








RESEARCH ARTICLE

Spatiotemporal interactions of a novel mesocarnivore community in an urban environment before and during SARS-CoV-2 lockdown

Julie L. P. Louvrier^{1,2}  | Aimara Planillo^{1,3}  | Milena Stillfried¹ | Robert Hagen¹  |
Konstantin Börner¹ | Sophia Kimmig¹  | Sylvia Ortmann¹  | Anke Schumann¹ |
Miriam Brandt¹  | Stephanie Kramer-Schadt^{1,2,3} 

¹Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany

²Institute of Ecology, Technische Universität Berlin, Berlin, Germany

³Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Gartenhaus, Berlin, Germany

Correspondence

Julie L. P. Louvrier

Email: louvrier@izw-berlin.de

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Abstract

1. Studying species interactions and niche segregation under human pressure provides important insights into species adaptation, community functioning and ecosystem stability. Due to their high plasticity in behaviour and diet, urban mesocarnivores are ideal species for studying community assembly in novel communities.
2. We analysed the spatial and temporal species interactions of an urban mesocarnivore community composed of the red fox *Vulpes vulpes* and the marten *Martes* sp. as native species, the raccoon *Procyon lotor* as invasive species, and the cat *Felis catus* as a domestic species in combination with human disturbance modulated by the SARS-CoV-2 lockdown effect that happened while the study was conducted.
3. We analysed camera trap data and applied a joint species distribution model to understand not only the environmental variables influencing the detection of mesocarnivores and their use intensity of environmental features but also the species' co-occurrences while accounting for environmental variables. We then assessed whether they displayed temporal niche partitioning based on activity analyses, and finally analysed at a smaller temporal scale the time of delay after the detection of another focal species.
4. We found that species were more often detected and displayed a higher use intensity in gardens during the SARS-CoV-2 lockdown period, while showing a shorter temporal delay during the same period, meaning a high human-induced spatiotemporal overlap. All three wild species spatially co-occurred within the urban area, with a positive response of raccoons to cats in detection and use intensity, whereas foxes showed a negative trend towards cats. When assessing the temporal partitioning, we found that all wild species showed overlapping nocturnal activities. All species displayed temporal segregation based on temporal delay. According to the temporal delay analyses, cats were the species avoided the most

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by all wild species. To conclude, we found that although the wild species were positively associated in space, the avoidance occurred at a smaller temporal scale, and human pressure in addition led to high spatiotemporal overlap.

5. Our study sheds light to the complex patterns underlying the interactions in a mesocarnivore community both spatially and temporally, and the exacerbated effect of human pressure on community dynamics.

KEYWORDS

activity patterns, camera trap, joint species distribution models, mesocarnivores, SARS-CoV-2 lockdown effect, spatial niche, temporal niche partitioning, urban ecology

1 | INTRODUCTION

Biotic communities are highly influenced by interspecific interactions such as predation, competition, parasitism or mutualism (Chesson, 2000; Letten et al., 2017). Predation or competition can play an important role in niche segregation with consequences such as lower population growth rate and smaller spatial ranges (Linnell & Strand, 2000; Parsons et al., 2019). Human-dominated landscapes can redefine the realised niche of a wildlife population, mostly because human activities may limit the growth and distribution of some species while favouring others, hence playing the role of the 'hyperkeystone' (i.e. a high-order species that regulates other keystone species Moll et al., 2021; Worm & Paine, 2016) directly or indirectly (Alberti et al., 2003; Smith et al., 2018). This makes urban areas an ideal setting to study the effects of species interactions on niche segregation.

The worldwide growing urbanisation can represent a permanent loss of natural habitat for wildlife species (Miller & Hobbs, 2002), together with changes of species communities with new species interactions (Beninde et al., 2015; Farinha-Marques et al., 2011; Johnson & Munshi-South, 2017). Urban ecosystems are considered ecologically novel due to the new conditions differing from conditions in natural habitats and the heavy influence of human activities (Lundholm & Richardson, 2010; Pickett et al., 2001; Shochat et al., 2006). Urban areas also host high densities of pet animals, which may represent direct negative interactions and disturbances (Lenth et al., 2008; Plaza et al., 2019). Because urban growth is an evolutionarily recent phenomenon, wildlife species have to rapidly adapt to these changes in habitat and communities (Smith et al., 2018).

Studying species interactions and niche segregation in an urban area can provide important insights into community functioning in novel environments (Parsons et al., 2019). Such information can inform management measures to protect threatened species, slow down the invasion of alien species (Pyšek et al., 2020) and help understanding how human alterations of communities could lead to changes in trophic cascades (Ricklefs, 1987).

Niche segregation can be studied based on the environmental features species select in any given environment, but also habitat use intensity and temporal shifts within the same spatial niche

(Ben-David et al., 1996; Zabala et al., 2009). Daily activity patterns can be adapted depending on environmental conditions, interference from competitors, food resource availability and human presence (Kronfeld-Schor & Dayan, 2003; Lesmeister et al., 2015; Oberosler et al., 2017; Pereira, 2010). As human activities are mostly concentrated during the day, some species have showed a shift in their diel activities towards nocturnal activities (Gaynor et al., 2018).

Mesocarnivores are ideal for studying community assembly in novel communities due to their high behavioural and trophic plasticity (Crooks & Soulé, 1999; Gehrt et al., 2011; Lombardi et al., 2017). The extirpation of larger competitors has facilitated mesocarnivores' population expansion in urban areas (Prugh et al., 2009), leading to increasing intra-guild competition over available sources (Greenwood et al., 1999). Because competition and predation are common among carnivore species and have been found to have consequences on spatial and temporal niche segregation (Carter et al., 2015; Swanson et al., 2016), studying their communities should be done while accounting for such interactions (Palomares & Caro, 1999; Parsons et al., 2019).

For mesocarnivores, several spatial niches and habitat utilisations are possible in urban areas, all with a different degree of human disturbance (Bateman & Fleming, 2012). These features can be used for different purposes for instance railways for movement paths (Lewis et al., 1993; Trewhella & Harris, 1990) and green areas as shelters (Adkins & Stott, 1998; Baker et al., 2000; Baker & Harris, 2007). Mesocarnivores display a diverse range of behaviours as a reaction to human activity (Barrueto et al., 2014; Sévêque et al., 2020; Smith et al., 2015; Wang et al., 2015; Wilmers et al., 2013). Some may benefit from human activities due to tolerance of the latter (McKinney, 2006), exploitation of anthropogenic resources (Newsome, 2015) and absence of predators (Crooks & Soulé, 1999).

Due to their similar ranges and habitat requirements, mesocarnivores may form hierarchies within the community (Cozzi et al., 2012; Kamler et al., 2012; Remonti et al., 2012). Such hierarchies, due to the novelty of the environment and species assembly, may differ from communities in natural habitats, with dominant species displaying tolerance to human disturbance and boldness rather than direct competitive advantage (Geffroy et al., 2015). Humans mediate the sympatry of competing carnivores, pushing also the dominant

species into the nighttime and hence forcing apparent coexistence (Moll et al., 2018; Sévêque et al., 2020).

Private gardens may represent an important source of food for mesocarnivores in urban environments, due to the presence of composts, preys and pet food (Baker & Harris, 2007; Contesse et al., 2004; Lewis et al., 1993). Due to that fact, we could expect a higher rate of visits than in other green parts of the city and consequently, higher rates of interactions between mesocarnivores. Pet cats are strongly linked to human presence, and their presence may therefore represent a factor to account for when studying mesocarnivore interactions in urban areas. Pet cats can indicate gardens with pet food left outside or in the trash, but also represent a disturbance for other wildlife species (Cechetti et al., 2021; Doherty et al., 2017; Medina et al., 2011).

Using camera trap data from multiple gardens across the city and from five consecutive sampling phases spanning two SARS-CoV-2 lockdown seasons, we studied the spatial and temporal niche segregation of the urban mesocarnivore community in Berlin, Germany.

More specifically, we wanted to investigate the effect of the presence of domestic cats and raccoons on the occurrence, habitat use intensity, nocturnality and temporal activity patterns of the native species, and the role of human pressure on the activity patterns of the whole novel community. Our hypotheses were (a) Urban variables (i.e. at large scale), representing human disturbance will affect the spatial distribution of the species, while (b) garden variables (i.e. at small scale), representing local shelter and food availability, together with species interactions will determine the use intensity by the species, (c) raccoons and cats will have negative effects on both native species distribution, habitat use intensity and nocturnality, (d) activity patterns in gardens will mostly be nocturnal due to avoidance of human activities, (e) species with positively correlated presence and use of gardens will show local temporal shifts of activity to avoid intra-guild competition, represented by a differentiation of time of delay after a focal species was present in a garden. According to allometric scaling laws of body size, we would expect that raccoons are dominant over foxes, foxes over cats and cats over martens, and that this will be expected in their times of delay, (f) a diminution in human activities represented by the SARS-CoV-2 pandemic lockdown will lead to an increase in detections and use of gardens, and consequently a negative effect on time of delay, that is, species will occur with a higher frequency in gardens.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out in the city state of Berlin, Germany (52°31'N, 13°24'E). Berlin is the capital and largest city in the country with a population of nearly 3.65 million people and an area of 892 km² (Amt für Statistik, 2017). Berlin encompasses densely populated areas interspersed with parks in the city centre and large green spaces and forests in the surroundings, with multiple residential

areas composed of family houses with gardens. The built-up area constitutes 48% of the city surface, green and open areas occupy 17.6%, forests 17.5%, roads 10.9% and water bodies 6% (Berlin Environmental Atlas, 2018). Green and open areas of Berlin include parks, private yards, allotments, cemeteries, recreational areas, sports grounds and street green. In total, Berlin contains more than 100 parks constituting an area of around 2,000 ha. Berlin's development of green areas results from the land-use history of the city, leading to an average 6 m² of green area per inhabitant in most of Berlin's sub-districts (Kabisch & Haase, 2014).

2.2 | Study species

The mesocarnivore community was composed of the native red fox *Vulpes vulpes* and native martens *Martes foina* and *Martes martes*, the invasive raccoon *Procyon lotor* and the feral/domestic cat *Felis catus*, directly associated with human activities. We excluded badgers *Meles meles* as their presence was rare. Study species are thoroughly described in Appendix 1.

2.3 | Data collection: Multi-season camera trap study

The camera trap study of urban mammals (www.wildtierforscher-berlin.de) is one of the scientific projects conducted by citizen scientists within the knowledge transfer project WTimpact (<http://www.wtimpact.de>; Appendix 2). We divided the area of Berlin into a regular grid of 287 × 2 km and accepted around 200 Berlin citizens per sampling phase with private gardens (either adjunct to their residential area or within an allotment), trying to get at least one participant per each 2 × 2 km grid per sampling phase to ensure spatial independence of the data. For each new sampling phase, we selected new citizen scientists while respecting this spatial grid. The camera traps took three consecutive pictures when triggered. We repeated this study for five sampling phases: first; October 7th–November 4th 2018, second; April 1st–April 28th 2019, third; September 30th–October 27th 2019, fourth; from March 30th–April 26th 2020 and fifth; September 28th–October 26th 2020 (Figure 1).

2.4 | Environmental variables

We obtained environmental variables at two spatial scales (Appendix 3):

1. The garden or allotment scale, provided by the citizen scientists: size of their garden (m²), the estimated tree cover in their garden (%), the height of the fence surrounding the garden (cm), and, if applicable, if the compost is closed or open.
2. The urban scale: environmental variables obtained from remote sensing data and available for the whole city coverage with a spatial resolution of 20 × 20 m that describe cover for wildlife (% tree

Camera trap locations and number of pictures from the urban mesocarnivore study in Berlin

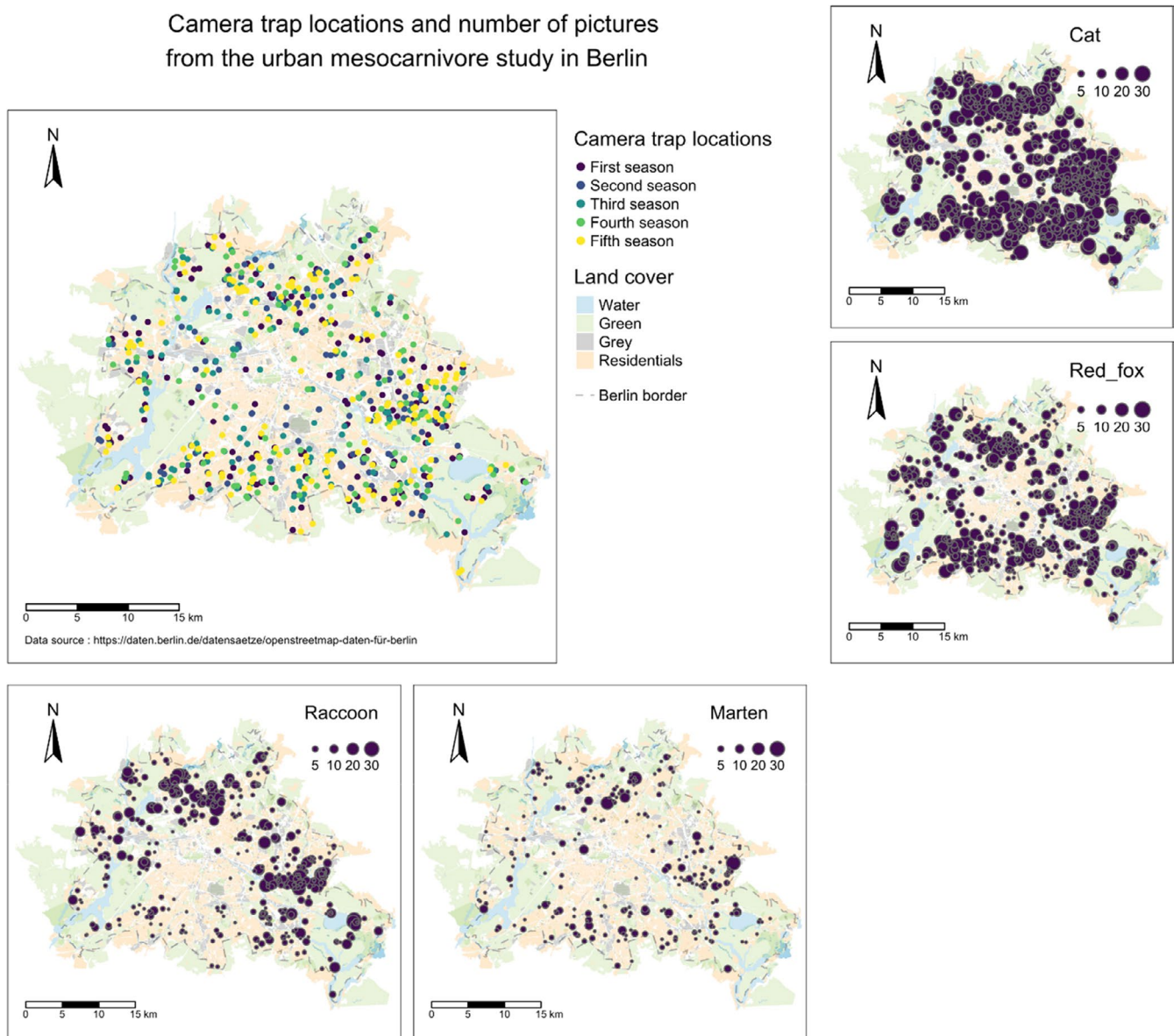


FIGURE 1 Camera trap locations in Berlin for the five sampling phases: fall 2018, spring 2019, fall 2019, spring 2020 and fall 2020, and number of days with pictures taken during those sampling phases

cover), and human disturbance (human population density, % impervious surface, noise). To represent environmental conditions surrounding gardens, environmental variables were averaged at a 100 m scale centred at the camera trap location, which is a broad enough spatial extent to examine urban effects given the small sizes of gardens (see Appendix 4).

2.5 | Data analysis

2.5.1 | Species' spatial analyses

We first checked for spatial overlap of mesocarnivore species by modelling mesocarnivore community assemblage in response to environmental covariates as well as the species associations using Joint

Species Distribution Models (JSDM) in a hierarchical Bayesian framework using the R package HMSC (Ovaskainen et al., 2017; Tikhonov et al., 2020). JSDMs are a multivariate method that analyses the response of multiple species to environmental drivers and allow to assess species associations in the residual variance after accounting for the environmental effects (Ovaskainen et al., 2017; Pollock et al., 2014; Warton et al., 2015). We analysed the urban mesocarnivore community spatial patterns using three complementary approaches: (a) a binary detection-non detection model ('detection' hereafter) based on the detection of each species at least once at a camera trap location during a sampling phase, (b) a relative use intensity model ('use intensity' hereafter) based on the number of independent pictures (i.e. filtered with a time difference of 30 min) of each species at a camera trap location during each sampling phase and (c) a nocturnality model ('nocturnality' hereafter) based on the proportion of independent

pictures taken at night over the total number of independent pictures taken at a camera trap location, per species and sampling phase. Only for the nocturnality model did we restrict the dataset to the nighttime between 6 p.m. and 6 a.m., corresponding to when wild species were mostly active, according to the activity pattern analyses.

In all three models, we included environmental variables related to four main groups: sampling phase, garden characteristics, local urban environmental variables and the effects of cats. All variables were included as fixed effects. Garden and urban environmental variables are summarised in Appendix 3. Given that cats are attached to the households they belong to (with the exception of stray cats), we considered them as explanatory variable associated with the environmental conditions. We therefore included cat presence (detection model), cat use intensity (use intensity model) or cat nocturnality (nocturnality model) as explanatory variable in the respective models. Finally, season was included to account for variability of mesocarnivores' activity within the year, as a binary categorical variable spring/fall. During our study, the epidemic of the Novel Coronavirus SARS-CoV-2 reached Berlin (Böhmer et al., 2020). The Berlin Senate established several contingency measures, resulting in lockdowns during spring and fall 2020 (GVBI, 2020). Consequently, human activities drastically decreased during this global shut-down, leading to an increase in wildlife sightings (Silva-Rodríguez et al., 2021), possibly representing a change of activity patterns of urban wildlife. To account for a possible change in urban mesocarnivores' space use and activity pattern in Berlin gardens, we created a binary variable of the SARS-CoV-2 lockdown, denoted covid/no_covid, referring to low (covid)/high (no_covid) human disturbance,

respectively. The computational details of the above method are described in Appendix 5.

2.5.2 | Temporal analyses

To test for temporal partitioning between the mesocarnivores of Berlin, we first filtered the pictures of the same species with a minimum time difference of 30 min to consider independent presence events. Using the R package CAMTRAPR (Niedballa et al., 2016), we compared the activity patterns of all four species by assessing the temporal overlap Δ_1 between each species (Ridout & Linkie, 2009). The coefficient ranges from 0 (no overlap) to 1 (complete overlap) and refers to the area under both density curves resulting from the activity patterns of each species.

To test for avoidance or attraction (Niedballa et al., 2019), we measured the time interval between the last picture of a species and the first picture of the focal species, hereafter called 'time of delay', for gardens where both species were detected. For the temporal analyses, we restricted the pictures to when wild species were mostly active, according to the activity pattern analyses, that is, between 6 p.m. and 6 a.m. (Figure 2). The time of delay for the red fox, as focal species, for instance, would be the time difference between the last picture of a raccoon, a cat or a marten, and the first picture of a fox. In our study, we then considered that the focal species would avoid another species if the time of delay was significantly greater than for its own species. In this case, we also analysed the time of delay of cats as a response variable, in contrast to the spatial analyses. Finally, to account for differences of probability of presences in

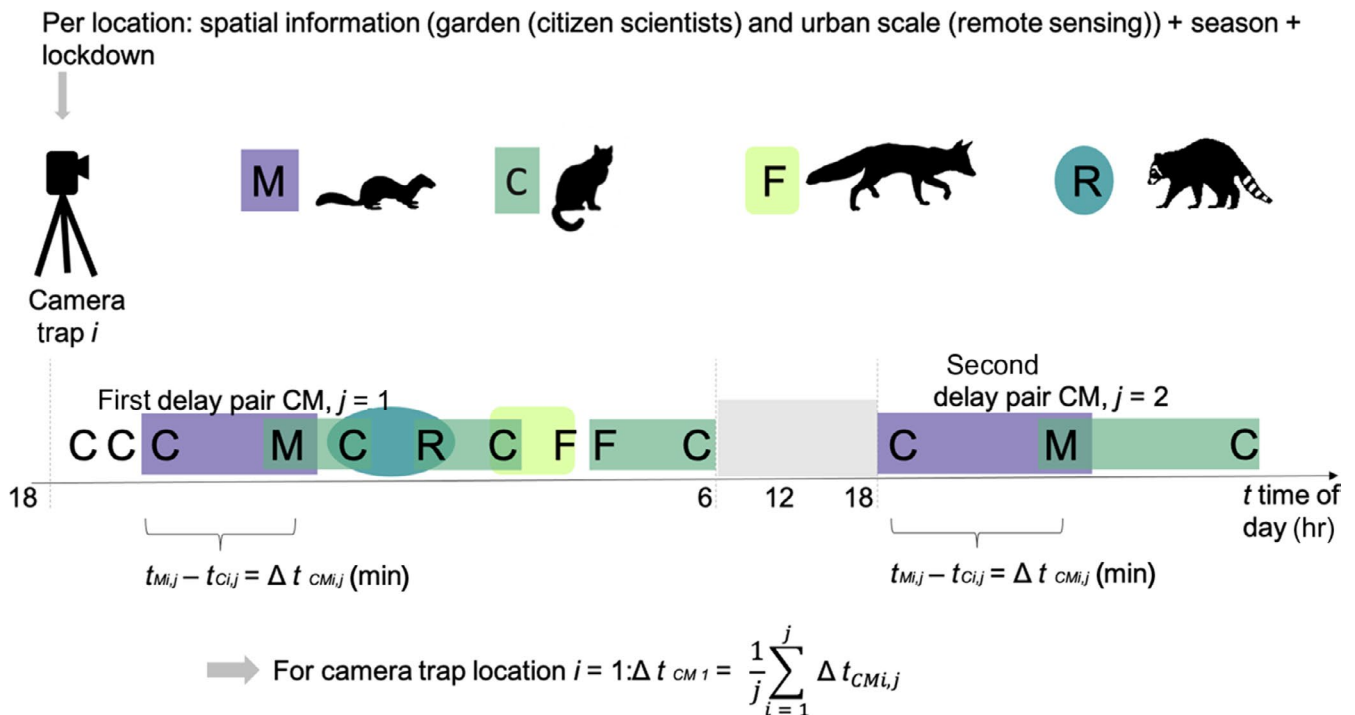


FIGURE 2 Representation of the measure of time of delay between two species of the mesocarnivore community of Berlin based on camera traps. Animal silhouettes by AP and MS

gardens, we ran pairwise regression of time of delay: we restrained the data to gardens where only the two species occurred and ran a similar regression with only one variable; the species after which the focal species was detected. Computational details are described in Appendix 5.

3 | RESULTS

In total, the number of camera traps used for this study varied between 116 and 150 camera traps per sampling phase (Appendix 6). By far, cats were the most detected species, with a total number of pictures between 2,204 and 3,144 per sampling phase, a maximum number of days detected at a site between 27 and 28 days, with an average between 8.98 and 10.35 days detected at a site. Martens, on the opposite, were the most elusive species, with a number of pictures taken between 50 and 302 per sampling phase, and a maximum number of days detected between 4 and 27 days, with an average between 0.42 and 1.31 days. Red foxes had a number of pictures between 316 and 1,194 per sampling phase, a maximum number of days during which they were detected between 17 and 27 days, with an average varying between 2.2 and 5 days. Raccoons had a total number of pictures between 244 and 1,022 per sampling phase, a maximum number of days during which they

were detected between 16 and 28 days, with an average between 1.7 and 4.3 days.

3.1 | Species' spatial analyses

The detection of mesocarnivore species in gardens was strongly influenced by the season and the effects of the SARS-CoV-2 lockdown (Figure 3a). For all species, detections during spring were lower than those during autumn. Additionally, fox detections increased when lockdown measures were active. Regarding the environmental variables, we found species-specific responses, although weaker than the response to season, as shown by lower standard coefficient values, pointing to a lack of clear spatial patterns in the urban area for the distribution of the species. The main variables showing some trends in the effect on mesocarnivore distributions were the existence of compost in the gardens, with a negative trend of gardens without compost, and a positive trend towards gardens with open compost in comparison to closed compost. Additionally, the presence of cats in the gardens had a negative trend on the presence of martens and foxes, but a positive one on the presence of raccoons. The use intensity of gardens followed a similar pattern (Figure 3b). The main difference was in the effect of cats. Although foxes still showed a negative trend towards cats, both marten's and raccoon's use intensity were positively associated with

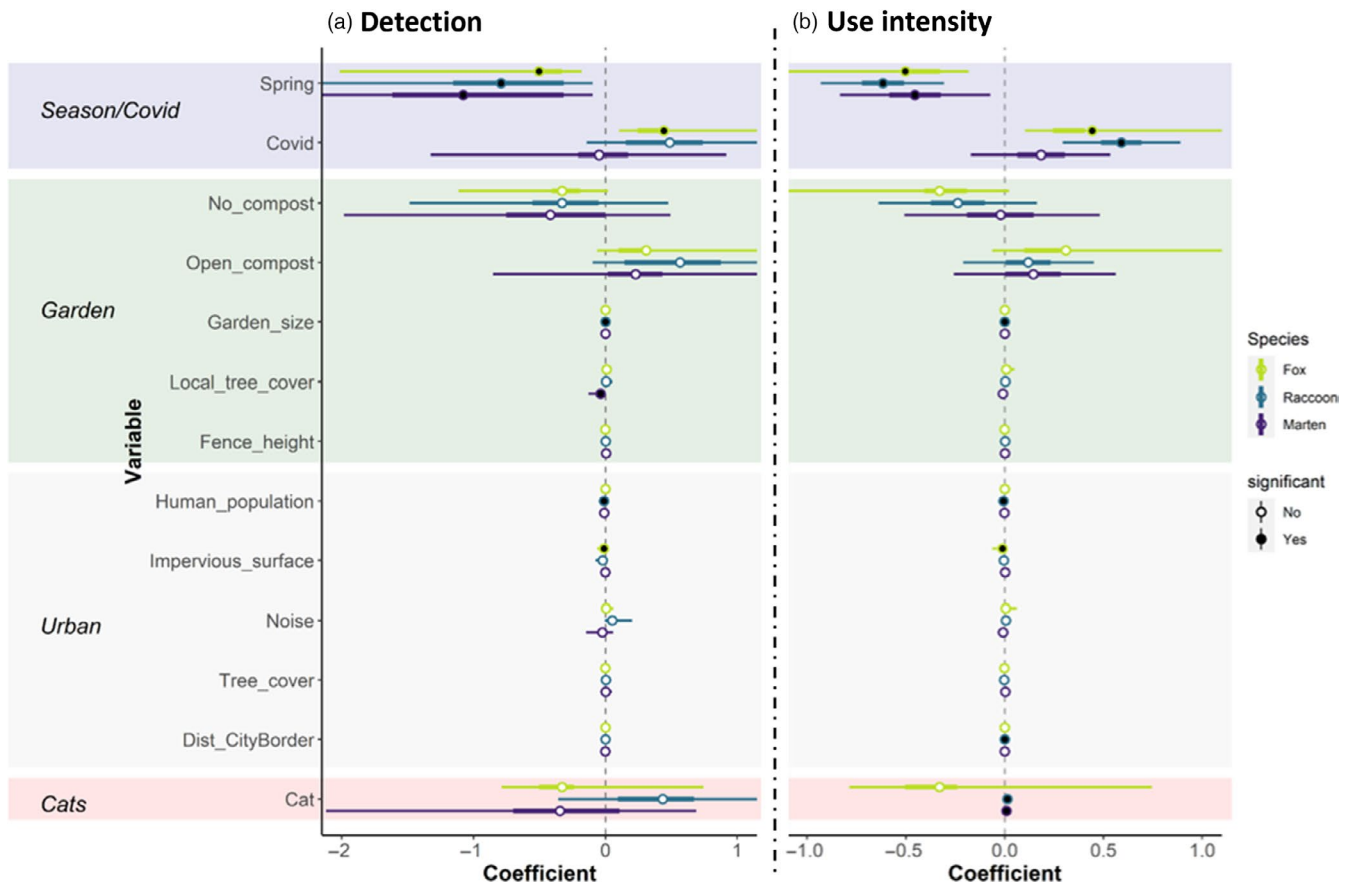


FIGURE 3 Effects of season including SARS-CoV-2 lockdown, garden covariates, urban covariates and presence of cats on the presence (a) and use intensity (b) of urban mesocarnivores in citizen's gardens of Berlin. Thin lines represent 95% credible intervals (CRI), and thick lines represent 50% CRI

the use intensity of cats. This effect was lower than the effect of season and lockdown measures. The nocturnality tendency of the species was not strongly associated with any of the study variables, although some trends appeared in the data (Appendix 7). During the SARS-CoV-2 lockdown, all species showed a tendency towards more nocturnal activity, as well as a positive correlation with cat nocturnal activity (Appendix 7).

The most relevant variables for fox detections (Figure 4a) were urban variables as well as the SARS-CoV-2 lockdown measures. Marten detections were mostly explained by the garden identities (random factor). Raccoon detections were mostly explained by garden characteristics and garden identities (random factor). Interestingly, use intensity variable importance showed an opposite pattern, where analysed variables explained most of the variance in marten use intensity, but only half of the variability of fox use intensity. Finally, foxes' and martens' nocturnality was mostly explained by garden identity, while variability in raccoon's nocturnality was mainly by garden characteristics and cat's nocturnality (Appendix 7).

When looking at the residual variance from the JSDM analyses, we found positive associations among all mesocarnivore species in the analyses for detections and use intensity, respectively (Figure 5), but not associations for nocturnality (Appendix 7). Finally, when inspecting the post-predictive power of our models, we could conclude that the detection model fitted the data quite well, while the use intensity model tended to slightly overestimate the output in comparison to the data (Appendix 8).

3.2 | Temporal analysis

The analyses of activity patterns showed that cats were the most diurnal species among the four mesocarnivore species (Figure 6).

Red foxes, raccoons and martens appeared to be nocturnal, with their activity mostly comprised between 6 p.m. and 6 a.m. No big differences of activity appeared among the sampling phases or after the SARS-CoV-2 lockdown measures (Appendix 9). All three wild carnivore species appeared to have overlapped nocturnal activities, with a coefficient of overlap above 0.8 for all species across all sampling phases (Appendix 9). We acknowledge that the estimates of Δ_1 might be biased because *campttrapR* uses a kernel estimator on a linear scale to measure overlap values. We recommend interpreting these results with caution.

The time of delay was mainly influenced by the species after which the focal species was detected (Figure 7), with a probability of direction above 0.8 for all species (Appendix 10). The highest values of probability of direction for the parameter 'species' for foxes were cat (1) and raccoon (0.95). The highest values for raccoons were cat (1) and fox (1), and the highest values for martens were fox (0.99) and cats (0.99). For cats, the highest value was only marten (1) (Appendix 10). The lockdown measures appeared to have a significant influence on foxes' time of delay and a probability of direction of 0.99. For cats and raccoons, the lockdown measure did not appear as significant but had a probability of direction of 0.96 and 0.95, respectively. For martens, the lockdown measure had a probability of direction of 0.74 (Appendix 10).

When predicting the time of delay (Figure 8), it appeared that raccoons waited the shortest after their own species, then martens, foxes and cats, in an increasing order. Cats appeared to wait the shortest after their own species, then foxes, raccoons and martens. Foxes appeared to wait the shortest after their own species, then martens, raccoons and cats and finally, martens appeared to wait the shortest after their own species, then raccoons, cats and foxes. Once the SARS-CoV-2 lockdown measures took place, the time

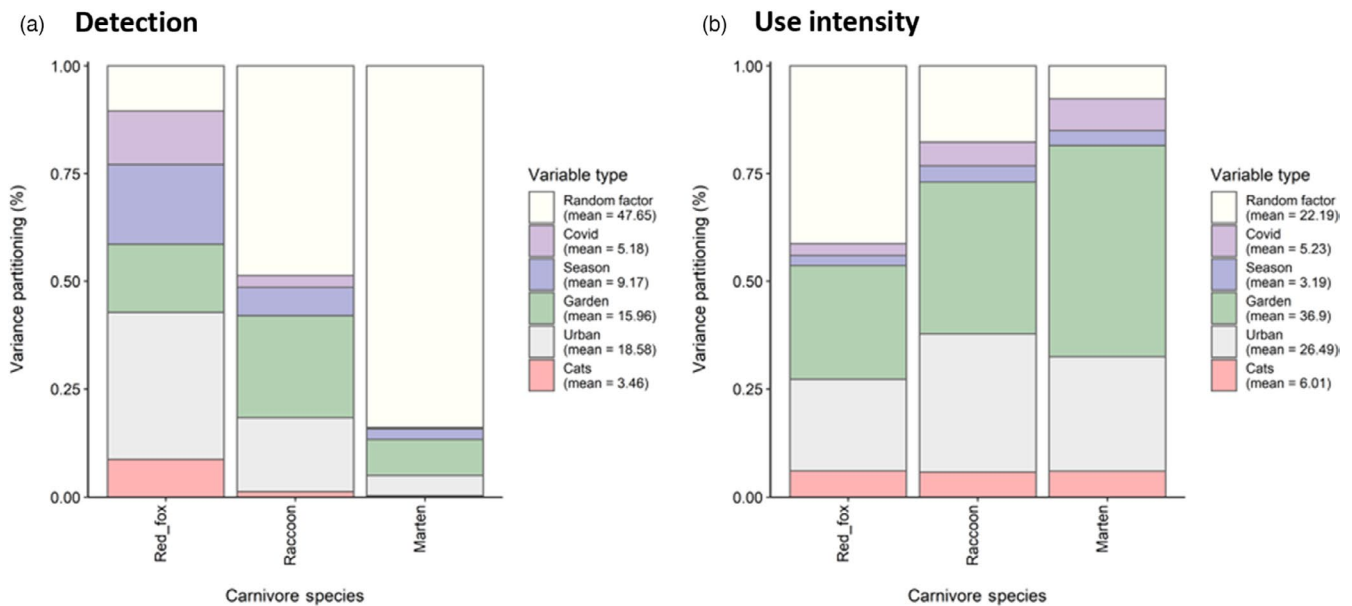


FIGURE 4 Relative importance of the different variable groups for the detection (a), use intensity (b) analyses, divided by mesocarnivore species. Variables were grouped into: season, SARS-CoV-2 lockdown effects, garden variables, urban variables and effects of cats. The random factor in all analyses refers to the garden identity. Mean values for all species in each analysis are shown to the right of the plots

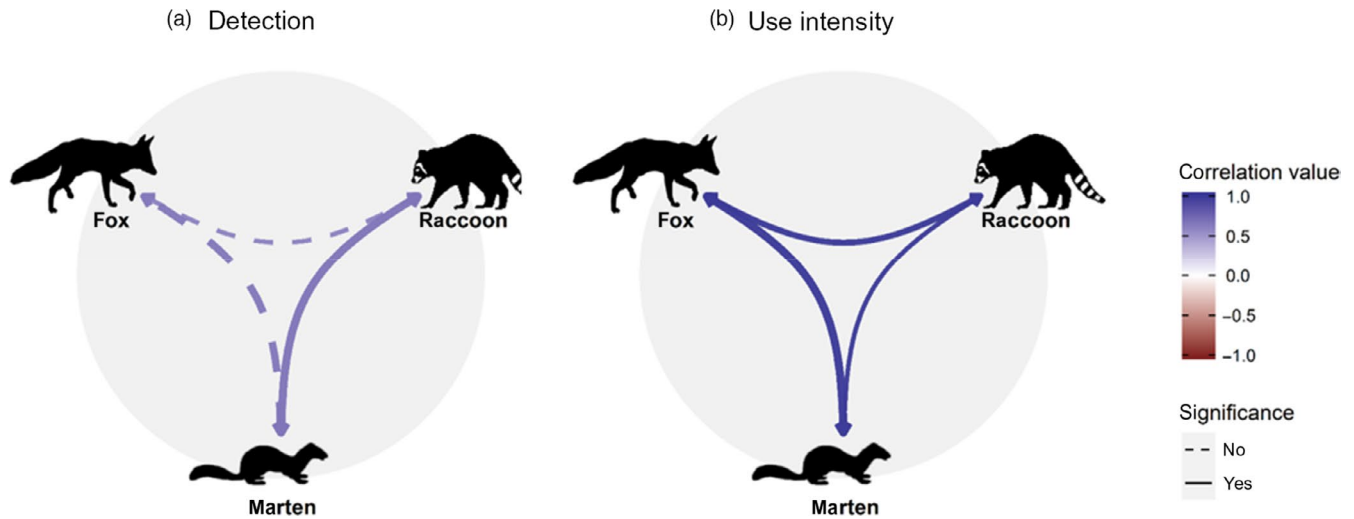


FIGURE 5 Species association in the residual variance of the JSDM analyses. Colour and width of the arrows represent the correlation value between two species. Solid lines are used for significant correlations and dashed lines are used for non-significant correlations. Animal silhouettes by AP and MS

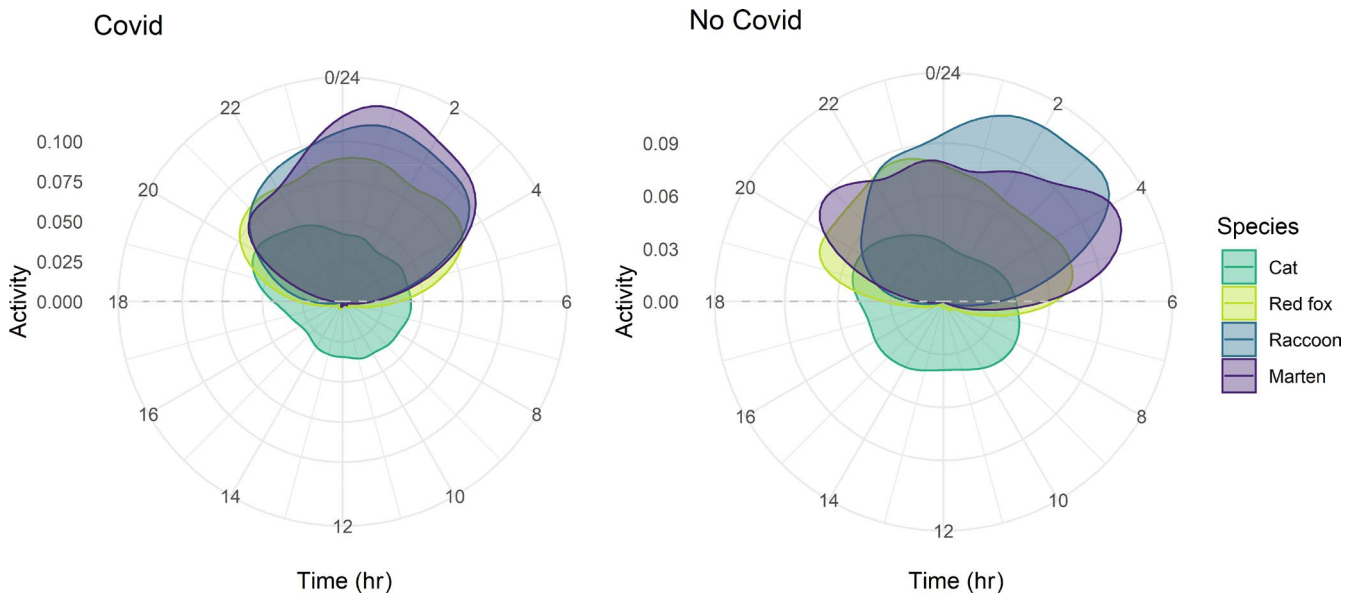


FIGURE 6 Activity patterns of each species composing the mesocarnivore community of Berlin, before the SARS-CoV-2 lockdown measures were in place (Covid) and were not in place (No Covid)

of delay decreased for all species except martens. Post-predictive power of our models showed a good fit of the data for each species (Appendix 8). The pairwise regressions showed similar results to the full models that we ran (Appendix 11).

4 | DISCUSSION

Past studies have assessed the spatial and temporal requirements of urban mesocarnivores (Moll et al., 2020; Parsons et al., 2019; Sévêque et al., 2020), our study combines both approaches and a temporal avoidance study at a small temporal scale, including native

species in combination with invasive and domestic species. The exceptional situation of the SARS-CoV-2 lockdown allowed us assessing the effects of a change in human activities on spatiotemporal requirements of urban mesocarnivores (Rutz et al., 2020). To respond to our hypotheses, local-scale garden variables determined the use intensity of gardens by the species, while landscape-scale urban variables and garden identities affected the spatial distribution of species. Raccoons and cats did not have negative effects on foxes' and martens' spatial requirements. Before we restrained the data to night only for the 'time of delay' analyses, activity patterns of wild species in gardens were mostly nocturnal due to avoidance of human activities, while cats' activity pattern occurred mostly

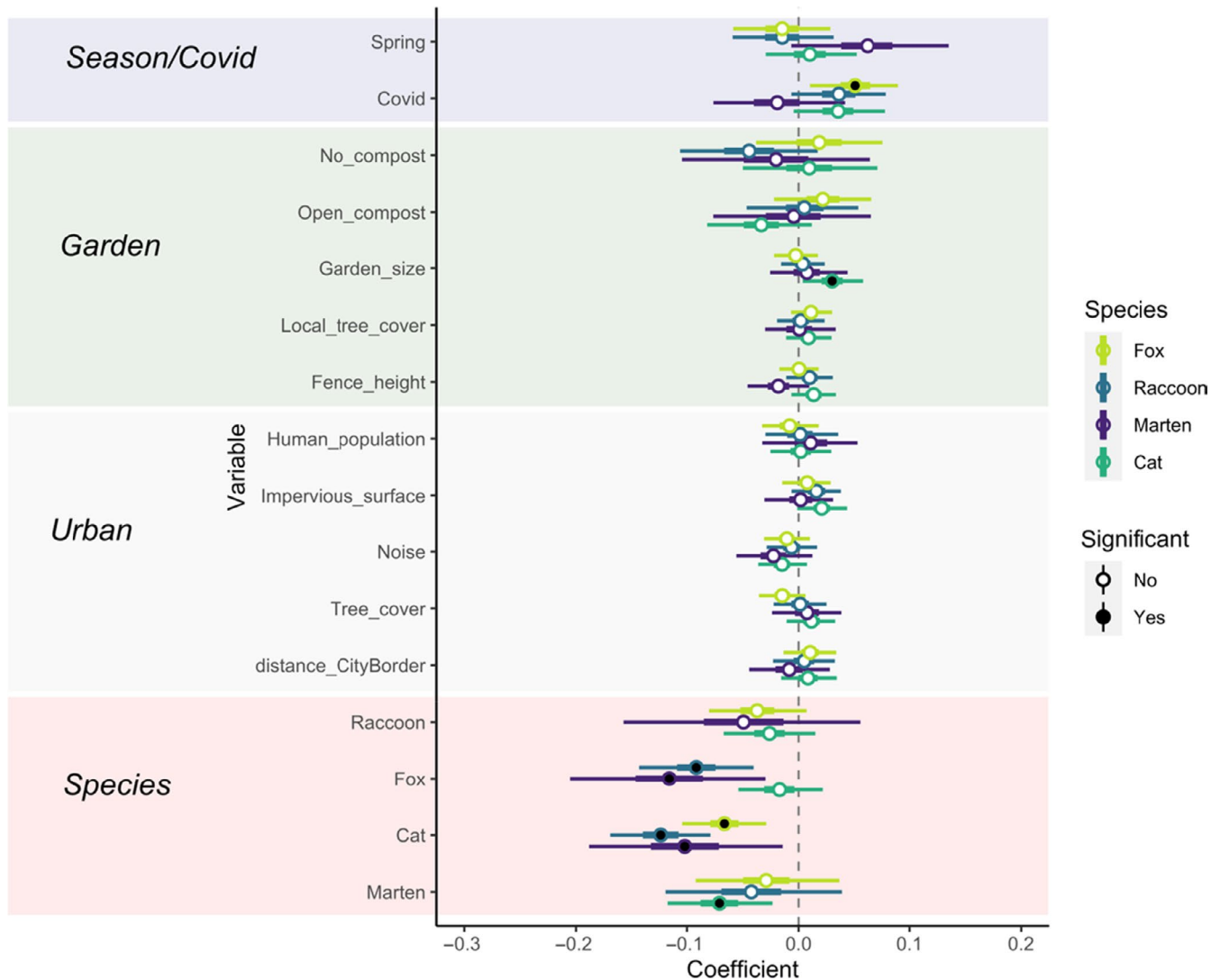


FIGURE 7 Effects of season, SARS-CoV-2 lockdown, garden covariates, urban covariates and first detected species, on the time of delay by urban mesocarnivores to get detected in gardens, and their 95% CRI estimated by the mixed model

during the daylight hours. Species with overlapping temporal niches displayed a differentiation of time of delay after a species was present in a garden. The avoidance appeared at a finer scale, the time of delay, for species with overlapping spatial and temporal niche. The hierarchy that appeared from our results are that cats are dominant over raccoons and foxes, displaying a more complex pattern than we hypothesised. A diminution in human activities represented by the SARS-CoV-2 pandemic lockdown led to a larger presence and use intensity of gardens and shorter time of delay.

4.1 | Environmental variable effects versus human activity effects

Overall, the fall season and lockdown measures positively influenced detection and intensity of use in comparison with the environmental variables that had a weaker effect. Mesocarnivores spatially segregated in gardens as an adaptation to human activities and season.

This was also visible in the increased nocturnal activity during lockdown, as people tended to be more present in their private gardens, forcing wildlife to be more nocturnal in gardens. Additionally, when lockdown measures were in place other anthropogenic food sources due to catering activities disappeared, leading to an increase of presence and use of gardens by wild mesocarnivores. Our analyses highlight the finding that mesocarnivores avoided human encounters above all, although not facing direct mortality risk (Moll et al., 2018; Stillfried et al., 2015). Hence, effects of human activities have the potential to cascade through communities even in urban systems where carnivores are habituated to human presence (Dorresteijn et al., 2015; Kuijper et al., 2016; Moll et al., 2018). Interestingly, one could expect a decrease in detections of cats during the lockdown measures due to owners keeping them inside to avoid transmission of SARS-CoV-2 through pets. Accordingly, we found a slight decrease in the number of cat pictures during the lockdown period (Appendix 6), but not big enough to conclude that such an effect occurred.

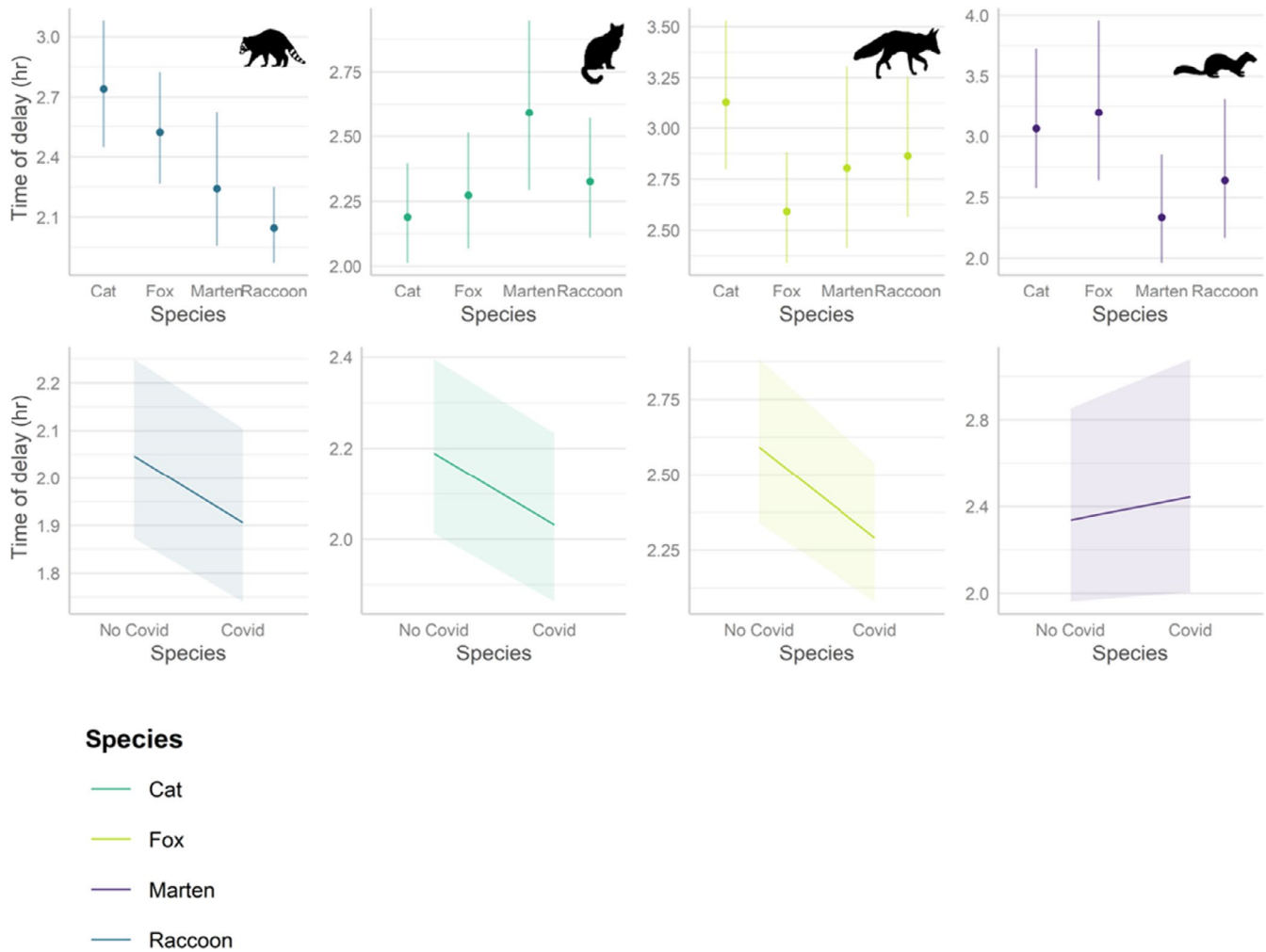


FIGURE 8 Predicted values of time of delay (hours) for each of the four mesocarnivore species of Berlin, depending on the species after which they were detected, and whether the SARS-CoV-2 lockdown was in effect or not

In spring, mesocarnivores appeared to be less present in gardens, which is corroborated by previous studies (Ables, 1969). In spring, gardens may not represent a main source of food due to a low productivity at this time of year. Additionally, mesocarnivores litter in spring, and restrain their activity closer to den sites (Marks & Bloomfield, 2006). In parallel, fall represents the season during which fox, raccoon and marten yearlings may start dispersing and looking for new territories (Fritzell, 1978; Harris & Trehella, 1988; Rosatte & Allan, 2009), hence exploring also new gardens. Note that the increase in detections during fall was not due to longer nights; when looking at the activity patterns during spring and fall (Appendix 9), we could see no difference in activity patterns, with a peak of activity similar between fall and spring. It is however important to keep in mind that in spring 2019 less pictures were taken for all the wild mesocarnivores. Although this season did not seem to differ in terms of covariates (Appendix 4), it remains however difficult to control for the yearly variation at very small scales, which could play a role in the results (Moll et al., 2020).

As cats could represent a source of nuisance for wildlife, gardens in which cats are present can also indicate a source of food as

owners may leave pet food in the trash and outside for their pets (Kalz, 2001; Theimer et al., 2015). Raccoons, as an invasive species and a bigger species than cats probably use cats as a proxy for pet food availability while foxes avoided cats although a previous study found that foxes could kill domestic cats in urban areas (Plumer et al., 2014). Finally, the number of pictures taken of martens was low in comparison with the other species. As a consequence, we consider that the results for martens have to be taken with caution.

4.2 | Urban scale versus local garden scale effects

On average, garden characteristics were more important for species' use intensity of the study area. Gardens have been found in another study to sustain the urban mammal communities specifically by maintaining high populations of prey species such as small rodents, and therefore attracting carnivore species (Hansen et al., 2020). For foxes, urban characteristics were more important for their presence; this may mean that the large-scale variables affected whether or not they would go in gardens, while the garden characteristics

at small scales would influence their use intensity, displaying a hierarchy between garden selection and use (Harris & Rayner, 1986; Rotenberry, 1985). However, for raccoons and martens, the detection was mostly explained by the garden identity, displaying an absence of spatial structure, or the absence of variables that could possibly explain their presence. Additionally, our study site is already confined within the border of a city, inside which environmental variability is high at very small scales, which could explain why for both the marten and the raccoon we found a high proportion of variance explained only by the random factor in the detection model. Our study is therefore a demonstration of the multi-scale processes underlying the community of mesocarnivores in urban environments and the influence of urbanisation and human activities on the balance of such a community (Moll et al., 2020; Parsons et al., 2019; Sévêque et al., 2020).

4.3 | Mesocarnivore sympatry patterns

The strong positive association among mesocarnivore species means positive co-occurrence of species in gardens for both detection and use intensity. Apart from environmental covariates, the presence of another species appeared positively correlated with the presence of the other two species. These results corroborate the fact that the study species all belong to the same guild, and therefore are more likely to use the same resources of food in a restrained environment (e.g. urban) with strong disturbances represented by human activities (Parsons et al., 2019). In this context, it is likely that the species will be positively associated, especially in gardens, which represent an unneglectable source of food or shelter from human disturbance (Sévêque et al., 2020).

4.4 | Interpretation of temporal analyses

As cats are mainly associated with humans, they consequently showed activity patterns that were parallel to human activities. The fact that wild species appeared to be nocturnal demonstrates that their activities were segregated to the nighttime to avoid human activities (Gaynor et al., 2018; Moll et al., 2018). When looking at the time of delay between the detection of a species and the detection of the second species we could not find that environment variables played a major role, only the species that was detected first and the lockdown measures did. These results confirm the hypothesis that when species compete for the same resources and their activities are constrained by human activities in urban areas and therefore the segregation happens at small temporal scales (Moll et al., 2018; Parsons et al., 2019).

Additionally, our results demonstrated a trend in the hierarchical levels displayed by the time of delay of the mesocarnivores of Berlin. For both foxes and raccoons, martens were the species after which they seemed to wait the shortest amount of time, and cats being the ones after which both of them waited the longest. Although cats'

presence seemed to positively influence the overall presence and use of gardens by raccoons, we could see that at the small temporal scale raccoons avoided cats the most. Consequently, at a smaller temporal scale cats represent a disturbance for mesocarnivores, invasive or not. It is interesting to note that the order after which cats wait does not seem to follow any form of rule, making the human-related pet species the dominant one.

In our dataset, the only rare species was the marten; hence, the time between the detection of another species and a marten might be long. However, because they are rare, the time of detection between a marten picture and another marten picture should even be longer, but what we found is the contrary in our results, with the shortest time being between two independent marten picture events, proving a strong avoidance of other species. The fact that the credibility intervals overlap might be due to the low detection rate of martens. When it comes to cats, because they are mostly diurnal, we believe that during the night, the probability of encountering them in gardens might be lower than the nocturnal species; consequently, the longest time of delay should also be between two cat pictures, but we observed the contrary, also proving an avoidance of the other species. Cats waiting the longest after martens might be due to both species having low encounter probabilities during the night in gardens. These results were confirmed by the pairwise regressions.

When the SARS-CoV-2 lockdown measures were implemented, we found that the general time of delay decreased, except for martens. In these times, we could observe that human activities decreased at the city scale, but people used their gardens more during the day, pushing wild species to be more nocturnal, therefore diminishing the window of time during which they may spend in gardens and forcing apparent coexistence. Our study highlights that urban landscapes created by 'hyperkeystone species' (Moll et al., 2021; Worm & Paine, 2016) are complex and responses by mesocarnivores translate at several spatiotemporal scales.

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COMPETING INTERESTS

We declare we have no competing interests.

AUTHORS' CONTRIBUTIONS

J.L.P.L., A.P. and S.K.-S. conceived the ideas and designed the methodology; M.S., R.H., K.B., S.K., S.O., A.S., M.B. collected and curated the data; J.L.P.L., A.P. and S.K.-S. led the writing of the manuscript.

All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.hdr7sqvjt> (Louvrier et al., 2021). Code and data also provided on the EcoDyn github account <https://doi.org/10.5281/zenodo.5676004> (Scherer et al., 2021).

ORCID

Julie L. P. Louvrier  <https://orcid.org/0000-0003-1252-1746>

Aimara Planillo  <https://orcid.org/0000-0001-6763-9923>

Robert Hagen  <https://orcid.org/0000-0002-4342-9216>

Sophia Kimmig  <https://orcid.org/0000-0002-4140-6002>

Sylvia Ortman  <https://orcid.org/0000-0003-2520-6251>

Miriam Brandt  <https://orcid.org/0000-0002-0490-9823>

Stephanie Kramer-Schadt  <https://orcid.org/0000-0002-9269-4446>

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SUPPORTING INFORMATION

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