorded. 29 occupied and 30 empty Goshawk nests were used in this study totalling 708 sample plots.

The same sample design from **Chapter I** (i.e. raptor nest sites and associated genuine and random references) was used to evaluate the spatial correlation of predators with biodiversity and their efficiency as biodiversity surrogates (**III**, **IV**). For that purpose two taxa were surveyed, birds and polypores (i.e. wood-decaying fungi). These species groups were chosen because they are good and established indicators of ecological value in the boreal forest (e.g. Kotiranta and Niemelä 1996, Virkkala and Rajasärkkä 2007). Birds were mapped within 250 m from the centre of the plots and polypores within 100 m. Moreover, for **Chapter IV,** existing protected areas were sampled in the same manner to compare the efficiency of the conservation criteria used hitherto as to the one otherwise delivered by the raptors or alternatively by reference sites. To be able to conduct the cost-efficiency analyses in **Chapter IV**, volumes of wood (m^3) were calculated for each forest stand within 250 m from the centre of every sample site based on data collected in the field. Cost of protection was calculated with the additive-value method (Oksanen-Peltola 1994) which is commonly used by Finnish regional Forest Centres and Environmental Centres.

2.4. Analyses

The main analyses in this thesis can be broadly organized in two categories. On the one hand, **Chapters I-III** are mainly based on different types of regression models. Because the sample sites were clustered around the raptor nests we used hierarchical models to account for spatial autocorrelation. In **Chapter I** we modelled occurrence of Flying Squirrel with Generalized Linear Mixed Models (Zuur et al. 2009) in relation to habitat and species identity. Additionally we compared occurrence patterns of the flying squirrel associated to the Goshawk between an area where the Ural Owl is present and where it is missing. In **Chapter II**, we used a Bayesian community model (adapted from Ovaskainen and Soininen 2011) to simultaneously fit bird abundance data from forest-dwelling bird species in relation to the Goshawk presence and distance from the nest while accounting for habitat effects. We used the community model to evaluate the change in community similarity over time and space. In **Chapter III** we used Bayesian inference to investigate the spatial association of different biodiversity metrics (i.e. species richness and abundance) for birds and polypores to the Goshawk and the Ural Owl. On the other hand, in **Chapter IV** we use numeric optimization models to compare the reserve selection strategies based on raptors with that of alternative approaches as well as to the existing protected areas. We maximized cost efficiency while accounting for complementarity among sites.

3. RESULTS AND DISCUSSION

3.1. Raptors affecting species distributions

Among studies investigating species distributions, the role that species interactions play in habitat selection has received little attention. This thesis highlights that predators can have both profound negative and positive effects shaping distribution patterns on other taxa (**I**, **II**). In **Chapter I**, while reference sites between Goshawk and Ural Owl had equal probability of hosting Flying Squirrels, the Flying Squirrel was nearly eight times more likely to be found at Goshawk nests sites than at Ural Owl nest sites (Figure 2a) in Suupohja, the region in which both predators co-occur. Given that habitat composition explaining the Flying Squirrel distribution was similar between nest sites of both raptor species, our results suggest that site selection based on presence of other species can override that based on physical habitat features (**I**). Additionally, in a natural experimental setting, we found that in Varsinais-Suomi where the Ural Owl is not part of the predator assembly, Flying Squirrels did not associate with the Goshawk (Figure 2b, **I**). This confirms that the way species are distributed is also conditional on the community setting in a flexible process that takes place at the individual level (Nathan et al. 2008).

Chapter II expands the scope, from a single case species to assess the impact that the Goshawk had on the forest bird assemblage. The bird community similarity gradually decreased during the years after the Goshawk had abandoned a nesting site (Figure 3), reinforcing the idea that predators can have a key role in the ecosystem (Ripple et al. 2014).

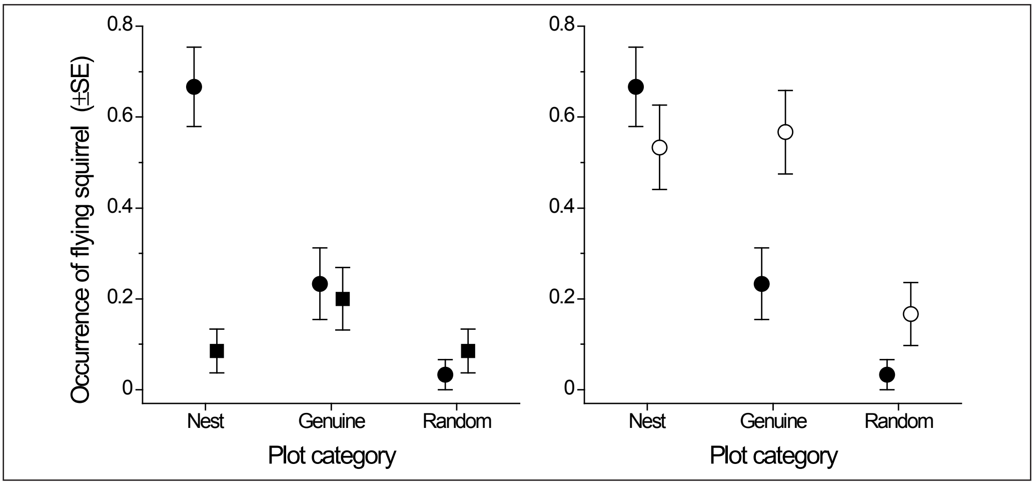

Figure 2. Probability (± SE) for flying-squirrels to occur in the three types of sampling plots in **(left)** relation to predator identity (Goshawk: black circles; Ural Owl: black squares), and **(right)** as compared between regions with different predator-community structure (black circles, both Goshawks and Ural Owls present; hollow circles, only Goshawks present).

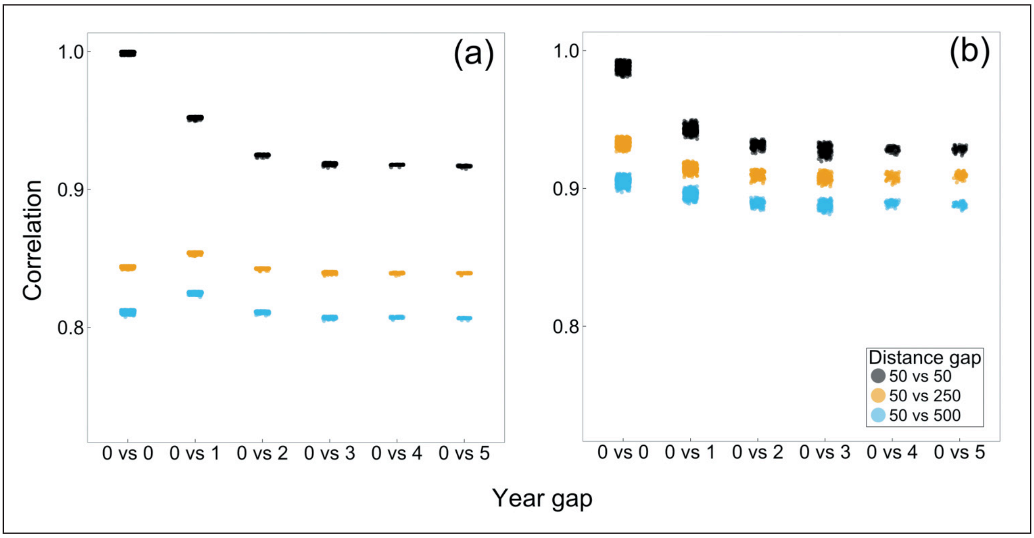

Figure 3. Change in community similarity for the prey assemblage **(a)** and for the non-prey assemblage **(b)** when moving away from the Goshawk nest and after a number of years after the Goshawk abandoned the nest. Habitat was set to the average value over the sample sites. We use as reference the sites at 50 m from the nest when the Goshawk was present (i.e. $T = 0$).

Moreover, this indicates that the effect that single species have on the habitat selection by other species may persist long after the keystone species has disappeared. To the best of our knowledge, this memory effect in response to other species interactions has been overlooked. It resembles, however, other findings pointing out that species occurrence after habitat perturbations (e.g. wild fires) can be partly explained by past habitat attributes (Knick and Rotenberry 2000) or the extinction debt concept, where species gradually perish years after habitat has been lost (Tilman et al. 1994, Hanski and Ovaskainen 2002, Kuussaari et al. 2009). We see two main reasons explaining this delay to adjust to non-Goshawk conditions by the bird assemblage. On the one hand, the tendency of many bird species to be philopatric; returning to breed where they bred previously or where they were born (Greenwood and Harvey 1982) may partly counterbalance the site selection based on up-to-date conditions. On the other hand, as several species are known to use indirect clues to assess other species presence (Thorson et al. 1998, Forsman et al. 2012), it is likely that the Goshawk nests or other cues remain as an indicator of the Goshawk presence even several years after the hawk has disappeared.

The impact that the Goshawk presence had on the bird assembly was, not surprisingly, more acute closer to the Goshawk nest (Figure 3). This is in line with other studies investigating the effect of raptors on other birds across space (Forsman and Mönkkönen 1998, Forsman et al. 2001, Thomson et al. 2006a) and underlines the relevance that predators have in creating heterogeneity across the landscape (Thomson et al. 2006b). Given the fact that structural features or small patches of scarce habitats promote diversity at the landscape scale (Davidar et al. 2001, Gibbons and Lindenmayer 2008, Timonen et

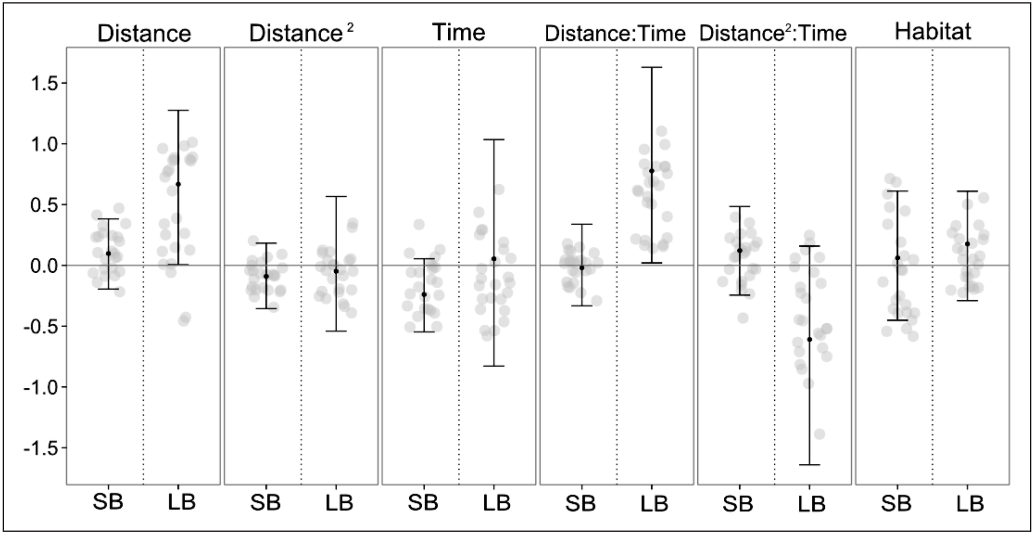

Figure 4. Mean assemblage responses (i.e. regression parameters) to the model covariates with 95% credibility intervals separately for the model with small species (SB) and with large species (LB). Note that, due to parameterization for time, positive parameter values for the time elements mean that the effect decreases with time. Species-specific mean estimates are represented with grey dots.

al. 2010), one might argue that heterogeneity delivered by predators could also promote biodiversity. However, further research should validate or contrast this idea.

Large predators are known to facilitate food resources to other species (Wilmers et al. 2003). However, in our studies we see two mechanisms, closely related under the risk of predation, by which species distributions are conditional on the predator presence. On the one hand, species that have high risk of predation by the focal predator are expected to avoid it (Lima and Dill 1990, Lima and Bednekoff 1999, Caro 2005). This is supported by the low occurrence of flying squirrels around Ural Owl nests (Figure 2, **I**), or the increase in numbers of large sized birds (i.e. preferred Goshawk prey) during the years after the Goshawk abandons the nest and as one moves away from the nest (Figure 4, **II**). Alternatively, as top predators can displace other subordinate predators they can act as protector species. Interestingly, although the Goshawk occasionally predates upon the Flying Squirrel (Selonen et al. 2010), the protection benefit that the squirrel receives against the Ural Owl appears to be enough to justify the spatial association with the Goshawk (see also Morosinotto et al. 2010). Among birds, some species of small sized birds were more common in the proximity of the occupied Goshawk nests and became scarcer during the years after the nest was abandoned. This suggests that some species may actively choose to breed in the proximity of the hawk and, therefore, supporting the heterospecific attraction hypothesis (Mönkkönen et al. 1999, Haemig 2001, Caro 2005, Lima 2009). However, this was not the general pattern for small bird species (Figure 4, **II**). Abundance of several species of small birds peaked at intermediate distances from the raptor nest or even showed a pattern more typical of large bird species. Thus, pointing

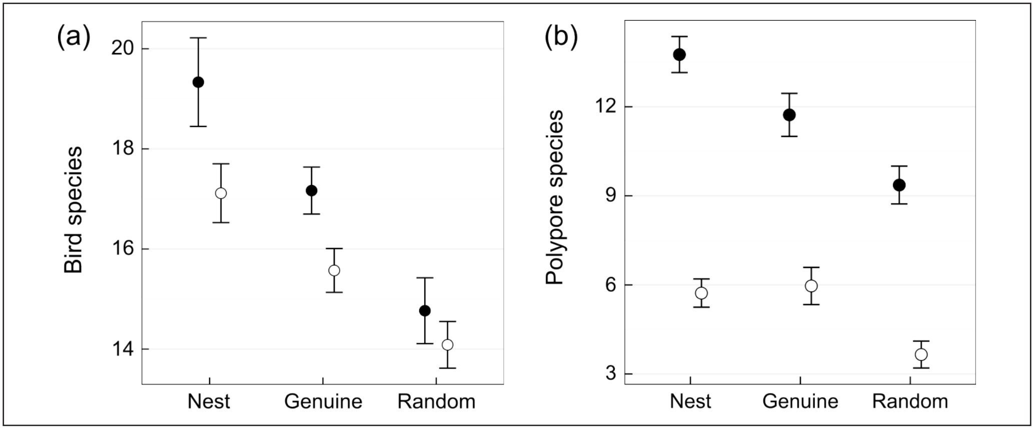

Figure 5. Number of recorded species (mean ±SE) in Goshawk (black circles) and Ural Owl clusters (hollow circles) for **(a)** birds and for **(b)** polypores.

towards avoidance of the Goshawk even when these small birds were unlikely to be hunted. This result contrasts with findings from other studies (Norrdahl and Korpimäki 1998, Mönkkönen et al. 2007). There are two main reasons that can justify this deviation from our expectations. First, it might be that the raptor attracts some smaller species of mesopredators (Morosinotto et al. 2012). This is in practice the case of the Great Spotted Woodpecker *Dendrocopos major* L., an opportunistic nest predator (Walankiewicz 2002), which was found to be associated to the Goshawk presence. Second, it is possible that some species are not entirely able to discern the Goshawk from the similar Sparrowhawk *Accipiter nisus* L., a predator specialized on small birds, and consequently fail to assess the real risk to be predated by the Goshawk.

3.2. Raptors to locate high biodiversity sites

When investigating the spatial relation of raptors with biodiversity metrics (**III**), both raptors showed to be associated to high biodiversity values (i.e. abundance and species richness, plus abundance and species richness of species of conservation concern). The Goshawk, however, performed better than the Ural Owl (Figure 5); Goshawk nest sites hosted higher biodiversity for both birds and polypores as compared to both genuine and random references. On the other hand, the Ural Owl nest sites were only better than both reference types with regards to bird biodiversity, whereas nest sites outperformed random references on polypore biodiversity but did not surmount genuine references. These results are in line with the findings reported by Sergio et al. (2006)top vertebrate predators have frequently been used as flagship or umbrella species to acquire financial support, raise environmental awareness and plan systems of protected areas. However, some have claimed that the utilization of charismatic predators may divert a disproportionate amount of funding to a few glamorous species without delivering broader biodiversity benefits, an accusation aggravated by the fact that the conservation of top predators

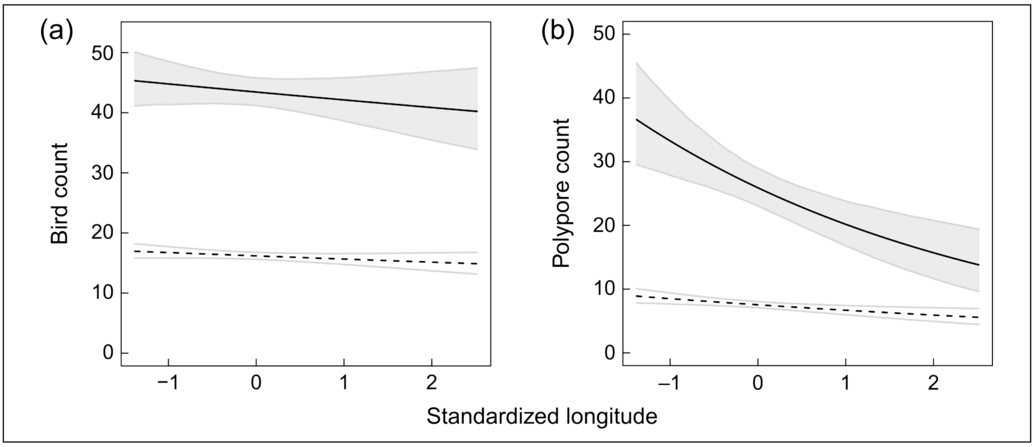

Figure 6. Change in average biodiversity and 95% credible intervals along the west–east gradient within the study area drawn from the posterior distributions for abundance (continuous line, grey shade) and species richness (broken line, white shade) separately for **(a)** birds and for **(b)** polypores.

is often complex, difficult and expensive. Therefore, tests are needed of whether apex predators may be employed to achieve ecosystem-level targets.2To test such a hypothesis, we compared the biodiversity values recorded at the breeding sites of six raptor species, differing widely in diet and habitat associations, with those observed at three types of control locations, (i and Martín and Ferrer (2013), adding further evidence that raptors could be used as surrogates of biodiversity. These findings oppose to few studies were raptors did not perform well as surrogates or, at least, not better than other taxa (Ozaki et al. 2006, Roth and Weber 2007, Jenkins et al. 2012). One potential cause of the mismatch between the biodiversity and the surrogate species previously reported may relate to the scale at which the surrogate is evaluated. Because habitat selection is typically more accurate at the nest stand level than further away (Johnson 1980, Penteriani et al. 2001, Fuller 2012), it is expected that using coarse scale data on the surrogates can dilute their efficiency. Thus, it is advisable to use fine scale data whenever it is available and scale up to investigate the extent of the surrogacy properties (Favreau et al. 2006).

The difference in surrogacy performance between both raptor species underlines the variation among surrogate species belonging to the same guild and presenting same habitat preference (here mixed spruce forest). There are two main reasons that can explain such differences. Given the fact that the Ural Owl does not build its own nests, one could expect that the species should be less demanding on the nest location habitat. Additionally, interspecific competition for the preferred nesting stands can result in the subordinate species (here the Ural Owl) occupying suboptimal and less diverse locations (Bosakowski et al. 1992, Kruger 2002).

The biodiversity metrics decreased along with a shift in vegetation complexity from the coast inland (Figure 6, **III**). Despite this decrease, both the Goshawk and the Ural Owl retained their association with diversity along the vegetation and biodiversity gradient. This shows that both raptor species select forest patches hosting more biodiversity than on average from those locally available irrespective of the biodiversity changes due to biogeographically reasons. Because validation of surrogate species is necessary, similar approaches challenging species of interest across gradients in the landscape can help to assess robustness and generalization of the surrogacy properties over large areas.

3.3. Cost-efficiency of using raptors as surrogates

When designing conservation networks under a cost-efficient scope and restricted to a low budget, it might be optimal to focus on more affordable sites (Juutinen et al. 2004). However, **Chapter IV** shows that protecting the cheaper random references still remained as the least advisable approach to complement existing protected areas even though they represented a higher diversity of habitats (Figure 7). The cost-efficiency analyses strengthen previous findings on spatial correlations of the raptors and biodiversity in which the Goshawk outperformed its references as well as to the Ural Owl (**III**). Additionally, one must note that we did not consider inventory costs in this study (Juutinen and Mönkkönen 2004). Because of their charisma, raptors are widely monitored by volunteers and institutions that submit information on raptor nest location to centralized databases (Saurola 2008). Therefore, information on raptor locations is more easily available and cheaper to extract than locating other potential sites (Martín and Ferrer 2013). Consequently, our results underestimate the economic performance of the raptors as surrogate species.

The use of a combination of surrogate species has been promoted under the rationale that, combined, several surrogates embrace further biodiversity than a single species. Multiple species would necessarily comprise a wider range of habitats and ecological requirements (e.g. McKenzie et al. 1989; Lambeck 1997). The conservation approach that was making use of both raptor nest sites together, performed better than the conservation approaches using the reference sites (Figure 7c). The difference was greater than when using single species approaches (Figure 7a, b). This is a reflection of complementarity between both raptor species and indicates that there is slight habitat segregation between the dominant Goshawk and the subordinate Ural Owl (Mikkola 1983, Solonen 1993). One can thus argue that using competing species can be a good strategy if aiming to maximize conservation of a certain habitat, as those would cover larger range of the within-habitat variation.

Existing protected areas hosted higher proportion of species not recorded elsewhere (especially true for polypores) and also represented an important share of the selected sites in all reserve selection models (particularly at lower budgets). This is not surprising as the protected areas comprise a wider variety of more unique habitats and have not been managed for longer. Yet, the number of Goshawk nest sites selected could equal and exceed the number of protected areas. It is likely that after more notorious and obvious sites were selected, the unsystematic conservation used hitherto has rendered the existing conservation network inefficient.

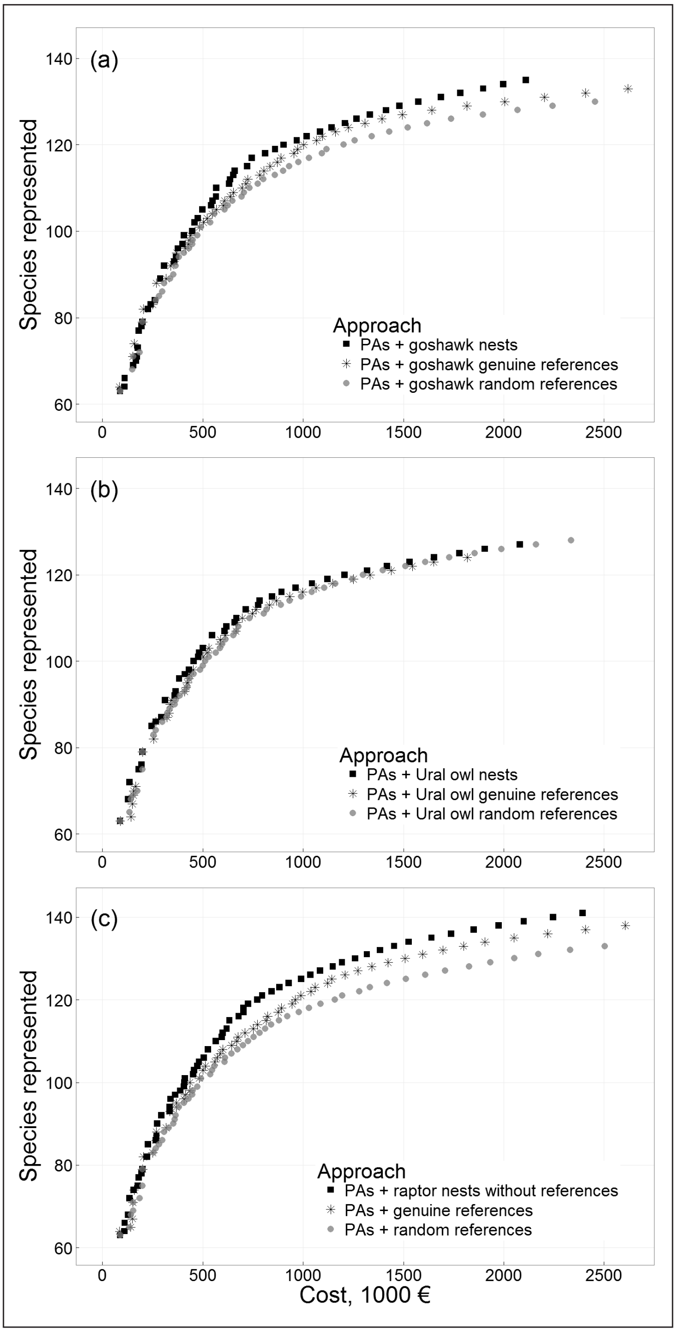

Figure 7. Performance of different conservation approaches where, in addition to protected areas (PAs), the reserve selection model was allowed to select (a) Goshawk nests, Goshawk related genuine sites or random sites, (b) Ural Owl nests, Ural Owl related genuine sites or random sites, and (c) both raptor nest sites, any kind of genuine site or any kind of random site.

4. CONCLUDING REMARKS

This thesis brings together fundamental ecology, conservation biology and cost-efficiency analyses to help clarify the role that raptors have in ecosystems and whether they can be of valuable use for conservation.

The results presented showcase the predators as keystone species. Raptors offer shelter to some species while may displace others (**I**, **II**), ultimately creating heterogeneity in the communities across time and space (**II**). Heterogeneity in habitat quality delivered by predators (Thomson et al. 2006b, **II**) can tentatively have similar effects than structural heterogeneity in enhancing biodiversity at larger scales. Research should, however, be directed to confirm this notion. Moreover, presence of highly interacting species can play important roles in the stability (resilience and resistance) of ecosystems in front of environmental perturbations (Tylianakis et al. 2008). Therefore, one could argue that top predators merit higher conservation effort in order to preserve their exceptional ecological function in the ecosystem (Sergio et al. 2008a, Ripple et al. 2014).

The fact that both raptor nest sites (especially with the Goshawk) hosted higher biodiversity (**III**) and provided more cost-efficient conservation (**IV**) is encouraging for three main reasons. First, as top predators stimulate high appeal among society, conservation efforts in line with protection of such species are more publicly acceptable (Fischer and Vanderwal 2007, Santangeli et al. 2012). Because conservation action is already biased towards charismatic species, it is important to evaluate how misleading using those species may be. Second, top predators are often threatened and, therefore, their coincidence with relevant locations for other taxa is a win-win scenario for conservation. Third, given that raptors are more conspicuous than other taxa and that thousands of nest locations are routinely collated yearly in databases, the use of raptor nest location to spot relevant sites for conservation could provide valuable information at no extra cost. A relevant finding is the fact that their surrogacy capacity persisted even if changing the environmental setting and regional biodiversity (**III**), indicating that raptors selected the best sites among the available stands in the area. This has clear implications if aiming to expand their use over large areas.

Even so, it is important to recognize the limitations of predators as surrogates of further biodiversity. For instance, some predators may displace other species of conservation interest (**I**, **II**). And even if the surrogacy function persists over ecological gradients (**III**), the change in the predator assembly can alter species-specific associations with the surrogate predator (**I**). Additionally, we here evaluated species with preference for coniferous forest. In order to effectively preserve other habitats, alternative species should provide better results. As a key example, using both predators boosted the cost-efficiency of raptor conservation approach as compared to reserve networks based on alternative sites (**III**). Therefore, while the use of top predators can effectively improve reserve selection used hitherto, top predators should not be considered the silver bullet in preserving biodiversity but rather a complement to a wide array of surrogates for biodiversity. Further research should address how to best integrate the importance that different species and other surrogates play in conservation planning.

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