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]

March 20, 2025

[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

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). Early focus was mainly on abiotic needs of a species (Grinellian niche; Grinnell, 1917) or its role within the food web (Eltonian niche; Elton, 1927; Mittelbach & McGill, 2019). In his "concluding remarks", Hutchinson (1957) revolutionized 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. This led to a large body of research using this definition to measure and compare the niche overlap of species from the same ecological guild (e.g., May, 1974; Pianka, 1974; Schoener, 1989) because coexistence theory predicted that the more competitive species would exclude other species with a too similar niche from a community (competitive exclusion principle, Hardin, 1960; Levin, 1970). Despite the later realization that species coexistence often cannot be explained just by the strength of competition without considering other effects like predation or variable environments (reviewed in Mittelbach & McGill, 2019), 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). One example for the use of niche overlap is the prediction of the spread of invasive neobiota based on their ecological preferences matched to the environmental conditions in the area compared to their region of origin (Broennimann *et al.*, 2012). 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). However, these research developments are not only crucial regarding the spread of neobiota, but also for native species reoccupying areas where they went extinct during the last centuries. 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 dense community, 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). 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) 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 these patterns often just focused on the interaction of two competitors, although ecological competitive networks usually consist of more than two species (Levine *et al.*, 2017). Rarely, a whole guild of a community was used 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). Even when more than two species' niches were analysed, these comparisons were done by pairwise comparisons without considering combined competitive effects from the guild (e.g., Korpimäki, 1986). 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.*, 2024).

The red kite is a bird of prey species occurring only in Europe with regionally very different population densities and trends, being present or increasing in some and being absent or decreasing in other areas (Heuck *et al.*, 2013; Mebs & Schmidt, 2014). More than half of its population breeds in Central Europe which makes it an important subject for conservation measures (Katzenberger *et al.*, 2021). In contrast to the aforementioned species, red kites are usually considered to be inferior in direct dominance-based interactions with other members from their guild, e.g. when defending a nest site against interspecific competitors (Dobler, 1990). Although the red kite has a quite large wingspan of up to 1.7 m, it is a light-weight and comparatively slender bird of prey (Mebs & Schmidt, 2014). Furthermore, this species is known for being less aggressive and young red kites, instead of defending themselves, fall into a state called "akinesis" and play dead when they are threatened (Mebs & Schmidt, 2014). 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 an extensive dataset with breeding attempts of red kites, buzzards, goshawks and eagle owls sampled for more than two decades. We compare the breeding niche of each species with the combined breeding niche of the other species to investigate similarities and differences between the species' breeding niches and from the overall community. Additionally, we do pairwise comparisons of the breeding niches of the competitors with the presumably most similar breeding niches; that is, red kites with buzzards and goshawks with eagle owls (Chakarov & Krüger, 2010; Mebs & Schmidt, 2014). This aims to provide possible explanations for the increasing number of breeding pairs of red kites within this area and the other species' breeding pair dynamics. We expect differences between the breeding niche preferences not in all, but in some of the measured traits, as stable coexistence does not necessarily need differences in all dimensions of competition (Mittelbach & McGill, 2019).

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). 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).

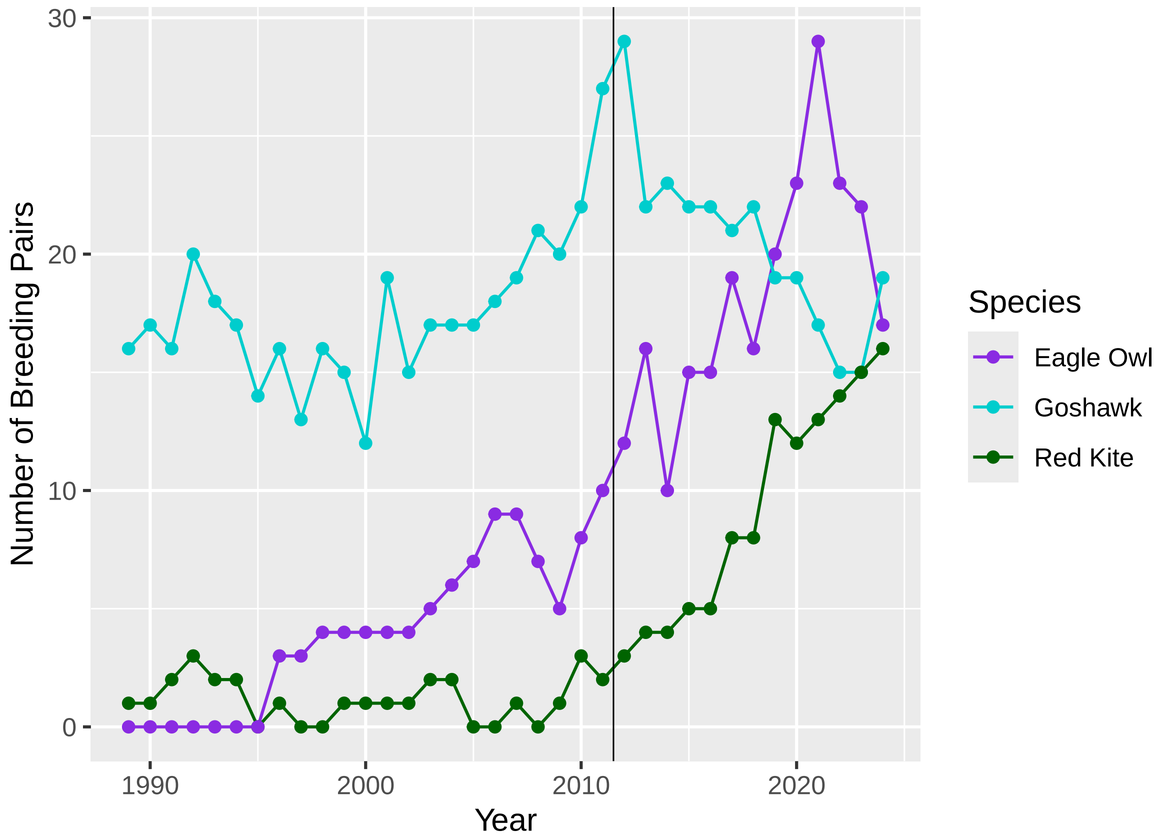

Figure 1: Population dynamics of eagle owls, goshawks, and red kites depicted by the number of breeding attempts in our study area since 1989. From 2012 onwards (black line), eagle owl and red kite breeding pair density increased whereas goshawk breeding pair density decreased.

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

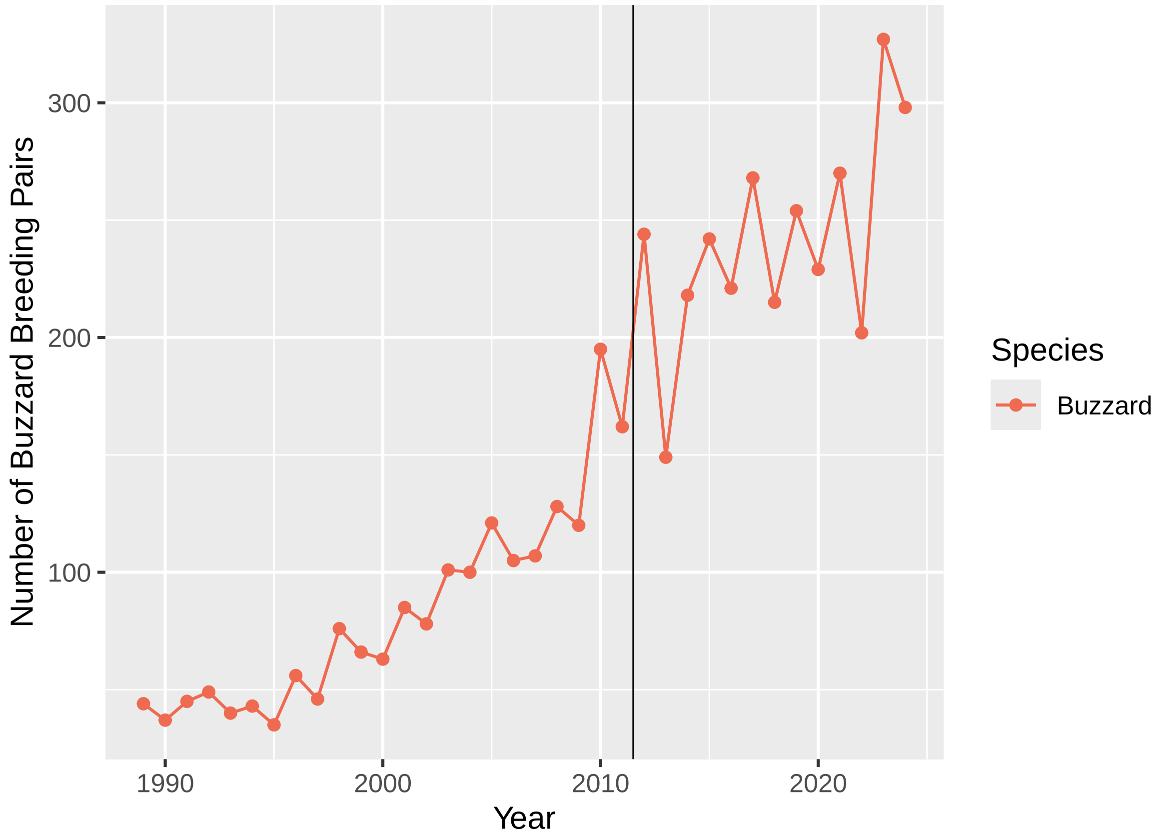

Figure 2: Population dynamics of common buzzards depicted by the number of breeding attempts in our study area since 1989. Buzzards increased a lot in breeding pair density, reaching above 200 breeding pairs first in 2012 (black line) and stayed above 200 breeding pairs with only one exception (2013).

bred at the 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). 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. The habitat type "forest" was not used in the shortest distance analysis because all four species' breeding attempts were located within forests; furthermore, distance to arable land almost always corresponded to the distance to the forest edge. 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. Additionally, it could be used to control if distances between breeding attempts were just sorted by habitat preferences or if a particular species was avoided more than expected by that. 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. 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).

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. Inside the radius of 1.5 km around red kite nests, arable land had a median (+IQR) share of 537.8+78.4 ha, forest of 85.9+37.5 ha, and settlement of 69.7+44.7 ha. For buzzards, arable land covered 502.7+159.0 ha, forest 88.7+75.9 ha, and settlement 85.4+64.7 ha. Goshawks had on average 465.9+222.0 ha of arable land, 105.5+154.8 ha of forest, and

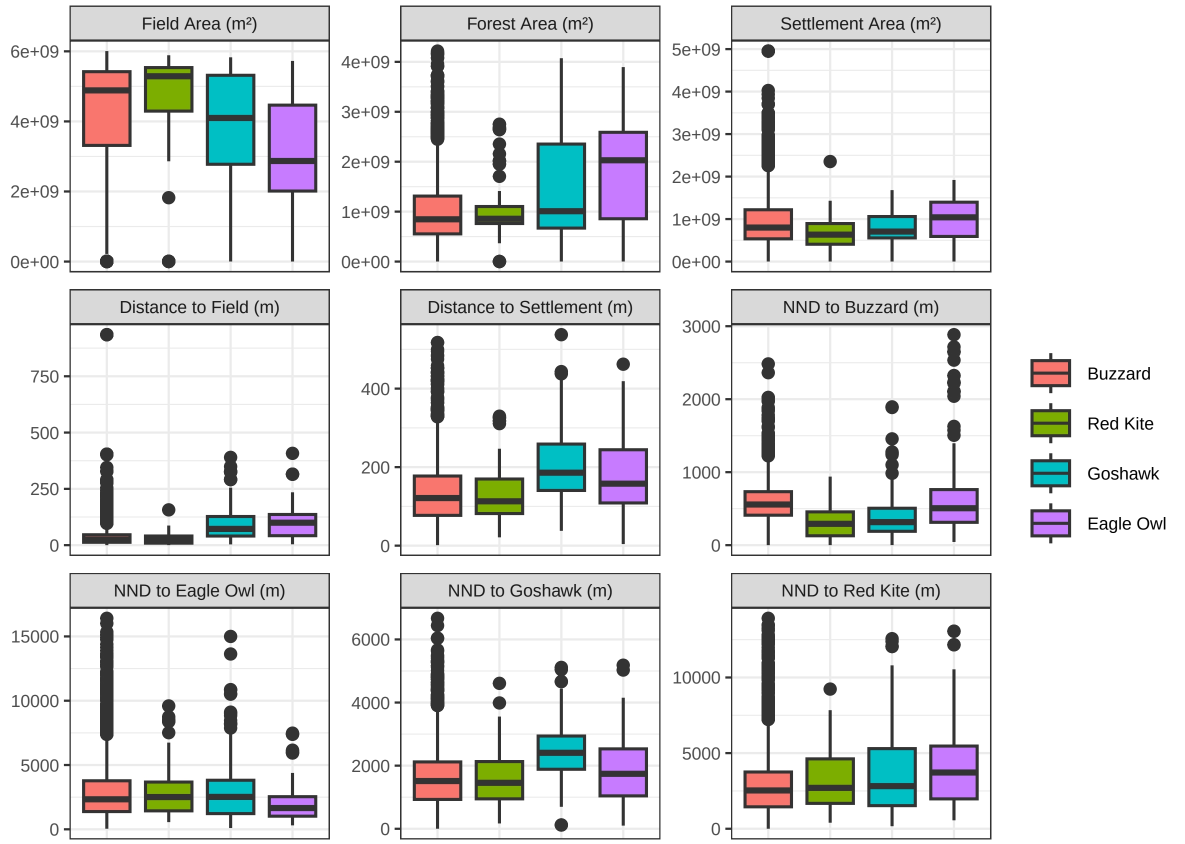

Figure 3: Boxplots depicting the niche spaces of buzzards, red kites, goshawks, and eagle owls for each measured dimension.

77.3+49.7 ha of settlement. The surroundings of eagle owl nests consisted of 301.7+210.7 ha arable land, 221.3+141.4 ha forest, and 111.5+68.2 ha settlement (Figure 3).

Red kites were breeding on average 23.5+31.7 m far from arable land and 113.0+88.0 m from settlements. The median distance of buzzards to arable land was 24.4+33.5 m and to settlements 121.3+100.3 m. For goshawks, the next arable land was on average 72.1+86.7 m away and the next settlement 185.8+118.1 m. Eagle owls had their nesting site 99.7+94.1 m distant from arable land and 157.9+135.5 m from settlements (Figure 3).

Regarding the NND, the median distances of red kites towards other breeding attempts were 2703.5+2941.5 m to other red kites, 292.2+327.6 m to buzzards, 1456.0+1181.3 m to goshawks, and 2507.8+2238.2 m to eagle owls. Buzzards bred on average 556.7+322.1 m distant to other buzzards, 2531.8+2302.3 m to red kites, 1512.9+1189.0 m to goshawks, and 2334.8+2396.8 m to eagle owls. The median distances for goshawks were 2406.7+1053.4 m to conspecifics, 2816.6+3770.3 m to red kites, 315.4+316.1 m to buzzards, and 2519.9+2592.2 m to eagle owls. For eagle owls, the closest breeding conspecific was usually 1654.3+1516.9 m far away, the closest red kite 3717.1+3491.7 m, the closest buzzard 506.1+448.5 m, and the closest goshawk 1741.5+1488.7 m (Figure 3).

Niche overlap of all four species

Red kites had differences in breeding niche preferences in only four out of nine dimensions. They had very narrow niches and low amounts of forest and settlement areas and were breeding most closely to open fields (Figure 4). 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.

In seven out of nine dimensions, buzzards had a niche overlap slightly smaller than 0.5, indicating differences in niche preferences compared to the community (Figure 4). Although these differences were not particularly pronounced, buzzards seemed to be able to retain a specific niche compared with the other species despite their high abundance. This 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

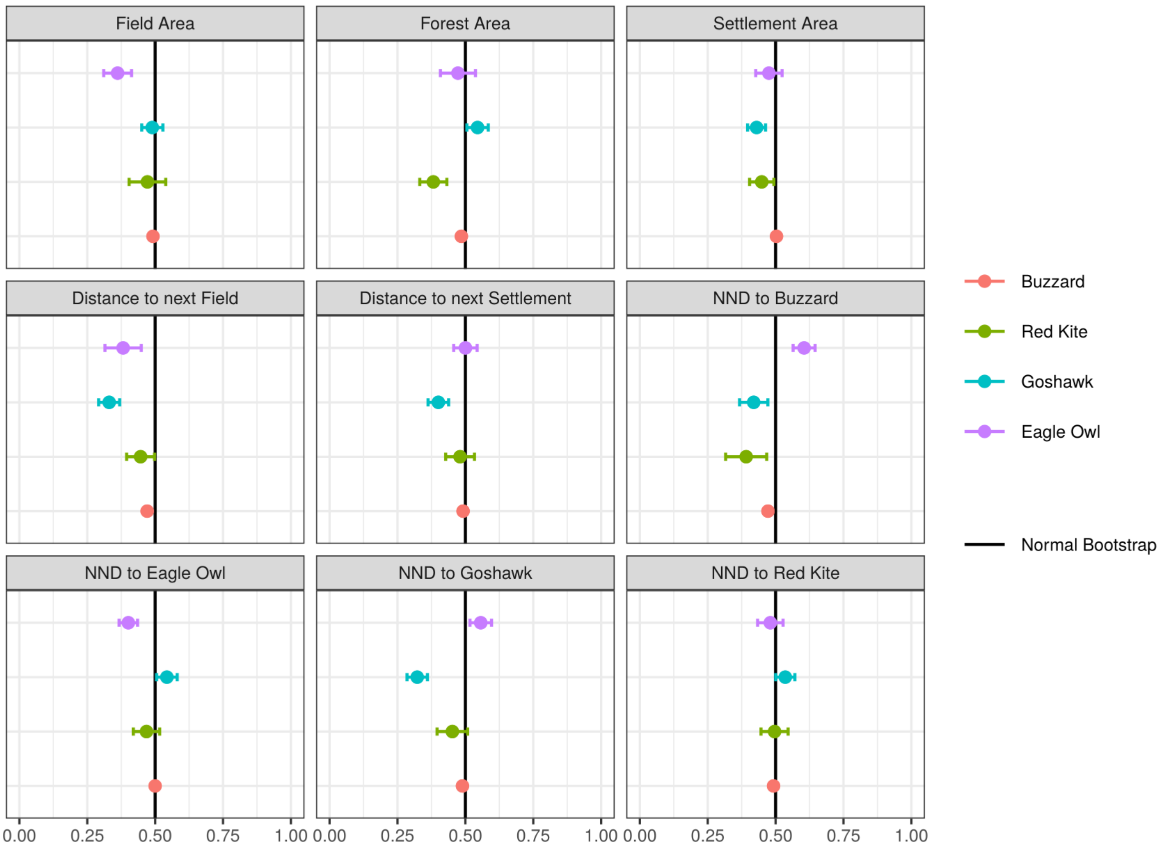

Figure 4: Niche overlap values ± confidence intervals of buzzards, red kites, goshawks, and eagle owls for each measured dimension. A shift to the left indicates a different niche space for the respective species from the rest of the community. A shift to the right indicates a large overlap with the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

relatively close to goshawks and to red kites as well, compared with the other species (Figure 3).

Goshawks had five dimensions with different niche preferences: 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). 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 larger than 0.5 for the respective dimensions (Figure 4).

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). The overall similar pattern of all three diurnal birds of prey to avoid close proximity to eagle owls might hint on the latter's strong predatory pressure and/or high competitiveness (Figure 3). For the NNDs to buzzards and to goshawks, eagle owls had a wider niche space enclosing most of the other species' niche (Figure 4).

Pairwise niche overlap between red kites and common buzzards

As shown in the multiple species overlap analysis, red kites showed relatively few distinct preferences from the other species, thus the overall comparison indicated a high level of competition for red kites within this community. The most similar pattern seemed to be with the common buzzard, which is also the most abundant competitor (Figures 2 and 3). Because of that, we decided to have a closer look how red kites were able to increase in breeding pairs even with this high level of competition and analysed the pairwise niche overlap of 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 1). 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 1). For the NND to buzzards, both species had significantly different niche spaces from each other (Table 1). Red kites were breeding consistently closer to buzzards than buzzards

Table 1: Niche overlap of buzzards and red kites for all measured dimensions separately and for the n-dimensional hypervolume. If the species' overlap value $\pm$ confidence intervals is smaller than 0.5, its niche differs significantly from the other species. If the overlap value $\pm$ 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

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 1). 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 just 0.42 (Table 1).

Pairwise niche overlap between goshawks and eagle owls

A second pairwise comparison was done for the other duo with mostly similar breeding niche preferences, goshawks and eagle owls. However, in contrast to red kites and buzzards, the population trends of goshawks during the observed time period was rather declining whereas eagle owls were increasing. 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 2). 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 2). 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 2). However, the symmetrical overlap does not contain a single dimension where goshawks and eagle owls differ as much from each other as red kites and buzzards do for NND to buzzards. Because of this, competition between goshawks and eagle owls for breeding territories might actually be more pronounced than between red kites and 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. Using a new method for comparison of multiple species' niche overlap, we found differences for each of the four species to

Table 2: Niche overlap of eagle owls and goshawks for all measured dimensions separately and for the n-dimensional hypervolume. If the species' overlap value $\pm$ confidence intervals is smaller than 0.5, its niche differs significantly from the other species. If the overlap value $\pm$ 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

the rest of their guild in some dimensions, meeting our expectations. These differences allow the species to reduce their breeding niche overlap and hence might lower their competition for breeding sites. One condition for coexistence of competing species in a community proposed by competition theory is that interspecific competition has to be lower than intraspecific competition (Chesson, 2000; Mittelbach & McGill, 2019), shown by significant differences of niche dimensions. The findings of the multiple niche overlap, based on a solid inference method using confidence intervals, then enabled us to do a pairwise comparison of the species pairs with the highest overlap (Parkinson *et al.*, 2018; Langthaler *et al.*, 2024) to get an even closer look on potential levels of competition. Furthermore, we were able to compare the breeding niche preferences of four raptorial bird species with very different population dynamics, both locally and globally (Mebs & Schmidt, 2014; Scherzinger & Mebs, 2020). These species are often investigated separately without much focus on their ecological interactions (e.g., Walls & Kenward, 2020; Aebischer & Scherler, 2023). This might be because birds of prey are difficult to study in large numbers due to their relative scarcity as big predators (Mebs & Schmidt, 2014). This study, however, shows that a comparative analysis of their ecology and interactions can contribute to a better understanding of their population dynamics.

Red kites were most similar in their breeding niche to common buzzards, which is also the most abundant competitor. However, despite their high abundance, buzzards seemed to retain a certain distance to other buzzard breeding pairs whereas red kites did not keep the same distance to buzzards. Apparently, red kites breeding close were tolerated more than other buzzards. This fits into the framework of higher intra- than interspecific competition enabling coexistence (Chesson, 2000) because buzzards seem to defend a certain area around their nest against competitors from their own species, but not against red kites. As "stabilizing niche differences include all factors that cause species to limit their own individuals more than they do those of other species" (Levine *et al.*, 2017), buzzards limit their own individuals more than red kites by showing a higher territoriality against conspecifics, by that potentially facilitating coexistence. 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. 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.*, 2024), and eagle owls (Boerner & Krüger, 2009; Mueller *et al.*, 2016; Gladow *et al.*, 2024) 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. Dobler (1990) also did not find interspecific territoriality in his study between red kites and goshawks, hinting on high general tolerance for red kites. Since we were doing our analysis in a community where intraguild predation (IGP) is also present, a big proportion of the above-mentioned aversion of buzzards against goshawks and eagle owls might actually come from defence behaviour against potential predators for adult buzzards or their offspring and therefore does not strictly resemble a reaction to competition but rather predation or a combination of both (Gladow *et al.*, 2024, 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. The breeding niche of red kites differed in four out of nine dimensions (smaller amount of forest area, larger amount of settlement area, shorter distance to fields, shorter NND to buzzards) from the overall community. Hence, red kites had the least amount of significantly different niche dimensions compared with the other three species. In an area as densely populated as ours, it is of course difficult to avoid close contact to other breeding pairs, as can be seen by the relatively large overlap with the rest of the raptor community. However, for some of the dimensions like distance to fields, red kites show a very narrow niche, expressing a strong preference to breed close to the forest edge. This is in accordance with literature, almost always describing red kites breeding attempts as being in proximity to open land (Trillmich, 1969; Stubbe, 1982; Mebs & Schmidt, 2014; Aebischer & Scherler, 2023). 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 different niche preferences to goshawks and eagle owls. This shows that despite the large number of buzzard breeding pairs in our sample, the other species also influence the niche overlap values.

Despite their high numbers and widespread distribution throughout the study area, buzzard breeding pairs differed in seven out of nine niche dimensions from their competitors. Most of the differences here as well were driven by differences to goshawks and eagle owls. 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. Nolte (1969) estimated in his study, conducted in a neighbouring area with similar size and landscape, that buzzards could breed there with up to 314 breeding pairs - if there would be no human disturbance, including settlements. However, because settlements were completely avoided, he only counted around 46 breeding pairs of common buzzards (Nolte, 1969). As the breeding pair dynamics in Figure 2 show, we had a similar population size during the 1990s. In recent years however, the number of pairs increased until it went above 300 for the first time in 2023 (Figure 2), matching almost exactly the estimations of Nolte (1969). It would be interesting to investigate how much of this population increase can be contributed to buzzards starting to breed closer or within human settlements. While it is still true that all four species, including buzzards, are mainly breeding away from settlements, many buzzards used nests close to or even within urban areas during the 12 years of this study (Figure 3).

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. This could be an explanation for the decline in breeding density in goshawks during the recent years (Figure 1). 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), presumably pushing goshawks into less favourable territories or preventing them to breed at all. 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 over 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. However, for goshawks the average distribution within these dimensions tended to be not as different from buzzards and red kites as it was for eagle owls (Figure 3). As shown by Chakarov & Krüger (2010), 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 preference for both species, but goshawks are less "extreme" or specialised in their breeding niche preferences 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 in 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 for 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. Whereas buzzards already breed in higher numbers close or even within larger settlements as discussed above, the goshawks' less flexible breeding ecology prevents that for now, making them more vulnerable to competitive exclusion by eagle owls. As the development of the number of breeding pairs for goshawks and eagle owls as well as the high breeding niche overlap of both species suggest, the upper population limit for birds with this breeding niche inside our study area seems to lie around 30 to 40 breeding pairs. How many of these are goshawk or eagle owl pairs is probably determined by eagle owl population development (Mueller *et al.*, 2016).

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.*, 2024), 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 (Lourenço & Rabaça, 2006; Sergio & Hiraldo, 2008; Mueller *et al.*, 2016; Scherzinger & Mebs, 2020).

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 better.

Using methods to compare the ecological niches of several species within a community or just a pair of species have both advantages and disadvantages. Within the ecological literature, discussions recently arose whether competition within a community can be estimated just by looking at the pairwise species interactions or if higher-order interactions emerge when more than two species compete with each other (Barabás *et al.*, 2016; Levine *et al.*, 2017; Gibbs *et al.*, 2022). Analysing the community or guild as a whole provided us with a more complete picture of the interactions between the different species (Levine *et al.*, 2017). However, emerging higher-order interactions can make such analyses and the interpretation of results very difficult (Gibbs *et al.*, 2022); but until now, the empirical evidence for such higher-order interactions is scarce (Levine *et al.*, 2017). Pairwise comparisons on the other hand allow for an easier analysis, although conclusions from these results can be misleading if both investigated species are influenced by other, not included species (Barabás *et al.*, 2016; Gibbs *et al.*, 2022). We therefore opted to do both: first, we looked at the niche overlap between all four species, and then took the species pairs which had the highest overlap and hence the greatest potential for competitive exclusion to look in detail at their ecological similarities (Parkinson *et al.*, 2018; Langthaler *et al.*, 2024). Although the method by Langthaler *et al.* (2024) does not explicitly include higher-order interactions, it provides a way to estimate the combined impact of several species on a focal species' niche, thus it can be used to go beyond pairwise interactions. In our study, the pairwise analyses between red kites and buzzards as well as goshawks and eagle owls were most informative about the dynamics within the populations. This indicates that, at least in this case, higher-order interactions do not seem to be very influential.

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. For example, buzzards exhibit large variation in the amount of field area around the nest but low variation in the distance to fields (Figure 3), indicating that open fields that are close by are an important factor for choosing a breeding site, but not that these fields have to be necessarily very large.

Conclusions

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 (Mittelbach & McGill, 2019). By analysing the niche overlap for different dimensions of their breeding niche, we could show that four raptorial bird species (red kite, common buzzard, northern goshawk and eagle owl) breeding in very high densities overlap a lot but still show key differences in their breeding niches. These differences - and where they are missing - might help to understand the dynamics of the different breeding pair numbers. Red kites and buzzards overlap to a large degree in all measured niche dimensions except NND 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 (Chesson, 2000). This might have enabled red kites to increase in breeding pair numbers during the last years despite sharing their habitat with so many buzzard pairs. Aggression experiments where buzzard pairs are confronted with red kite models and compared to the reaction to buzzard models could help to understand these mechanisms better. 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.

Author Contributions (CRediT)

Kai-Philipp Gladow: Conceptualization (Equal), Data curation (Equal), Formal analysis (Equal), Investigation (Lead), Methodology (Equal), Project administration (Lead), Software (Supporting), Resources (Supporting), Supervision (Equal), Validation (Equal), Visualization (Supporting), Writing - original draft (Lead); **Jonas Beck**: Data curation (Equal), Formal analysis (Equal), Methodology (Equal), Software (Equal), Resources (Supporting), Validation (Equal), Visualization (Equal), Writing - review & editing (Equal); **Patrick B. Langthaler**: Data curation (Equal), Formal analysis (Equal), Methodology (Equal), Software (Equal), Resources (Supporting), Validation (Equal), Visualization (Equal), Writing - review & editing (Equal); **Nayden Chakarov**: Conceptualization (Supporting), Funding acquisition (Equal), Methodology (Supporting), Resources (Equal), Supervision (Supporting), Writing - review & editing (Equal); **Oliver Krüger**: Conceptualization (Equal), Funding acquisition (Equal), Methodology (Supporting), Project administration (Supporting), Resources (Equal), Supervision (Equal), Writing - review & editing (Equal).

Acknowledgements

This work was supported by the Friedrich-Ebert-Stiftung (FES) and the Bielefeld University's Young Researchers Fond to KPG and the German Research Foundation (DFG; project number 398434413), as part of the SFB TRR 212 (NC3; project numbers 316099922 and 396780709) to OK and NC. We thank all people involved in mapping the breeding locations of the four species alongside the authors, in recent years namely Meinolf Ottensmann, Hugo Pereira, Tim Maximilian Rapp and Tony Rinaud.

Declarations of interest

There are no conflicting interests to declare.

1 References

Adler, P.B., Smull, D., Beard, K.H., Choi, R.T., Furniss, T., Kulmatiski, A., Meiners, J.M., Tredennick, A.T. & Veblen, K.E. (2018) Competition and coexistence in plant communities: Intraspecific competition is stronger than interspecific competition. *Ecology Letters* **21**, 1319–1329.

Aebischer, A. & Scherler, P. (2023) *Der Rotmilan - Ein Greifvogel im Aufwind.* Haupt Verlag AG, Bern, 2 edn.

Anaya-Rojas, J.M., Bassar, R.D., Potter, T., Blanchette, A., Callahan, S., Framstead, N., Reznick, D. & Travis, J. (2021) The evolution of size-dependent competitive interactions promotes species coexistence. *Journal of Animal Ecology* **90**, 2704–2717.

Auguie, B. & Antonov, A. (2017) gridExtra: Miscellaneous Functions for "Grid" Graphics.

Barabás, G., J. Michalska-Smith, M. & Allesina, S. (2016) The Effect of Intra- and Interspecific Competition on Coexistence in Multispecies Communities. *The American Naturalist* **188**, E1–E12.

Beschta, R.L. & Ripple, W.J. (2016) Riparian vegetation recovery in Yellowstone: The first two decades after wolf reintroduction. *Biological Conservation* **198**, 93–103.

Boerner, M. & Krüger, O. (2009) Aggression and fitness differences between plumage morphs in the common buzzard (Buteo buteo). *Behavioral Ecology* **20**, 180–185.

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.J., Randin, C., Zimmermann, N.E., Graham, C.H. & Guisan, A. (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography* **21**, 481–497.

Chakarov, N. & Krüger, O. (2010) Mesopredator Release by an Emergent Superpredator: A Natural Experiment of Predation in a Three Level Guild. *PLoS ONE* **5**, 8.

Chase, J.M. & Leibold, M.A. (2003) *Ecological Niches: Linking Classical and Contemporary Approaches.* University of Chicago Press.

Chesson, P. (2000) Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology, Evolution, and Systematics* **31**, 343–366.

Cowie, R.H., Bouchet, P. & Fontaine, B. (2022) The Sixth Mass Extinction: Fact, fiction or speculation? *Biological Reviews* **97**, 640–663.

Dayan, T. & Simberloff, D. (2005) Ecological and community-wide character displacement: The next generation. *Ecology Letters* **8**, 875–894.

Dobler, G. (1990) Brutbiotop und Territorialität bei Habicht (Accipiter gentilis) und Rotmilan (Milvus milvus). *Journal für Ornithologie* **131**, 85–93.

Elton, C.S. (1927) *Animal Ecology.* The Macmillan Company, New York.

Gibbs, T., Levin, S.A. & Levine, J.M. (2022) Coexistence in diverse communities with higher-order interactions. *Proceedings of the National Academy of Sciences* **119**, e2205063119.

Gladow, K.P., Jablonski, M., Chakarov, N. & Krüger, O. (2024) A top predator does not provoke stronger defense than a mesopredator in an intraguild prey .

Grinnell, J. (1917) The Niche-Relationships of the California Thrasher. *The Auk* **34**, 427–433.

Hardin, G. (1960) The Competitive Exclusion Principle. *Science* **131**, 1292–1297.

Heuck, C., Brandl, R., Albrecht, J. & Gottschalk, T.K. (2013) The potential distribution of the Red Kite in Germany. *Journal of Ornithology* **154**, 911–921.

Holt, R.D. (2009) Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* **106**, 19659–19665.

Holt, R.D. & Polis, G.A. (1997) A Theoretical Framework for Intraguild Predation. *The American Naturalist* **149**, 745–764.

Hutchinson, G.E. (1957) Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology* **22**, 415–427.

Junker, R.R., Kuppler, J., Bathke, A.C., Schreyer, M.L. & Trutschnig, W. (2016) Dynamic range boxes – a robust nonparametric approach to quantify size and overlap of n-dimensional hypervolumes. *Methods in Ecology and Evolution* **7**, 1503–1513.

Katzenberger, J., Gottschalk, E., Balkenhol, N. & Waltert, M. (2021) Density-dependent age of first reproduction as a key factor for population dynamics: Stable breeding populations mask strong floater declines in a long-lived raptor. *Animal Conservation* **24**, 862–875.

Korpimäki, E. (1986) Niche Relationships and Life-History Tactics of Three Sympatric Strix Owl Species in Finland. *Ornis Scandinavica (Scandinavian Journal of Ornithology)* **17**, 126–132.

Krüger, O. (2002a) Analysis of nest occupancy and nest reproduction in two sympatric raptors: Common buzzard Buteo buteo and goshawk Accipiter gentilis. *Ecography* **25**, 523–532.

Krüger, O. (2002b) Interactions between common buzzard *Buteo buteo* and goshawk *Accipiter gentilis* : Trade-offs revealed by a field experiment. *Oikos* **96**, 441–452.

Krüger, O. & Lindström, J. (2001) Lifetime reproductive success in common buzzard, *Buteo buteo* : From individual variation to population demography. *Oikos* **93**, 260–273.

Langthaler, P.B., Gladow, K.P., Krüger, O. & Beck, J. (2024) A Novel Method for Nonparametric Statistical Inference for Niche Overlap in Multiple Species. *Biometrical Journal* **66**, e202400013.

Levin, S.A. (1970) Community Equilibria and Stability, and an Extension of the Competitive Exclusion Principle. *The American Naturalist* **104**, 413–423.

Levine, J.M., Bascompte, J., Adler, P.B. & Allesina, S. (2017) Beyond pairwise mechanisms of species coexistence in complex communities. *Nature* **546**, 56–64.

Lourenço, R.F. & Rabaça, J.E. (2006) Intraguild Predation by Eagle Owls in Europe. *Airo* **16**, 63–68.

Mammen, U. & Stubbe, M. (1996) Der Greifvogelhorst in seiner populationsökologischen Bedeutung - The nest of raptors in their ecological meaning. *Populationsökologie Greifvögel- und Eulenarten* pp. 87–111.

Marini, L., Økland, B., Jönsson, A.M., Bentz, B., Carroll, A., Forster, B., Grégoire, J.C., Hurling, R., Nageleisen, L.M., Netherer, S., Ravn, H.P., Weed, A. & Schroeder, M. (2017) Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography* **40**, 1426–1435.

May, R.M. (1974) On the theory of niche overlap. *Theoretical Population Biology* **5**, 297–332.

Mebs, T. & Schmidt, D. (2014) *Die Greifvögel Europas, Nordafrikas, Vorderasiens.* Kosmos.

Merling de Chapa, M., Courtiol, A., Engler, M., Giese, L., Rutz, C., Lakermann, M., Müskens, G., Horst, Y., Zollinger, R., Wirth, H., Kenntner, N., Krüger, O., Chakarov, N., Mueller, A.K., Looft, V., Grünkorn, T., Hallau, A., Altenkamp, R. & Krone, O. (2020) Phantom of the forest or successful citizen? Analysing how Northern Goshawks (Accipiter gentilis) cope with the urban environment. *Royal Society Open Science* **7**, 201356.

Mittelbach, G.G. & McGill, B.J. (2019) *Community Ecology.* Oxford University Press.

Morosinotto, C., Villers, A., Thomson, R.L., Varjonen, R. & Korpimäki, E. (2017) Competitors and predators alter settlement patterns and reproductive success of an intraguild prey. *Ecological Monographs* **87**, 4–20.

Mueller, A.K., Chakarov, N., Heseker, H. & Krüger, O. (2016) Intraguild predation leads to cascading effects on habitat choice, behaviour and reproductive performance. *Journal of Animal Ecology* **85**, 774–784.

Nolte, M. (1969) *Die Siedlungsdichte Und Siedlungsweise Des Maeusebussards (Buteo Buteo) Im Ravensberger Land.* Bielefeld.

Ousterhout, B.H., Serrano, M., Bried, J.T. & Siepielski, A.M. (2019) A framework for linking competitor ecological differences to coexistence. *Journal of Animal Ecology* **88**, 1534–1548.

Parkinson, J.H., Kutil, R., Kuppler, J., Junker, R.R., Trutschnig, W. & Bathke, A.C. (2018) A Fast and Robust Way to Estimate Overlap of Niches, and Draw Inference. *The International Journal of Biostatistics* **14**.

Pfeiffer, T. & Meyburg, B.U. (2015) GPS tracking of Red Kites (Milvus milvus) reveals fledgling number is negatively correlated with home range size. *Journal of Ornithology* **156**, 963–975.

Pianka, E.R. (1974) Niche Overlap and Diffuse Competition. *Proceedings of the National Academy of Sciences* **71**, 2141–2145.

Pocheville, A. (2015) The Ecological Niche: History and Recent Controversies. *Handbook of Evolutionary Thinking in the Sciences* (eds. T. Heams, P. Huneman, G. Lecointre & M. Silberstein), pp. 547–586, Springer Netherlands, Dordrecht.

R Core Team (2024) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ripple, W.J., Beschta, R.L., Fortin, J.K. & Robbins, C.T. (2014) Trophic cascades from wolves to grizzly bears in Yellowstone. *Journal of Animal Ecology* **83**, 223–233.

Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12**, 982–998.

Rodriguez Curras, M., Manlick, P.J. & Pauli, J.N. (2025) Carnivore community reassembly provides a test of Eltonian niche conservatism. *Oikos* **n/a**, e10625.

Scherzinger, W. & Mebs, T. (2020) *Die Eulen Europas: Biologie, Kennzeichen, Bestände*. Kosmos.

Schoener, T.W. (1989) I.1 Ecological Niche. *Ecological Concepts: The Contribution of Ecology to an Understanding of the Natural World, Symposium British Ecological Society* (ed. J.M. Cherrett), pp. 3–13, Blackwell Scientific Publications, Cambridge.

Sergio, F. & Hiraldo, F. (2008) Intraguild predation in raptor assemblages: A review. *Ibis* **150**, 132–145.

Sergio, F., Marchesi, L. & Pedrini, P. (2003) Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. *Journal of Animal Ecology* **72**, 232–245.

Sippel, S., Meinshausen, N., Fischer, E.M., Székely, E. & Knutti, R. (2020) Climate change now detectable from any single day of weather at global scale. *Nature Climate Change* **10**, 35–41.

Stubbe, M. (1982) Brutdichte und Altersstruktur einer Rotmilan-Population - Milvus milvus (L., 1758) - im nördlichen Harzvorland der DDR im Vergleich zum Mäusebussard Buteo buteo (L., 1758). *Archiv für Naturschutz und Landeschaftsforschung* **22**, 205–214.

Trillmich, F. (1969) Zur siedlungsdichte von rotmilan (milvus milvus) und mäusebussard (buteo buteo) bei hildesheim. *Vogelwelt* **90**, 98–108.

Walls, S. & Kenward, R. (2020) *The Common Buzzard*. Bloomsbury Publishing.

Wickham, H. (2016) *Ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Wickham, H., Pedersen, T.L., Software, P. & PBC (2024) Gtable: Arrange 'Grobs' in Tables.

Wickham, H. & RStudio (2023) Tidyverse: Easily Install and Load the 'Tidyverse'.