

Does spatial co-occurrence of carnivores in a Central European agricultural landscape follow the null model?

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Abstract Spatiotemporal heterogeneity in the distribution of resources, interspecific competition and predation are important factors determining the spatial distribution and co-occurrence of many animal taxa. Here, we use data from scent station field studies and permutation-based null model analyses to test whether spatial co-occurrence of different carnivores' species is non-random in a Central European landscape that has been strongly modified and fragmented through human activity. In general, our results suggest a higher degree of spatial co-occurrence of different carnivore species than expected by chance; though it should be noted that this difference was not detectable under the conservative form of the null model. On the other hand, our data do not provide evidence for a significant degree of spatial segregation at the interspecific level. In conclusion, our results imply that antagonistic interactions, such as interspecific competition and predation, are not the dominant factors shaping spatial distribution of carnivores. Consequently, we suggest that the high degree of spatial co-occurrence might be a

consequence of spatial heterogeneity in distribution of resources that are shared at the interspecific level.

Keywords Carnivores · Co-occurrence · Interspecific competition · Mesopredator release · Agricultural landscape

Introduction

The current European landscape has been markedly affected by the expansion of agriculture and urban development, which has led to the destruction and fragmentation of many natural habitats (Faaborg et al. 1993; Vitousek et al. 1997). Habitat loss and the reduction in size of large habitat patches concentrates native organisms within smaller and more isolated habitat remnants, which may result in an increase in direct and indirect interactions both between conspecific and interspecific individuals (Nee and May 1992; Hanski 2008). Competition between key trophic species, such as carnivores, could have a strong effect on the whole carnivore community as an important factor structuring their populations and determining spatial distribution of individual species (Crooks and Soulé 1999). For example, interspecific competition and/or predation between dominant members of a carnivore guild may reduce population densities, cause local extinction or affect spatial distribution of subordinate carnivore species (Polis et al. 1989; Creel and Creel 1996; Palomares and Caro 1999). These factors are important, therefore, as regards conservation of carnivore populations.

Interspecific interactions between carnivore species have been intensively studied in recent years, especially within the context of the 'mesopredator release hypothesis' (Crooks and Soulé 1999; Lloyd 2007; Rayner et al. 2007; Helldin et al. 2006; Elmhagen et al. 2010). Under the most typical scenario predicted by this hypothesis, extinction of sensitive carnivore species (i.e. top predators) due to fragmentation of natural habitats will result in the release of interspecific

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interactions between top predators and mesopredators and, consequently, an increase in mesopredator populations. This may have a dramatic effect on trophic interactions within an ecosystem, inducing declines in prey species due to an increase in predation pressure (Crooks and Soulé 1999; Rayner et al. 2007).

Top predators “sensu stricto” have disappeared in many areas due to fragmentation and loss of natural habitats (Crooks and Soulé 1999; Crooks 2002). Carnivores persisting in fragmented landscapes following the extinction of top predators, however, often show pronounced differences in body mass and in competitive abilities. As in the case of the classical top predator–mesopredator(s) model, it is possible that the spatial distribution and population size of these species will also be shaped by antagonistic interspecific interactions (see for example McDonald et al. 2007). Such antagonistic interactions are expected to result in segregated distribution of different species, i.e. a lower degree of spatial co-occurrence than expected by chance. Alternatively, different habitat preferences due to segregated niches may also result in segregated distribution at the interspecific level. In fragmented landscapes, however, other processes in addition to antagonistic interactions may lead to aggregated distributions of different carnivore species. For example, spatial variation in the quality or accessibility of resources essential for more than one species may cause those species to co-occur more often than expected by chance (e.g. Šálek et al. 2010).

In agricultural landscapes of Central Europe, the red fox (3–10 kg), Eurasian badger (4–20 kg), stone marten (*Martes foina*, 0.9–2.1 kg), pine marten (*Martes martes*, 0.8–1.6 kg), polecat (*Putorius putorius*, 0.5–2 kg), stoat (*Mustela erminea*, 0.15–0.35 kg) and least weasel (*Mustela nivalis*, 0.03–0.16 kg) co-exist sympatrically. A non-native carnivore species, the domestic cat (*Felis catus*, 1.2–8 kg), co-occurs in the same area, though its activity is mostly concentrated near human settlements where their resting sites are mainly situated (Barratt 1997; Germain et al. 2008). Small mammals are the most important prey for most of the carnivores inhabiting Central European agricultural landscapes (Jedrzejewski and Jedrzejewska 1992; McDonald et al. 2000; McDonald 2002) and, based on their diet spectrum, they can be classified as either primary specialists (such as the small mustelids *M. nivalis* and *M. erminea*) with small mammals comprising 77–85 % of the diet (e.g. Martinoli et al. 2001; Elmeros 2006; Lanszki and Heltai 2007); or mesocarnivore generalists, where small mammals comprise a smaller proportion of the diet, varying between 25 and 70 % (Bertolino and Dore 1995; Prigioni and De Marinis 1995; Genovesi et al. 1996; Goldyn et al. 2003). The diet of the Eurasian badger is also composed of a variety of food items; invertebrates and fruits, however, are the most important items and the proportion of small mammals usually does not exceed 35 % (Goszczyński et al. 2000). All the carnivores display mainly crepuscular or

nocturnal activity (e.g. Lodé 1995; Doncaster and MacDonald 1997; Kowalczyk et al. 2003; Sidorovich et al. 2008) and they inhabit a wide range of habitat types (Gehring and Swihart 2003; Pita et al. 2009). Our previous research, however, has shown that in a landscape affected by intensive agriculture, carnivores generally prefer small forest fragments over larger blocks and that activity is mainly focused along the prey-rich habitat edges (Šálek et al. 2009; Šálek et al. 2010; Svobodová et al. 2011; Červinka et al. 2011).

The main aim of this study was to test the hypothesis that spatial co-occurrence of carnivores in agricultural landscape is non-random, i.e. that the presence of a given carnivore is affected by the presence/absence of the remaining members of this guild, resulting in a higher or lower degree of spatial co-occurrence than expected by chance. To do this, we analysed a large carnivore spatial distribution dataset based on presence/absence data gathered using scent stations along habitat edges (i.e. forest-farmland edges, corridors). Our statistical approach was based on the comparison of real carnivore spatial distribution data with a hypothetical distribution derived from null models (Gotelli 2000) which assumes visits to individual localities by individual predators are not affected by the presence/absence of other carnivore species. Deviation of our data from the null model would suggest that the distribution of carnivore visits is non-random, i.e. biased either toward higher co-occurrence or toward higher avoidance of interspecifics than expected by chance. Due to the correlative nature of the input data, the null model approach does not allow recovery of the causative factors leading to observed patterns; however, it is often the only possible means of analysing complex patterns and interactions in community ecology (Gotelli 2000). For example, an examination of the causes of observed spatial distribution patterns would require an unfeasible level of controlled population density manipulation for individual species, as well as other factors that may affect co-occupancy, such as prey density.

As the effect of interspecific carnivore interactions on spatial distribution have not previously been studied in European agricultural landscapes, we believe that our contribution based on null model analysis represents a first logical step that may stimulate and direct further research in this field.

Material and methods

Study area

We compiled a database using data from six independent field studies focused on carnivore distribution in intensive agricultural landscapes in the Czech Republic (Table 1), performed between 2005 and 2010 in south Bohemia

Table 1 Summary of field experiments used to evaluate spatial co-occurrence of carnivore species

Source	Habitat	Study area (km ²)	Year	Season	Design	Sampling days	Sampling spots
Šálek et al. 2009	Corridor	95	2005–2006	Spring	Independent sample spots	5	41
Šálek et al. 2010	Forest edge+corridor	250	2006–2007	Spring	Independent sample spots	5	100
Svobodová et al. 2011	Forest edge	60	2006–2007	Spring	Independent sample spots	5	40
Červinka et al. 2013	Corridor	700	2008–2009	Spring+autumn	Independent sample spots	5	228
Červinka et al. 2013	Corridor	340	2009–2010	Spring	Independent sample spots	5	120
Červinka et al. 2011	Forest edge	1,502	2008–2009	Spring	Two sample spots at the same site, 0 and 25 m from the habitat edge	8	154

(49°0'44.010"N, 14°20'27.451"E) and south Moravia (48°52'18.616"N, 16°24'59.472"E). The total study area for all six field studies comprised 2,602 km². The landscape in this area has been highly modified by intensive agricultural practices and urbanisation over the last 60 years, with the most significant changes occurring in landscape structure; principally, the reduction in size of already fragmented vegetation and non-agricultural patches and changes in agricultural management, including an increase in soil fertilisation and a switch from spring to autumn sowing (Lipský 2000; Boucníková and Kučera 2005).

The study region has a flat or gently rolling landscape (altitude varying from 210 to 520 m) composed of a mosaic of agricultural land dominated by crop and hayfields and extensively used pastures, a variety of human-made fish ponds, human settlements, gardens, orchards and non-agricultural habitats with scattered vegetation (e.g. corridors). Highly fragmented forest remnants, consisting of small patches of secondary coniferous or mixed forest, are embedded within the agriculture land. Crop fields are mainly used for intensive cultivation of cereals, maize and legumes, while grasslands are composed almost exclusively of production hayfields (mown twice a year) or extensive pastures. The agricultural matrix is composed of relatively short (<70 cm) vegetation in the pre-harvest period. During the harvest season, however, the vegetation is high and dense with an average height of 1–1.5 m.

Our study focuses on the analysis of carnivore co-occurrence in two habitats characterised by high densities of small mammals, the principal prey of carnivores (e.g. Šálek et al. 2010):

1. Forest-farmland edges: usually fringed with *Quercus robur* and forest trees such as *Picea abies*, *Pinus sylvestris*, *Populus tremula* and *Betula pendula*. The shrub layer is dense, consisting mainly of shrubs and saplings of canopy trees (*Corylus avellana*, *Prunus spinosa* and *Acer platanoides/pseudoplatanus*). This habitat type is characterised by dense and diverse herbaceous vegetation originating mainly from the nearby hayfield, though many understory species are also present.
2. Corridors: consisting primarily of narrow strips of shrubby vegetation and dense long-stemmed grasses around watercourses, with widths ranging from 2 to 12 m and lengths ranging from 200 m up to several kilometres. Shrubs were dominated by either *P. spinosa* or *Salix* spp. in mesic and more humid habitats, respectively. *Calamagrostis epigejos*, *Festuca rubra*, *Arrhenatherum elatius* and *Geum urbanum* were typical understory species in mesic corridors, while *Filipendula ulmaria*, *Lysimachia vulgaris* and *Scirpus sylvatica* were dominant in the understory layer of humid habitats. Long-stemmed vegetation was comprised primarily of *Phalaris arundinacea* and *Carex* spp.

We did not include data on carnivore distribution from forest and grassland interiors as carnivores rarely visit these habitat types, probably due to low small mammal abundance (see Šálek et al. 2009; Šálek et al. 2010). In addition, preliminary analyses suggested that statistical power to detect any deviation from random distribution based on poor quality habitat data that have been collected is extremely low (Šálek et al. unpubl. data).

Carnivore survey

Various methods have been developed to assess carnivore distribution and habitat utilisation (e.g. Gompfer et al. 2006; Long et al. 2008), all of which must take account of specific ecological and behavioural features of carnivores, such as wariness of humans, nocturnal activity, secretive habits and low population densities (Sargeant et al. 2003). For our research, we decided to use scent stations, one of the most widely used methods for large spatial-scale carnivore observations (e.g. Linhart and Knowlton 1975; Zielinski and Stauffer 1996; Crooks and Soulé 1999; Gehring and Swilhart 2003; Mortelliti and Boitani 2007; Long et al. 2008). For a detailed description of the methodology, see Šálek et al. (2009) or Šálek et al. (2010). In brief, scent stations were monitored for five to eight consecutive days. Presence of footprints was checked every morning or, in one case (Červinka et al. 2011), every second morning (see

Table 1). In the case of rainfall, the observation was interrupted and restored scent stations were checked again after 2 days. Slight heterogeneities in design between individual field studies were controlled statistically, thus they cannot bias our conclusions (see the Statistics section for further details). Identification of carnivores was based on footprint dimensions and shape characteristics (Anděra and Horáček 2005). We excluded data on domestic dogs from our analysis as their occurrence is mostly dependent on human activity (see Lenth et al. 2008) and stray or feral domestic dogs are rare or absent in our study area (M. Šálek, personal observation). Footprints that were not unambiguously assigned to a given species were also excluded from the dataset.

Data analysis

In most field studies, spatially unclustered scent stations (i.e. minimal distance between adjacent scent stations <500 m) were used (Šálek et al. 2009; Šálek et al. 2010; Svobodová et al. 2011; Červinka et al. 2013). Individual scent stations were assumed to correspond to “sampling spots”, i.e. spatial units that were used in subsequent statistical analyses (see below). For technical reasons, scent stations were clumped into spatially non-independent groups in one study (Červinka et al. 2011), the distance between individual scent stations in this group being <100 m. As carnivores exploit home ranges that exceed this spatial-scale considerably (Gittleman and Harvey 1982; MacDonald et al. 2004), these scent station groups were treated as sampling spots.

Multiple visits to a given sampling spot by the same carnivore species could have been caused by the same individual. To avoid this source of pseudo-replication, we considered individual carnivore species to be either present or absent at the scent station during a given temporal replication at a given field study. Thus, like the vast majority of previous studies focusing on community co-occurrence patterns (reviewed in Gotelli 2000; Gotelli and McCabe 2002), our analysis uses set binary presence/absence matrices, where individual matrices (i.e. strata that were used as constraints for generation of null communities, see below) correspond to a given temporal replication during a given field study; matrix rows corresponding to individual species and columns to individual sampling spots. This type of database is useful for analysis of co-occurrence patterns at a temporal scale corresponding to individual matrices (i.e. 5–8 days, see Table 1). Interactions between individuals of different species that determine the pattern of their spatial co-occurrence, however, may also operate on a finer temporal scale. To take such interactions into account, it is hypothetically possible to run an analysis where individual days within temporal replicates of individual field studies are treated as separate units (i.e. individual presence/absence matrices). Aside from the

above mentioned problem with pseudo-replication, we felt that this type of analysis was inappropriate for our dataset. First, we used the whole sampling period (i.e. 5–8 days of scent station exposure) as the basic temporal unit in order to reduce sampling error for a given community due to false negative records. If we had used the day-by-day data, the effect of false-negative observations would increase and inflate our analysis. Second, day-by-day data would enable us to analyse the concurrence pattern for a 24-h period only, which may be too rough a temporal scale to detect short-term effects. Finally, although interactions at a fine temporal scale (i.e. in the order of hours) may be interesting from an ethological point of view, its applicability in other, possibly more important, contexts, such as biodiversity conservation (i.e. the conservation of both carnivore species and the biota affected by their impact), is questionable.

The major aim of this contribution is to evaluate the null hypothesis that the probability of spatial co-occurrence between different carnivore species is similar to that expected by chance. To do this, we compared our presence/absence data with null models. These generate null communities (i.e. communities where species distribution is not affected by interactions) using randomisation of original presence/absence matrices. Several null model types have been proposed for analysis of spatial association patterns at the interspecific level (reviewed in Gotelli 2000). As conclusions derived from different null models may vary, we used two types in this study, the fixed–equiprobable (FE) model and the fixed–fixed (FF) model. These have previously been shown to exhibit appropriate statistical properties, i.e. reasonably low rates of Type I and II errors (Gotelli 2000), and are commonly used for analysis of similar data (e.g. Azeria et al. 2012). Whereas the FF null model is conservative in detecting aggregated distributions (i.e. higher co-occurrence than expected by chance), the FE model is conservative in detecting segregation patterns (i.e. lower co-occurrence than expected by chance; see for example Gotelli 2000; Azeira et al. 2012). Under the FE null model, the total number of sampling spots visited by individual species remains unchanged (i.e. fixed row totals) but presence/absence observations of individual species are randomly redistributed among sampling spots. Under the FF model, both number of species observed at individual sampling spots and presence/absence totals for individual species are maintained (i.e. both fixed rows and columns). To control for potential bias that may arise due to heterogeneity between individual field studies or between-year differences in abundance of individual carnivore species, visits of individual carnivore species were randomly redistributed only among sampling spots corresponding to a particular temporal replication for a given field study. Using these constraints, we generated 1,000 randomised matrices for both FF and FE. These randomised matrixes were constructed using the function `permatswab` implemented in the R (v. 2.11.1 software, R

Development Core Team 2010) package Vegan (Oksanen et al. 2010).

As a first step, we tested whether spatial distribution of individual carnivore species pairs exhibited an aggregated or segregated pattern, using the Sorensen index of association (SOR; Dice 1945) to quantify the degree of spatial co-occurrence between all possible species pairs (e.g. Azeria et al. 2012). SOR was extracted from community matrixes using the function `betadiver` implemented in Vegan. Association between species pairs was considered non-random if the corresponding SOR was not included in 95 % CI derived from permutations.

We further tested whether there was any general community-wide co-occurrence pattern, irrespective of the species involved in individual interactions. The community-wide association index corresponds to the mean of association indices across all pairwise interactions ($n=21$ in our case). Its significance was assessed by comparison of the observed community-wide index with the distribution of permutation-based community-wide indices. In addition, we converted these community-wide association indices into standardised effect sizes (SEs) using the formula described in Gotelli and McCabe (2002): $SES = (I_{Obs} \times I_{sim}) / \delta_{sim}$, where I_{Obs} is the observed index of association between a given species pair and I_{sim} and δ_{sim} are the mean null model based index of association and its standard deviation. We used four different types of association matrix to compute community-wide SEs (e.g. see Azeira et al. 2012), the SOR, the Jaccard index (JAC; Jaccard 1901), the checkerboard score index (CU; Stone and Roberts 1990) and the recently proposed standardised version of CU, the StCU (Azeria et al. 2009). SE values greater than 1.98 indicate a significantly segregated distribution (at $\alpha=0.05$) in the case of CU and StCU and aggregated distribution in the case of the SOR or JAC indices, and vice versa when SE values are less than -1.98.

Finally, we tested whether there was any association between the tendency to prefer/avoid sites where heterospecifics occur and body mass difference between individual carnivore species (a proxy of carnivore competitive ability), as implied by the mesopredator release hypothesis. To achieve this, we computed SEs for individual species pairs and performed linear regression between these pairwise SEs and pairwise absolute body mass differences. Data on carnivore body mass in the Czech population was obtained from Anděra and Horáček (2005). We used mid-values reported by these authors, an average of female and male body mass mid-values being used if a given species exhibited sexual dimorphism in this parameter.

Domestic cats were frequently detected during field work and may have had a large effect on the outcome of our analysis as its distribution is affected by distance to human settlements (Ferreira et al. 2011). All analyses, therefore,

were performed for both the whole database and for data with records of domestic cat excluded.

Results

We used 496 records of seven carnivore species at 683 sampling spots to evaluate carnivore co-occurrence patterns. We documented the occurrence of least weasel (60 [8.8 %] localities visited), stoat (95 [13.9 %] localities visited), polecats (European polecat and steppe polecat, 67 [9.8 %] localities visited), martens (pine marten and stone marten, 82 [12.0 %] localities visited), Eurasian badger (15 [2.2 %] localities visited), red fox (71 [10.4 %] localities visited) and domestic cat (106 [15.5 %] localities visited).

Based on SORSs, just one and five species pairs out of 21 were proved to co-occur significantly more frequently than expected by chance under the FF and FE null models, respectively (Table 2). Interestingly, most of the pairwise association indices that proved to be significant were interactions between the domestic cat and other carnivores (four out

Table 2 Observed Sorensen association index (SOR; Dice 1945) scores and permutation-based confidence intervals for individual species pairs computed under the Fixed–Fixed (FF) and Fixed–Equiprobable (FE) null models (Goletti 2000). Significant differences between observed data and null model outputs ($\alpha=0.05$) are in bold

Species pair	FF null model SOR (\pm 95 % CI)	FE null model SOR (\pm 95 % CI)
Cat–fox	0.1387 (0.2543~0.1156)	0.1387 (0.2080~0.0693)
Cat–badger	0.1186 (0.1186~0.0169)	0.1186 (0.1016~0.0000)
Cat–marten	0.2333 (0.2555~0.1222)	0.2333 (0.2111~0.0777)
Cat–polecat	0.1893 (0.2248~0.0946)	0.1893 (0.1893~0.0710)
Cat–stoat	0.1938 (0.2244~0.1020)	0.1938 (0.1836~0.0714)
Cat–weasel	0.1754 (0.2456~0.1052)	0.1754 (0.1988~0.0701)
Fox–badger	0.0470 (0.1182~0.0000)	0.0470 (0.0941~0.0000)
Fox–marten	0.1224 (0.2176~0.0816)	0.1224 (0.1904~0.0544)
Fox–polecat	0.1323 (0.2058~0.0731)	0.1323 (0.1764~0.0441)
Fox–stoat	0.1595 (0.2085~0.0858)	0.1591 (0.1717~0.0490)
Fox–weasel	0.1304 (0.2173~0.0724)	0.1304 (0.1884~0.0434)
Badger–marten	0.1087 (0.1304~0.0000)	0.1087 (0.1086~0.0000)
Badger–polecat	0.0246 (0.1234~0.0000)	0.0246 (0.0987~0.0000)
Badger–stoat	0.0370 (0.1111~0.0000)	0.0370 (0.0925~0.0000)
Badger–weasel	0.0481 (0.1204~0.0000)	0.0481 (0.0969~0.0000)
Marten–polecat	0.1258 (0.2097~0.0839)	0.1258 (0.1818~0.0419)
Marten–stoat	0.1764 (0.2235~0.0941)	0.1764 (0.1882~0.0588)
Marten–weasel	0.1655 (0.2482~0.1103)	0.1655 (0.2068~0.0689)
Polecat–stoat	0.1006 (0.1886~0.0628)	0.1006 (0.1635~0.0503)
Polecat–weasel	0.0746 (0.1940~0.0597)	0.0746 (0.1641~0.0298)
Stoat–weasel	0.1490 (0.2236~0.0869)	0.1490 (0.1739~0.0618)

of five cases under the FE model). No species pair exhibited significantly negative association.

Irrespective of association index type, whole community association indices suggest a significantly higher degree of co-occurrence than expected under the FE null model. The difference remained significant even when data for the domestic cat was excluded. Nevertheless, the domestic cat's contribution to co-occurrence pattern strength was considerable as SESs were approximately two times higher for analyses including domestic cat data. Contrary to FE, the FF model did not recover any deviation for the null expectation (Table 3).

We found no correlation between absolute carnivore body mass difference and pairwise SESs using linear regression. Results remained non-significant irrespective of association index type used for calculation of SES and presence of domestic cat data.

Discussion

Habitat fragmentation and human-induced habitat loss force species to occupy ever decreasing and more isolated patches of suitable habitat, often resulting in an increase in the frequency of interspecific interactions (Nee and May 1992; Wiens 1993; Hanski 2008). Interspecific competition is an important factor structuring carnivore communities and as such may affect a whole cascade of trophic relationships. Therefore, it is highly appropriate to consider such interactions and apply them to biodiversity conservation (e.g. Crooks and Soulé 1999; Rayner et al. 2007). Interactions

between carnivores may be characterised either as a direct predatory impact (i.e. interspecific predation; Palomares and Caro 1999) or through competition for resources such as food, den sites or territories (Ritchie and Johnson 2009). For example, larger, more dominant species may out-compete subordinate species, causing behavioural changes in their activity patterns or habitat use (Linnell and Strand 2000). Consequently, these antagonistic interactions are predicted to result in the segregated spatial distribution of different carnivore species (Connor and Simberloff 1979; Gotelli 2000). Contrary to this prediction, however, null model analysis of whole community patterns provides no evidence for the segregated distribution of carnivores inhabiting intensive agricultural landscapes, at least at the temporal scale encompassing our field studies (5–8 days). In addition, none of the species pairs evaluated by pairwise comparison in this study exhibited a significant bias toward segregated distribution. If interspecific interactions play an important role in the spatial structuring of a given community, differences in the dominance rank or competitive ability between any two species would be reflected in the strength of spatial segregation. We found no support for this, however, because the correlation between the strength of spatial association and absolute value of body mass difference (a proxy for dominance rank difference) for all species pairs was not significant. This analysis supports our conclusion that antagonistic interactions are unlikely to shape the spatial distribution of carnivores substantially in an intensive agricultural landscape.

In general, our whole community analysis indicated that carnivores tend to co-occur more frequently than expected based on the null FE null model. The difference between our observations and the outcome of the null model was not significant using the FF model. Nevertheless, it is worth noting that the FF model is conservative with respect to the detection of aggregated distributions (Gotelli 2000) and at the same time is not as sensitive when using matrices of low fill, which was the case with our dataset (matrix fill=0.10). Our previous research has shown that mesocarnivore activity is generally concentrated in patches where their principal prey, small mammals, are found in high densities, i.e. in corridors along the edges of small residual forest fragments (Šálek et al. 2010; Červinka et al. 2011, 2013). We hypothesise, therefore, that aggregated distributions detected in the carnivore community are predominantly driven by preferences for high quality foraging patches shared at the interspecific level. There is, however, an alternative explanation for the observed pattern. The spatial co-occurrence of carnivore species may also be associated with similar micro-habitat preferences for special vegetation structures/patches, such as dense shrub or canopy cover, that provide shelter and protection against avian predators (Lozano et al. 2003; Blaum et al. 2007; Mangas et al. 2008). Further, forest edges or corridors in fragmented

Table 3 Community-wide analysis of co-occurrence patterns based on data for all carnivore species detected and for all carnivores without the domestic cat. Standardised effect sizes (SES; Goletti and McCabe 2002) and permutation-based *p* values were computed under the fixed–fixed (FF) and fixed–equiprobable (FE) null models (Goletti 2000) for four association indices: C-Score (CU; Stone and Roberts 1990), standardised C-Score (CUS; Azeira et al. 2009), Jaccard index (JAC; Jaccard 1901) and Sorensen index (SOR; Dice 1945). Significant differences between observed data and null model outputs ($\alpha=0.05$) are in bold

	Index	FF null model		FE null model	
		SES	<i>p</i>	SES	<i>p</i>
All species	CU	-1.264	0.204	-4.609	<0.001
	stUS	-0.062	0.994	-4.080	<0.001
	JAC	-0.853	0.418	4.288	0.002
	SOR	-1.055	0.320	4.363	<0.001
Without domestic cat	CU	1.359	0.154	-2.527	0.018
	stCU	1.309	0.200	-2.100	0.049
	JAC	-1.708	0.080	2.307	0.036
	SOR	-1.760	0.070	2.311	0.040

landscapes could serve as important dispersal/movement structures within an individual home range (Rondinini and Boitani 2002; Šálek et al. 2009), which could also lead to increased frequency of interspecific carnivore interactions.

Interestingly, the domestic cat appeared to play an important role in the occurrence of aggregated carnivore distributions in our study area. Four out of five significant pairwise tests under the FE model included the domestic cat. Although our data still suggest a significantly higher co-occurrence than expected after the removal of the domestic cat from our analyses, the difference in the magnitude of the effect decreased by approximately half. As we are not aware of any direct mechanism that could explain such a strong influence of the domestic cat, we hypothesise that the effect was mediated indirectly. For example, some free-ranging carnivore species may be attracted to human settlements (characterised by high domestic cat activity) due to increased resource densities, as previously documented for several mesocarnivore species (Prange and Gehrt 2004; Ordeñana et al. 2010; reviewed in Bateman and Fleming 2012).

Methodological constraints (discussed above) meant that our analyses of carnivore co-occurrence were evaluated at a temporal scale corresponding with the duration of individual experiments (i.e. 5–8 days). Thus, we cannot exclude the possibility that the high co-occurrence of intraguild carnivore competitors in the same habitat could have been mediated by mechanisms that we were unable to evaluate. For example, one species may visit sampling spots at different times of day to avoid direct confrontation with another (Johnson et al. 1996; Jędrzejewski et al. 2000; Linnell and Strand 2000; Harrington et al. 2009). In addition, the spatial segregation of habitats at a relatively fine scale might facilitate the co-occurrence of more species (Linnell and Strand 2000; Sidorovich et al. 2009). Further research, which utilises finer temporal and spatial scales to monitor carnivore activity (e.g. Moruzzi et al. 2002), may shed more light on this topic.

In conclusion, this study showed that the spatial distribution of carnivores in an intensive agricultural landscape exhibits a higher degree of spatial co-occurrence among species than could be expected by chance, at least in habitats with high prey densities. This suggests that potential risks resulting from spatial association with intraguild competitors/predators are low or that they are overshadowed by the potential benefits resulting from use of the same patch (see also Davis et al. 2011). Further research is necessary to provide support for one or other of these two alternatives. For example, the spatial pattern of carnivore spatial co-occurrence could differ between habitats with contrasting resource abundance. Additionally, whereas carnivore species co-occur more than could be expected by chance in prey-rich habitats, as shown in this study, they could be distributed randomly, or co-occur less than expected, in prey-poor habitats (such as forest and grassland interiors) because the

resultant benefits of spatial co-occurrence would be low and potentially overshadowed by the costs or risk. Alternatively, manipulative experiments (e.g. Vanak et al. 2009) could also prove useful in assessing these alternatives.

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