Alike but still different: coexistence of four raptor species explained by breeding niche overlap

Kai-Philipp Gladow*[1], Jonas Beck[2],
Patrick B. Langthaler[2], Nayden Chakarov[1], Oliver Krüger[1]

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[1] Department of Animal Behaviour, Bielefeld University, Germany
[2] Department of Artificial Intelligence and Human Interfaces, Paris Lodron University of Salzburg, Austria

* Correspondence: kai-philipp.gladow@uni-bielefeld.de

Abstract

Understanding how species competing for similar resources coexist and influence each other has been, and still is, one of the big questions of community ecology. This question has often been tackled by comparing ecological niches of species pairs, although usually more than just two species compete for the same resources. We analysed the niche overlap of the breeding niche of four raptorial bird species (red kites, common buzzards, northern goshawks and eagle owls) living in sympatry in very high densities using a large sample size of n = 3439 breeding attempts from over 12 years. Using a new method to measure multiple species niche overlap, we show that each species overlaps a lot with the rest of the community but still shows key differences in its respective breeding niche. Afterwards, we take a closer look at the species pairs with the highest niche overlap. Red kites and buzzards overlap to a large degree in all measured niche dimensions except nearest neighbour distance to buzzard breeding pairs. Apparently, buzzards seem to be more territorial against their conspecifics than against red kites, meaning intraspecific competition is higher than interspecific competition. This might have enabled red kites to increase in breeding pair numbers during the last years despite sharing their habitat with many buzzard pairs. Goshawks lack such a key difference to eagle owls, being very similar in their breeding niche in all measured dimensions. As a consequence, goshawks fail to avoid competition and presumably predation by the dominant eagle owl, constraining the possibility for stable coexistence and explaining their reduction in breeding pairs as eagle owls increase, and vice versa. Experimental designs to test for direct behavioural reactions to intra- and interspecific competitors and territory intruders could help to understand these mechanisms better.

Keywords: birds of prey, breeding habitat, coexistence, competitive exclusion, ecological niche, intraguild predation, niche overlap

Introduction

The ecological niche has been a key concept in ecology for many decades, and measuring it has a history of almost 100 years (Pocheville, 2015). Hutchinson (1957) defined the ecological niche concept by describing the niche of a species as an n-dimensional hypervolume, where every dimension represents a measurable trait of the species which influences the ability of the species to coexist within a community (Chase & Leibold, 2003; McPeek, 2022). This set a tight link between coexistence theory and competition research (e.g., Hardin, 1960; Levin, 1970; May, 1974; Pianka, 1974; Schoener, 1989). However, modern coexistence theory highlights many different influences on the probability of species coexistence, be it other, more direct interaction types (like predation, McPeek, 2022), stochasticity, or spatially and temporally heterogeneous environments (Chesson & Huntly, 1997; Chesson, 2000). However, comparing ecological niches still provides important insights into the ecological similarities between species (Krüger, 2002a; Chase & Leibold, 2003; Broennimann *et al.*, 2012) or into the ability of species to adapt to new or changing environments (Holt, 2009). Larger niche overlaps also reduce the probability for stable species coexistence in competition-based consumer-resource models (Chesson, 2000; Mittelbach & McGill, 2019). Understanding why some species are able to increase their geographical range or their population size in a certain area whereas others are decreasing is becoming a key knowledge, especially since human-induced change is rapidly accelerating (Sippel *et al.*, 2020; Cowie *et al.*, 2022). For example, eagle owls (Chakarov & Krüger, 2010) and wolves (Ripple *et al.*, 2014) were able to colonize formerly abandoned areas and have profound impact on the community structure, partly via intraguild predation on smaller predators (Mueller *et al.*, 2016; Beschta & Ripple, 2016). This clear hierarchical dominance of top predators may allow them to establish themselves in an already densely populated area, but for less dominant predators, it can be more difficult to spread into these areas as they are not only facing competition with other mesopredators, but also suffer from mesopredator suppression by top predators (Ritchie & Johnson, 2009; Terraube & Bretagnolle, 2018). For a species to successfully invade a community and coexist with their competitors, theory predicts that intraspecific competition within the established species has to be higher than interspecific competition between the established and the invading species (invasibility criteria, Chesson, 2000; McPeek, 2022) and research on competing pairs of plant species has found empirical evidence for this (Adler *et al.*, 2018). Hence, reducing niche overlap is one possibility to reduce interspecific competition and increase the likelihood of coexistence (Mittelbach & McGill, 2019). When mesopredators start to colonize areas already populated by other species of their ecological guild, another possible strategy to reduce niche overlap can be changes in behaviour, like different activity times or occupation of distinct habitats compared with competitors (Dayan & Simberloff, 2005).

In general, analyses of competitive interactions often just focused on pairwise interactions, although ecological competitive networks usually consist of more than two species (e.g., Korpimäki, 1986). Hence, the additive and indirect effects emerging from the interactions of multiple competitors have to be considered for a complete understanding of these networks (Levine *et al.*, 2017). However, a whole guild of a community was used only rarely to assess the competitive interactions between species (Levine *et al.*, 2017) and most of this work was done on a theoretical rather than an empirical level (e.g., Barabás *et al.*, 2016). Furthermore, many methods on niche overlap often suffer from potentially weak statistical inference because they assume normally distributed data (e.g., Schoener, 1989). We use the recently published method of Langthaler *et al.* (2024) to estimate niche overlaps of n-dimensional hypervolumes for more than two species simultaneously, while providing inference to discriminate between similar and distinct niche spaces using confidence intervals. This method is fully non-parametric and thus robust against heavily skewed datasets and differences in sample size, which is very common in ecological data (Langthaler *et al.*, 2024).

In our long-term study area, red kites (*Milvus milvus*) were only present with one or two breeding pairs for about 20 years but started to increase steeply since 2012 (Figure 1). However, the area is already densely populated by common buzzards (*Buteo buteo*, Figure 2), northern goshawks (*Accipiter gentilis*, Figure 1) and Eurasian eagle owls (*Bubo bubo*, Figure 1). These documented breeding pair densities are among the highest ever reported in the literature for common buzzards and eagle owls and high for northern goshawks (Gladow *et al.*, 2025).

In contrast to the aforementioned species, red kites are usually considered to be competitively inferior in direct dominance-based interactions with other members from their guild, e.g. when defending a nest site against interspecific competitors (Dobler, 1990). Regarding their breeding habitat, it is known that red kites prefer open landscapes with fields and meadows for their long and far-reaching hunts (Aebischer & Scherler, 2023). However, it is not known if these preferences can persist while spreading into an area densely populated by other birds of prey, where other species, especially common buzzards, occupy the majority of possible breeding territories. Although these species' distributions overlap largely in the Western Palaearctic (Mebs & Schmidt, 2014) and research on common buzzards and red kites has been done extensively in this biogeographic region (Walls & Kenward, 2020; Aebischer & Scherler, 2023), studies comparing their ecological preferences directly, especially for breeding sites, are usually descriptive in nature and do not deal with the questions of coexistence or competitive exclusion (e.g., Trillmich, 1969; Stubbe, 1982). This is even more surprising because red kites and buzzards do occur in very similar habitats (Walls & Kenward, 2020; Aebischer & Scherler, 2023). The situation for comparisons of buzzards or red kites with other members of their guild, like goshawks or eagle owls, are similar (but see Dobler, 1990; Chakarov & Krüger, 2010; Mueller *et al.*, 2016).

In this study, we use more than two decades of data on breeding attempts of red kites, buzzards, goshawks, and eagle owls to quantify and compare their breeding niches. We define the breeding niche as a nine-dimensional environmental space describing the conditions under which a breeding attempt is made. We first compare the breeding niche of each species with the combined breeding niche of all other species in the guild, and then conduct targeted pairwise comparisons between the most similar presumed competitors (red kites vs. buzzards, goshawks vs. eagle owls; Chakarov & Krüger, 2010; Mebs & Schmidt, 2014). Our overarching goal is to understand how a behaviourally subordinate mesopredator such as the red kite can increase in breeding density within a community already saturated by ecologically similar raptors.

To make this question explicit and testable, we address the following hypotheses:

1. The four raptor species occupy distinct breeding niche hypervolumes in multivariate environmental space, such that each species' breeding niche overlaps only partially with the combined niche of the remaining guild.
2. Red kites show their greatest niche overlap with common buzzards, but their breeding niche is shifted along at least some environmental dimensions, resulting in reduced overlap compared to what would be expected if both species used breeding habitats identically.
3. Niche differentiation relevant for coexistence is concentrated in a subset of the nine

measured environmental dimensions rather than expressed equally across all dimensions, consistent with the prediction that stable coexistence does not require species to differ in every aspect of their niche (Mittelbach & McGill, 2019).

By testing these hypotheses with a non-parametric, multivariate niche-overlap framework at the scale of a whole predator guild, we aim to link long-term population dynamics of red kites and their competitors to explicit patterns of breeding niche differentiation and overlap.

Material and Methods

Study area

The study area is located west of the city of Bielefeld in North Rhine-Westphalia and Lower Saxony, Germany (52.06 N and 8.30 E). It measures 300 km^2 in size and includes three different natural regions: the largest part in the north consists of a hilly terrain with mostly rural landscape and small to medium sized deciduous forests (mainly European beech *Fagus sylvatica*); the Teutoburg Forest in the center is a low mountain range with larger forested areas containing predominantly beech as well as European spruce (*Picea abies*); the south is similar to the north, although its dominating tree species is Scots pine (*Pinus sylvestris*) growing on sandy soils. Research on raptors has been done in this study area since 1975, with the main focus on common buzzards since 1989 (Krüger & Lindström, 2001). Additionally, northern goshawks, red kites and Eurasian eagle owls as well as their interactions have been studied there (e.g., Krüger, 2002a; Mueller *et al.*, 2016).

Population dynamics of the four raptor species

Since 1989, all breeding attempts of common buzzards, northern goshawks and red kites are being mapped for the whole study area (see Krüger & Lindström, 2001; Gladow *et al.*, 2025). Mapping was done by checking each forest in the study area in early spring for raptor nests and confirming breeding attempts (nest occupancy) later in the breeding season. Since 1996, eagle owl breeding attempts are being mapped as well. There is knowledge of only one eagle owl pair breeding in this area in the preceding years. Breeding pair density of the four species were compiled to compare their population trends and densities. During the last 12 years, all four species showed some interesting changes in their breeding population trends. Red kites had been almost absent from the area until then, but started to increase rapidly from year to year up to 16 breeding pairs in 2024 (Figure 1).

The common buzzard population has increased more than eightfold between 1989 and 2024 from around 12 breeding pairs per 100 km^2 to over 100 breeding pairs per 100 km^2, but started to fluctuate a lot since the beginning of the 2010s (Figure 2). Equally impressive has been the re-colonization of the study area by eagle owls, from 1 breeding pair per 100 km^2 to a maximum of over 9 breeding pairs per 100 km^2, with most of the new territories appearing from 2010 onwards (Figure 1). In slight contrast, the population dynamics of the goshawk show a stable population size with between 5 and 7 breeding pairs per 100 km^2, but decreased fast after a high level in 2012 (Figure 1). The densities of common buzzards and eagle owls are among the highest ever reported, and for goshawks above average for central Europe (Mebs & Schmidt, 2014).

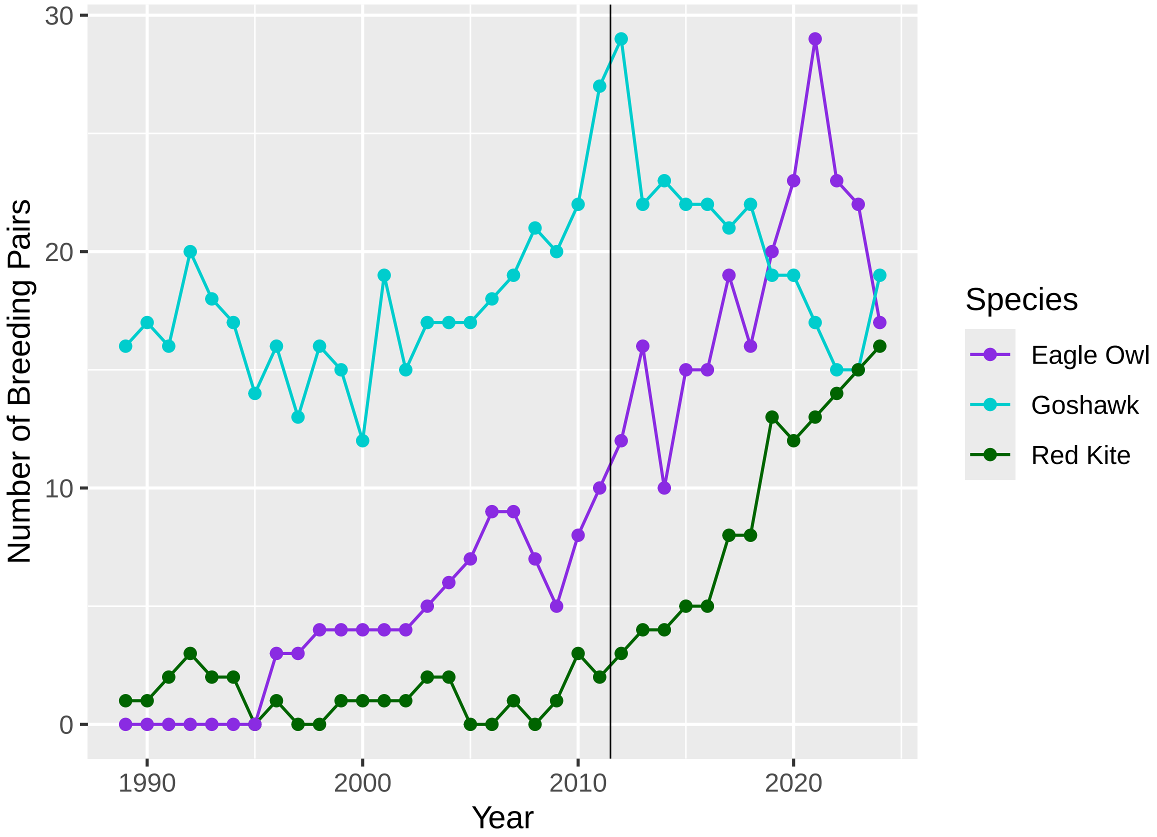

Figure 1: Population dynamics of eagle owls, goshawks, and red kites depicted by the number of breeding attempts in our study area since 1989. From 2012 onwards (black line), eagle owl and red kite breeding pair density increased whereas goshawk breeding pair density decreased.

Data collection

We decided to take the apparent change in population dynamics in our research area as a threshold for our analysis. Hence, we used all breeding attempts of the four species since 2012 (until 2023) to compare their habitat preferences. We considered each breeding attempt to be independent, even if there had been another attempt at the same site in previous years. We did so because of several reasons. First, breeding pairs have to make a new decision where to breed every year again. Even if the same individuals bred at the

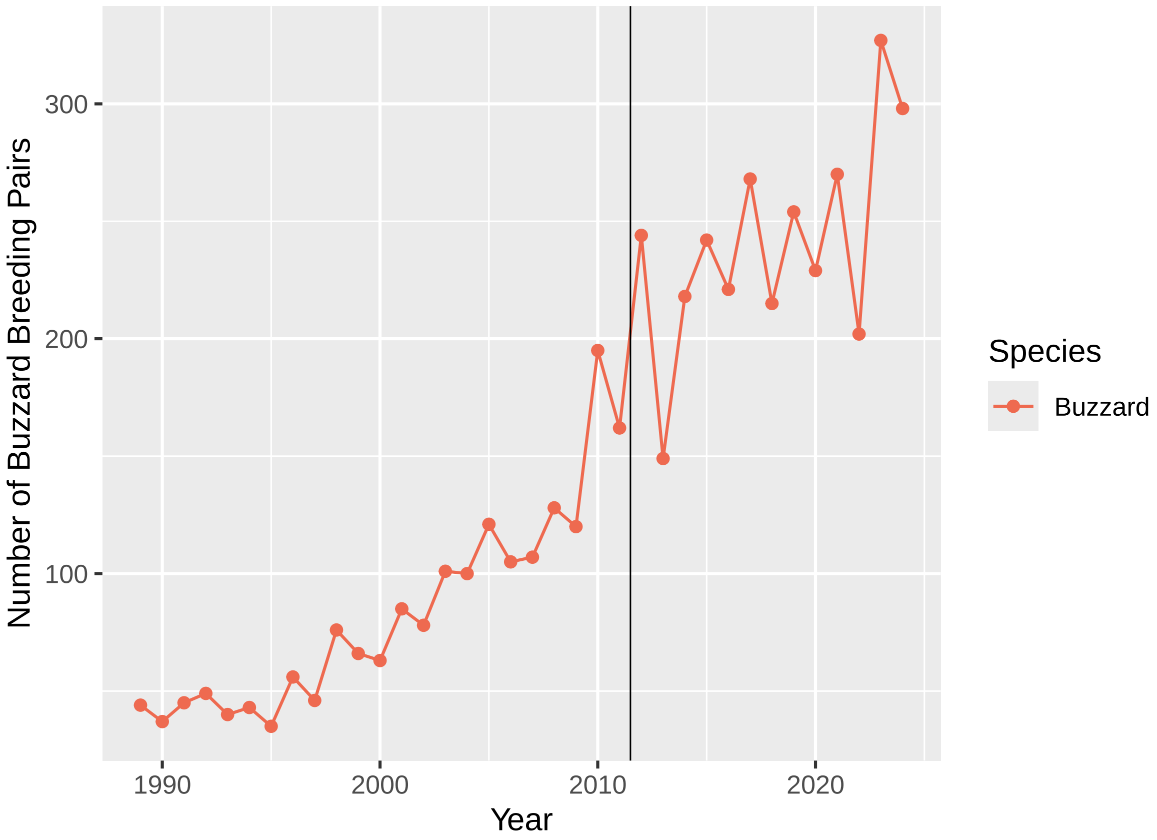

Figure 2: Population dynamics of common buzzards depicted by the number of breeding attempts in our study area since 1989. Buzzards increased a lot in breeding pair density, reaching above 200 breeding pairs first in 2012 (black line) and stayed above 200 breeding pairs with only one exception (2013).

same location as the year before, they did so because they actively chose that location over other nesting sites. It is known from many bird of prey species that the re-use of nests used in the previous years depends on the breeding success and the habitat quality (Mammen & Stubbe, 1996; Krüger & Lindström, 2001). Hence if nesting sites were chosen several times for breeding, this reflects the good quality of the surrounding habitat. So by using the absolute number of attempts and by that including some nest surroundings several times, we accounted for the territory quality (Junker *et al.*, 2016). To control for potential statistical issues caused by this, we ran an additional analysis with the inclusion of each nest surrounding only once (see Supplementary Material). The results of this smaller subset resembled the results of the larger analysis and allowed for the same conclusions presented here, hence we used the whole dataset for analysis. We used the geographic information system QGIS (version 3.22) to collect habitat properties for all breeding attempts. The collected variables were divided into three categories: amount of habitat type within a 1.5 km radius around the breeding site, shortest distance from the nest to that habitat type and nearest neighbour distance (NND) to other intra- and interspecific breeding attempts. The habitat types chosen were arable land (including meadows), forest, and settlement area. We chose these variables because 1) our study site is dominated by them, whereas other habitat types (like larger water bodies or marshland) are almost non-existent, and 2) these habitat properties have been shown to be important for bird of prey breedings in the past (Mebs & Schmidt, 2014). NND to other breeding pairs of the same or of other species was collected to investigate if some species were breeding especially close or far away from other species, hinting at niche partitioning or territoriality. A radius of 1.5 km around the nests was chosen because it describes the 50 per cent home range of red kites (Pfeiffer & Meyburg, 2015) and eagle owls have been shown to impact intraguild prey within this radius around their nest the most (Sergio *et al.*, 2003).

Statistical analysis

Analyses were done in R (R Core Team, 2024) using the packages *DynRB*, *ggplot2*, *gridExtra*, *tidyverse*, and *gtable* (Junker *et al.*, 2016; Wickham, 2016; Auguie & Antonov, 2017; Wickham & RStudio, 2023; Wickham *et al.*, 2024). We used the method developed by Langthaler *et al.* (2024), which is not yet integrated in an R package. In general, this method calculates an overlap for the different niche spaces of several species at the same time (see Langthaler *et al.*, 2024). For each niche dimension (e.g., breeding distance to settlements), the niche distribution of one species is compared with a reference distribution calculated from the combined niche space of the other considered species. We applied the fully nonparametric inference framework of Langthaler *et al.* (2024) to quantify niche overlap among multiple species. For each ecological variable (niche dimension), the empirical distribution of a species was compared with a reference distribution formed by the pooled observations of all other species in the community. The resulting overlap estimator $I_j \in [0, 1]$ quantifies how similar the species' niche distribution is to this community reference along dimension j. Statistical inference is based on rank-based resampling: for each dimension, we obtained 95 % bootstrap confidence intervals from 10,000 resamples of the observed data, following Langthaler *et al.* (2024). The reference value of 0.5 corresponds to the situation where the species' distribution is, on average, equally similar to the reference distribution. Hence, if the entire confidence interval lies below 0.5, the species occupies a significantly different niche space in that dimension. Confidence intervals including 0.5 indicate no statistically discernible difference. In ecological communities, species seldom compete with just one other species but several, hence analysing this combined competitive impact displays the situation in a multi-species guild more adequately (Mittelbach & McGill, 2019). However, to get a more detailed view on the interactions of red kites with buzzards and of goshawks with eagle owls, we additionally did pairwise comparisons of the red kite's and the buzzard's niche as well as the goshawk's and eagle owl's niche using the method from Parkinson *et al.* (2018) implemented in the *DynRB* package (function *ranks_ OV*, Junker *et al.*, 2016).

Table 1: Median ± interquartile ranges (IQR) for each measured niche dimension and for all four species. Dist. = Distance; NND = Nearest Neighbour Distance.

Dimension	Red Kites	Common Buzzards	Northern Goshawks	Eagle Owls
Field Area (ha)	537.8 ± 78.4	502.7 ± 159.0	465.9 ± 222.0	301.7 ± 210.7
Forest Area (ha)	85.9 ± 37.5	88.7 ± 75.9	105.5 ± 154.8	221.3 ± 141.4
Settlement Area (ha)	69.7 ± 44.7	85.4 ± 64.7	77.3 ± 49.7	111.5 ± 68.2
Field Dist. (m)	23.5 ± 31.7	24.4 ± 33.5	72.1 ± 86.7	99.7 ± 94.1
Settlement Dist. (m)	113.0 ± 88.0	121.3 ± 100.3	185.8 ± 118.1	157.9 ± 135.5
Buzzard NND (m)	292.2 ± 327.6	556.7 ± 322.1	315.4 ± 316.1	506.1 ± 448.5
Eagle Owl NND (m)	2507.8 ± 2238.2	2334.8 ± 2396.8	2519.9 ± 2592.2	1654.3 ± 1516.9
Goshawk NND (m)	1456.0 ± 1181.3	1512.9 ± 1189.0	2406.7 ± 1053.4	1741.5 ± 1488.7
Red Kite NND (m)	2703.5 ± 2941.5	2531.8 ± 2302.3	2816.6 ± 3770.3	3717.1 ± 3491.7

Results

Descriptive analysis

From the 12 years from 2012 to 2023, 2881 breeding attempts of buzzards, 246 of goshawks, 208 of eagle owls and 104 of red kites were used for the analysis. The different values for each dimension and species can be found in Table 1.

Niche overlap of all four species

Red kites exhibited significant differences compared with the raptor community in only four out of nine dimensions of their breeding niche. They had very narrow niches and low amounts of forest and settlement areas and were breeding most closely to open fields (Figure 4, Table S1). Compared with the other species, red kites were breeding closer to buzzards, which aligns with similarities between red kites and buzzards for the dimensions without niche differences.

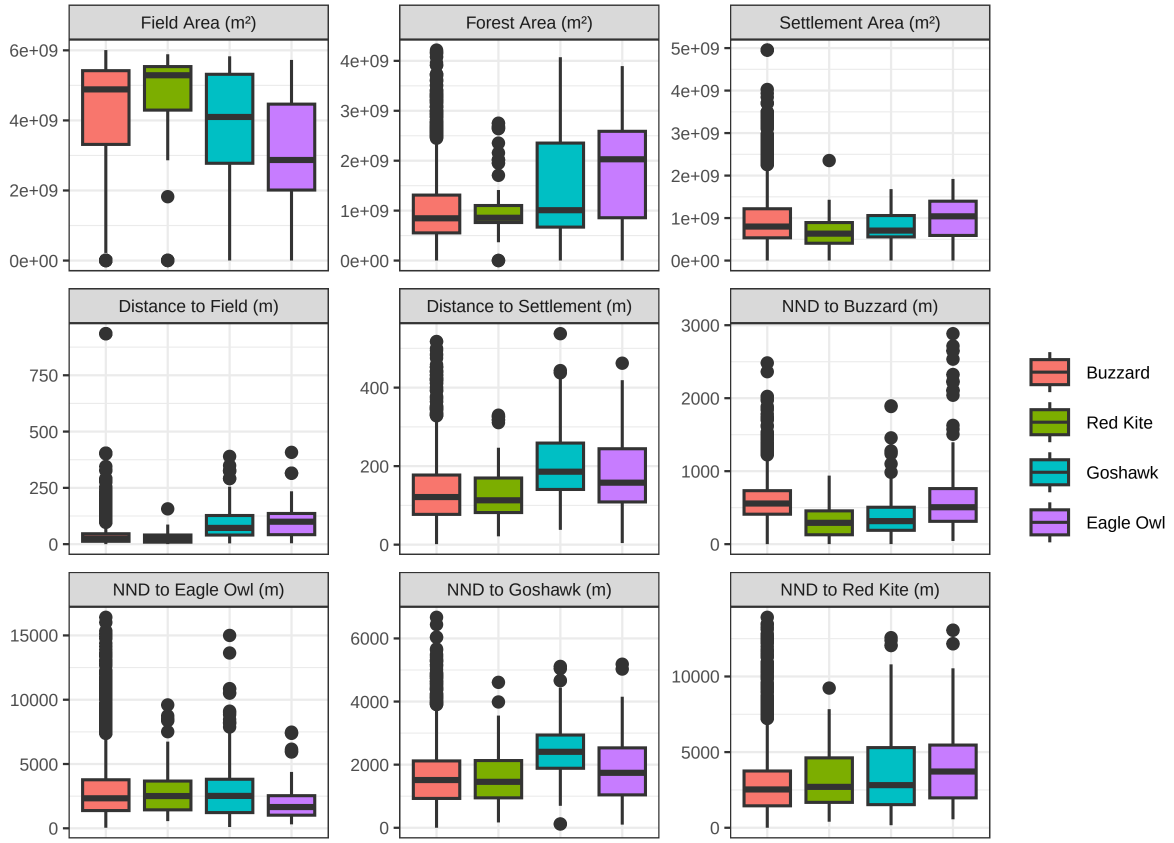

Figure 3: Boxplots depicting the niche spaces of buzzards, red kites, goshawks, and eagle owls for each measured dimension.

In seven out of nine dimensions, buzzards had a niche overlap significantly smaller than 0.5, indicating differences in their breeding niche compared to the community (Figure 4, Table S1). Their niche contained relatively large amount of field area in close proximity, less wooded areas and relatively close to settlements (Figures 3 and 4). They bred further away from other buzzards than the other species did, highlighting intraspecific territoriality and probably competition; on the other hand, buzzards were not repelled from breeding relatively close to goshawks and to red kites as well, compared with the other species (Figure 3).

Goshawks differed in five dimensions significantly from the raptor community in their

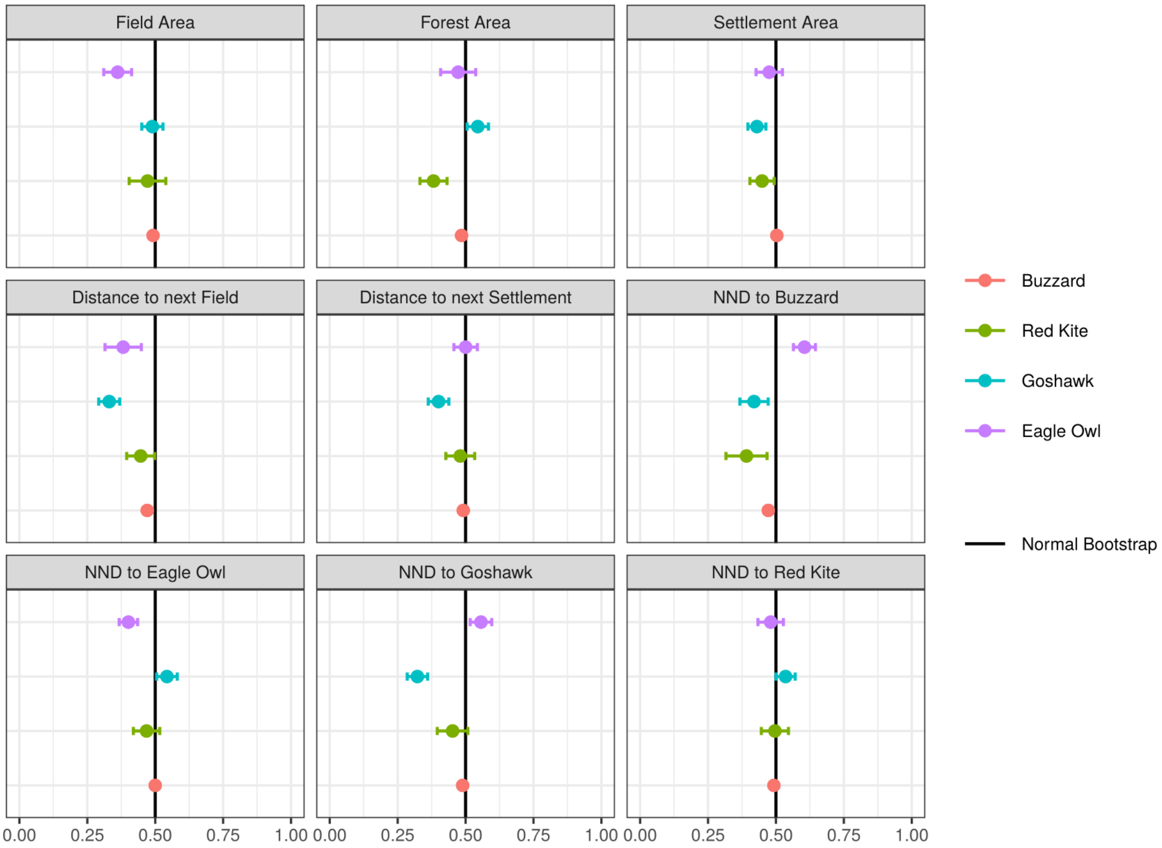

Figure 4: Niche overlap values ± confidence intervals of buzzards, red kites, goshawks, and eagle owls for each measured dimension. A shift to the left indicates a different niche space for the respective species from the rest of the community. A shift to the right indicates a large overlap with the rest of the community, often enclosing the other species' niche spaces. See Table S1 for the model output.

breeding niche: a very narrow niche with few urban areas; a large distance to open fields and to settlements; a low NND to buzzards; and a high NND to other goshawks (Figures 3 and 4, Table S1). Additionally, goshawks had a very wide niche space regarding the amount of forest area and the NNDs to eagle owls and to red kites, enclosing most of the niche space occupied by the other species (Figure 3). This is shown by goshawks having a niche overlap value significantly larger than 0.5 for the respective dimensions (Figure 4, Table S1).

Eagle owls were breeding at sites with the least amount of field area compared with the other species and also relatively far away from open fields; in contrast, they had their nests significantly closer to other eagle owls than buzzards, red kites and goshawks (Figures 3 and 4, Table S1). For the NNDs to buzzards and to goshawks, eagle owls had a significantly wider niche space enclosing most of the other species' niche (Figure 4, Table S1).

Pairwise niche overlap between red kites and common buzzards

We found that buzzards differed significantly from red kites in the amount of forest and settlement areas and in NND to goshawks, mostly because of a broader niche space compared with red kites (Table 2). Red kites, on the other hand, had almost always a big overlap with the buzzards' niche, and with respect to the amount of forest area, were even completely enclosed by it (Table 2). For the NND to buzzards, both species had significantly different niche spaces from each other (Table 2). Red kites were breeding consistently closer to buzzards than buzzards did towards their conspecifics (Figure 3). This is the most pronounced difference between red kites and buzzards for all of the analysed breeding niche dimensions and contrasts with their otherwise large overlap in breeding niche. This can also be observed in the symmetrical niche overlap calculated from the different species' overlap values (Table 2). The n-dimensional niche overlap was high with a value of 0.884 and in almost all of the nine dimensions, red kites and buzzards had a symmetric overlap of more than 0.9. The only difference was the NND to buzzards, where the symmetric overlap was 0.42 (Table 2).

Table 2: Niche overlap of buzzards and red kites for all measured dimensions separately and for the n-dimensional hypervolume. If the species' overlap value ± confidence intervals is smaller than 0.5, its niche differs significantly from the other species. If the overlap value ± confidence intervals is bigger than 0.5, its niche is completely enclosed by the other species' niche. The symmetrical overlap shows the overall similarity for both species' niches. The n-dimensional overlap does not provide CIs. Dist. = Distance; NND = Nearest Neighbour Distance.

	Common Buzzard			Red Kite			
Dimension	Overlap	lower CI	upper CI	Overlap	lower CI	upper CI	Sym. Overlap
Field Area	0.482	0.440	0.524	0.469	0.427	0.511	0.904
Forest Area	0.390	0.354	0.427	0.604	0.568	0.640	0.942
Settlement Area	0.450	0.422	0.479	0.525	0.497	0.553	0.945
Field Dist.	0.482	0.442	0.523	0.517	0.477	0.557	0.997
Settlement Dist.	0.489	0.452	0.527	0.509	0.471	0.546	0.996
Buzzard NND	0.372	0.336	0.409	0.282	0.245	0.319	0.420
Eagle Owl NND	0.469	0.432	0.506	0.530	0.492	0.567	0.994
Goshawk NND	0.462	0.425	0.500	0.532	0.495	0.570	0.983
Red Kite NND	0.503	0.465	0.541	0.493	0.455	0.531	0.992
n-dimensional	0.454	-	-	0.487	-	-	0.884

Pairwise niche overlap between goshawks and eagle owls

We found that eagle owls differed significantly from goshawks in the amount of urban area and distance to buildings as they were breeding closer to human settlements and included more of that area around their breeding site (Table 3). The goshawk's breeding niche differed in the amount of field area and in the NND to buzzards. Furthermore, for NND to eagle owls, they had a wider niche and enclosed the eagle owl's breeding niche. Thus, both species differed from each other in some dimensions, but they never did this for the same dimension because one species' niche was always partially covered by the (wider) niche of the other species (Figure 3, Table 3). This can be seen as well in the symmetrical niche overlaps, which are on average lower for the different dimensions than for the buzzard-kite comparison (between 0.7 and 0.9), and in the n-dimensional overlap (0.820, Table 3). However, the symmetrical overlap does not contain a single

Table 3: Niche overlap of eagle owls and goshawks for all measured dimensions separately and for the n-dimensional hypervolume. If the species' overlap value ± confidence intervals is smaller than 0.5, its niche differs significantly from the other species. If the overlap value ± confidence intervals is bigger than 0.5, its niche is completely enclosed by the other species' niche. The symmetrical overlap shows the overall similarity for both species' niches. The n-dimensional overlap does not provide CIs. Dist. = Distance; NND = Nearest Neighbour Distance.

	Eagle Owl			Goshawk			
Dimension	Overlap	lower CI	upper CI	Overlap	lower CI	upper CI	Sym. Overlap
Field Area	0.495	0.444	0.545	0.416	0.366	0.467	0.824
Forest Area	0.463	0.411	0.514	0.452	0.401	0.504	0.837
Settlement Area	0.352	0.299	0.405	0.535	0.482	0.588	0.753
Field Dist.	0.464	0.408	0.520	0.513	0.457	0.569	0.952
Settlement Dist.	0.407	0.352	0.462	0.549	0.494	0.604	0.894
Buzzard NND	0.412	0.362	0.463	0.446	0.396	0.497	0.735
Eagle Owl NND	0.595	0.543	0.647	0.330	0.278	0.382	0.785
Goshawk NND	0.339	0.285	0.392	0.525	0.471	0.579	0.712
Red Kite NND	0.516	0.461	0.572	0.448	0.393	0.504	0.925
n-dimensional	0.443	-	-	0.463	-	-	0.820

dimension where goshawks and eagle owls differ as much from each other as red kites and buzzards do for NND to buzzards.

Discussion

Within a community of raptorial birds, we analysed the amount of breeding niche overlap to answer the question how different species with similar habitat preferences are able to coexist despite one of the highest bird of prey densities ever reported. We were especially interested how red kites, formerly not present as breeding pairs in this area, were able to invade and establish themselves in this community. One condition for coexistence of competing species in a community proposed by modern coexistence theory is that interspecific competition has to be lower than intraspecific competition (Chesson, 2000;

Mittelbach & McGill, 2019), visible by the significant differences of niche dimensions. Using a new method for comparison of multiple species' niche overlap, we found that each of the four species differed from the rest of the guild in at least some of the nine breeding niche dimensions (Langthaler *et al.*, 2024). These differences reduce niche overlap and are consistent with stabilizing niche differences that may help to keep interspecific competition lower than intraspecific competition. The multiple-species comparison then guided targeted pairwise analyses of the most similar competitors (Parkinson *et al.*, 2018), allowing us to relate patterns of niche segregation to the very different population trajectories of red kites, buzzards, goshawks and eagle owls at both local and larger scales.

Red kites had the greatest breeding niche overlap with common buzzards, the numerically dominant competitor, which matches their broadly similar habitat use described in previous studies (Mebs & Schmidt, 2014; Walls & Kenward, 2020; Aebischer & Scherler, 2023). However, buzzards kept a greater distance to conspecific breeding pairs than to red kites, whereas red kites did not avoid nesting close to buzzards. This suggests that buzzards exhibit stronger territorial behaviour towards conspecifics than towards red kites, so that intraspecific competition in buzzards exceeds interspecific competition with red kites. This may constitute a stabilizing mechanism for coexistence: buzzards limit their own individuals more than they limit red kites (Chesson, 2000; Levine *et al.*, 2017). When buzzards are confronted with taxidermic models of conspecifics in their territory, they usually show a high level of aggression (Krüger, 2002b; Boerner & Krüger, 2009). Models of goshawks (Krüger, 2002b; Gladow *et al.*, 2025), and eagle owls (Boerner & Krüger, 2009; Mueller *et al.*, 2016; Gladow *et al.*, 2025) also spark highly aggressive responses, also indicating low tolerance. Additional experiments with taxidermic models of red kites to check for a lower level of aggression would be desirable; expectations based on the findings in our study should be that similar reactions to red kites are rather unlikely. Interspecific aggression between buzzards and red kites has also rarely been documented in earlier studies, e.g. Trillmich (1969) observed aggression towards red kites only in the direct vicinity of the nest. Dobler (1990) did not find interspecific territoriality in his study between red kites and goshawks, hinting on high general tolerance for red kites.

In our system, intraguild predation (IGP) is also present (Chakarov & Krüger, 2010). Hence, a big proportion of the above-mentioned aversion of buzzards against goshawks and eagle owls might actually come from defence behaviour against potential predators and therefore does not strictly resemble a reaction to competition but rather predation or a combination of both (Gladow *et al.*, 2025, discussed in more detail below). If the observed interaction patterns between red kites and buzzards are stable and generalisable can only be determined by studying the same niche dimensions in other regions. As Ousterhout *et al.* (2019) point out, local environmental gradients can influence the strength of intra- and interspecific competition. What is valid for our populations might not be the case for other study areas. For example, food availability or distribution of suitable habitats could potentially lead to buzzards being more tolerant of conspecifics than of red kites, or not tolerant at all if the breeding sites are too close (Ousterhout *et al.*, 2019).

One of our main goals was to shed light on the similarities and differences of the steadily increasing number of red kite breeding attempts compared with the other, already present species within our study area. Red kites had the least amount of significantly different niche dimensions compared with the other three species. The overall large similarity with the buzzards' breeding niche is likely to explain most of the overlapping niche dimensions for red kites; since buzzards make up most of the extant breeding pairs, similarities and dissimilarities with buzzards influence the niche overlap values the most (Langthaler *et al.*, 2024). However, for the amount of forest area, amount of settlement area and distance to fields, differences of red kites from the other species were mainly driven by a different breeding niche to goshawks and eagle owls. These differences indicate a low level of interspecific competition for breeding sites, so that coexistence of eagle owls and goshawks with red kites is not limited by their breeding niche (Levine *et al.*, 2017; Mittelbach & McGill, 2019).

Despite their high abundance, buzzards differed in seven out of nine niche dimensions from their competitors, with most of the differences were driven by differences to goshawks and eagle owls as well. In general, out findings are in accordance with the literature about common buzzard breeding sites (Mammen & Stubbe, 1996; Walls & Kenward, 2020). Particularly interesting, however, are the relative proximity to urbanised areas and the higher nearest neighbour distance to other breeding buzzards. Buzzards in our study area bred closer to settlements than traditionally reported, and the local population size has now reached values that earlier work had projected as only attainable in the absence of human disturbances and settlements (Nolte, 1969). An increased tolerance to settlements likely drives the rising breeding pair numbers of buzzards, but it does so in a way that primarily expands their niche into human-modified habitats rather than increasing direct niche overlap with other raptors. As a consequence, urbanisation can create new “release” habitats for generalists, as has been shown also in other predators (e.g., Gil-Fernández *et al.*, 2020).

Whereas buzzards and red kites show a very distinct difference in one niche dimension (NND to buzzards), which might allow red kites using very similar habitats as buzzards to breed nearby them, goshawks' and eagle owls' niches overlap to a large amount for all of the measured dimensions and lack any significant difference. In the light of their population developments, this points to a high level of interspecific competition, with the dominant eagle owl constraining coexistence of goshawks (Chesson, 2000; McPeek, 2022). Earlier studies have shown that eagle owls which re-occupy territories in their former range often replace goshawks and use almost the same breeding niche (Mueller *et al.*, 2016), effectively displacing them. Competitors with larger body size have in most cases a competitive advantage (Anaya-Rojas *et al.*, 2021). Additionally, the intraguild predation pressure of eagle owls exerted on goshawks let the owl dominate the hawk (Chakarov & Krüger, 2010; Scherzinger & Mebs, 2020). As can be seen in the breeding niche regarding distance to urban areas, goshawks prefer to breed relatively far away of humans; however, because big and remote forests get more and more diminished by forestry and spruce forests vanish from bark beetle infestation and dryness due to climate change (Marini *et al.*, 2017), goshawks cannot evade eagle owls that easily any more.

As such, the goshawk's breeding niche shows clear patterns of a "sandwich position" between its niche preferences and the competition by eagle owls (Chakarov & Krüger, 2010; Mueller *et al.*, 2016). Most of its niche differences come from the comparison with buzzards and red kites, whereas high similarity to eagle owls persists. As shown by Krüger *et al.* (2025), eagle owls took over almost the same breeding niche as goshawks used to have during their re-establishment, pushing the latter out of their old territories. Our analysis supports this by showing a similar breeding niche for both species, but goshawks are less specialised in their breeding niche when breeding in sympatry with eagle owls. The relatively wide variation for the NND to eagle owls, enveloping most of the variation of the other three species, is also in line with comparison with this: where it is possible, goshawks try to breed far away from eagle owls, but some pairs have to take the risk and breed close to their intraguild predator. Goshawks were known to live in general at large distances to human settlements (Mebs & Schmidt, 2014), partly because of their preference for large forests but also their inconspicuous behaviour (Dobler, 1990; Krüger, 2002a). While there are more and more examples of goshawks breeding in urban areas (Merling de Chapa *et al.*, 2020), this analysis still shows that they are choosing to breed the furthest away from settlements of all four of the investigated species. Thus, the goshawks' less flexible breeding ecology seems to make them more vulnerable to competitive exclusion by eagle owls.

Eagle owls have a very broad niche, highlighting plasticity and tolerance of different environments (Scherzinger & Mebs, 2020). However, within this broad niche space, eagle owls still show preferences, like a small amount of open field area and breeding at a relatively large distance to it. They also breed closer to other eagle owls compared with the other raptorial birds; since the average distance between eagle owl pairs is still higher than 1.5 km, that is possibly not due to a low level of territoriality but a clear pattern of all other species trying to avoid predation by eagle owls (Sergio *et al.*, 2003; Chakarov & Krüger, 2010; Mueller *et al.*, 2016). This picture becomes especially clear when compared with the NND to goshawk breeding pairs: buzzards, red kites and eagle owls breed closer to goshawks than other goshawks do; apparently, none of them fears predation as much as buzzards, red kites and goshawks fear predation by eagle owls. Direct behavioural reactions of buzzards to both eagle owl and goshawk models close to buzzard nests appeared to be similar in aggression level (Gladow *et al.*, 2025), but regarding nest choice, there seems to be a higher aversion against eagle owls. This emphasizes the ecological role of eagle owls as apex predators in these bird communities, shaping the spatial distribution of other predators via intraguild predation and size-induced competitive exclusion (Lourenço & Rabaça, 2006; Sergio & Hiraldo, 2008; Mueller *et al.*, 2016; Terraube & Bretagnolle, 2018).

Until now, there is no clear theoretical or empirical evidence how large the influences of predation and competition on species coexistence are in relation to each other, although predation is often thought to have a more direct and thus higher impact (Holt & Polis, 1997; Mittelbach & McGill, 2019). Because of this, the question arises if analysing niche overlap to estimate species coexistence makes sense at all in a community of raptorial birds with intraguild predation. But as we have an interplay of competition and predation in our system, the breeding niche overlap might not only represent the level of competition, but also the risk of predation during the breeding season (Chakarov & Krüger, 2010). Since a higher niche overlap in this case means a higher likelihood of breeding in similar areas, the species with greater body size is able to exert predatory pressure on its competitor or its offspring (Anaya-Rojas *et al.*, 2021). Eagle owls do so on all other species present (Mueller *et al.*, 2016; Scherzinger & Mebs, 2020), and goshawks are able to prey on buzzards and red kites (Mebs & Schmidt, 2014). However, because we show that the breeding niches of eagle owls and goshawks overlap a lot and are very distinct from buzzards and red kites, the goshawk might be the one species which is suffering substantially more from lethal and especially non-lethal effects of intraguild predation than the other birds of prey. Hence calculating niche overlap can help not only to estimate the level of competition but also the level of predation, and in this case better explain the breeding pair dynamics of goshawks. Furthermore, predation clearly does not always trump over competition since Morosinotto *et al.* (2017) showed that intraspecific competition can limit a species more even with intraguild predation by the competitor. Nevertheless, more empirical research on the relative importance of competition and predation in IGP systems is needed to understand this interplay and top-down limitations better (Terraube & Bretagnolle, 2018).

One limitation which we have chosen deliberately is the focus on breeding niche parameters. We are aware that for a complete coexistence analysis of these four species, other factors like competition for food or interactions outside the breeding season are important as well (Mebs & Schmidt, 2014; Mittelbach & McGill, 2019). Nevertheless, we are confident that the variables chosen by us resemble the most important factors for birds of prey choosing nesting sites within this study area and thus enabled us to accurately measure their breeding niche (Chakarov & Krüger, 2010; Walls & Kenward, 2020; Aebischer & Scherler, 2023). The difficulty of analysing different niche dimensions (either separately or in combination) is that the relative importance of certain dimensions for competition is hard to estimate (Hutchinson, 1957; Chase & Leibold, 2003). We looked at nine different variables (amount of field, forest, and urban area, distance to fields and settlements, NND to all four species) which are most likely important for these species to choose a breeding location (Mebs & Schmidt, 2014). Of course, not all included factors are equally relevant for each of the considered species; however, the level of variation around the population mean seems to show the importance of single dimensions for most breeding pairs of a species.

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