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Individual specialization in the use of space by frugivorous bats

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Abstract

1. Natural populations are not homogenous systems but sets of individuals that occupy subsets of the species' niche. This phenomenon is known as individual specialization. Recently, several studies found evidence of individual specialization in animal diets. Diet is a critical dimension of a species' niche that affects several other dimensions, including space use, which has been poorly studied under the light of individual specialization.
2. In this study, which harnesses the framework of the movement ecology paradigm and uses yellow–shouldered bats *Sturnira lilium* as a model, we ask how food preferences lead individual bats of the same population to forage mainly in different locations and habitats.
3. Ten individual bats were radiotracked in a heterogeneous Brazilian savanna. First, we modelled intraspecific variation in space use as a network of individual bats and the landscape elements visited by them. Second, we developed two novel metrics, the spatial individual specialization index (*SpatIS*) and the spatial individual complementary specialization index (*SpatICS*). Additionally, we tested food-plant availability as a driver of interindividual differences in space use.
4. There was large interindividual variation in space use not explained by sex or weight. Our results point to individual specialization in space use in the studied population of *S. lilium*, most probably linked to food–plant distribution.
5. Individual specialization affects not only which plant species frugivores consume, but also the way they move in space, ultimately with consequences for seed dispersal and landscape connectivity.

KEYWORDS
Cerrado, Chiroptera, ecology of individuals, interindividual variation, Phyllostomidae, plant–animal interactions, spatial ecology

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Patricia Kerches-Rogeri and Bernardo Brandão Niebuhr shared first authorship.

1 | INTRODUCTION

Most ecological studies assume that individuals of the same population behave as equivalents (Bolnick et al., 2003). However, growing evidence, mainly from dietary studies, points out that individuals use different subsets of their population's total niche. Interindividual variations or even individual specialization have been observed in several animal taxa, such as gastropods, crustaceans, arachnids, insects, fishes, amphibians, reptiles, birds and mammals (Araújo, Bolnick, & Layman, 2011; Bolnick et al., 2003), all over the world (Araújo & Costa-Pereira, 2013).

As defined by Bolnick et al. (2003) individual specialization occurs when individuals use a subset of the total niche of their population, so that the niche of an individual specialist is substantially narrower than its population's niche for reasons not attributable to sex, age or morphology. Individual specialization may imply trade-offs, so that if an individual improves its efficiency in consuming a given resource type, it will lose its ability to consume other resource types (Bolnick et al., 2003). Those trade-offs may occur in several aspects of foraging, such as prey search, recognition, capture and digestion, and their relation to individual specialization may be understood within the context of optimal foraging theory (Svanbäck & Bolnick, 2005).

Those trade-offs may be reflected also in movement patterns (Spiegel, Leu, Bull, & Sih, 2017), although most studies focus on diet only (reviewed by Araújo et al., 2011). Nevertheless, movement ecology has been receiving increasing attention, especially after a conceptual framework was developed (Nathan et al., 2008). According to this framework, the movement of organisms is the result of the interaction between four components: internal state, movement capacity, navigation capacity and external factors. This framework was amplified by making it explicit that each individual may differ on these components—why, how and where they move, as well as on how they perceive and are influenced by resources, other organisms and the environment in general—so that each individual moves differently from the others (Jeltsch et al., 2013). Furthermore, Spiegel et al. (2017) recently proposed a conceptual framework for personality-dependent spatial ecology, connecting individual specialization to animal personality and movement, and several studies have started to connect space use and diet to understand individual

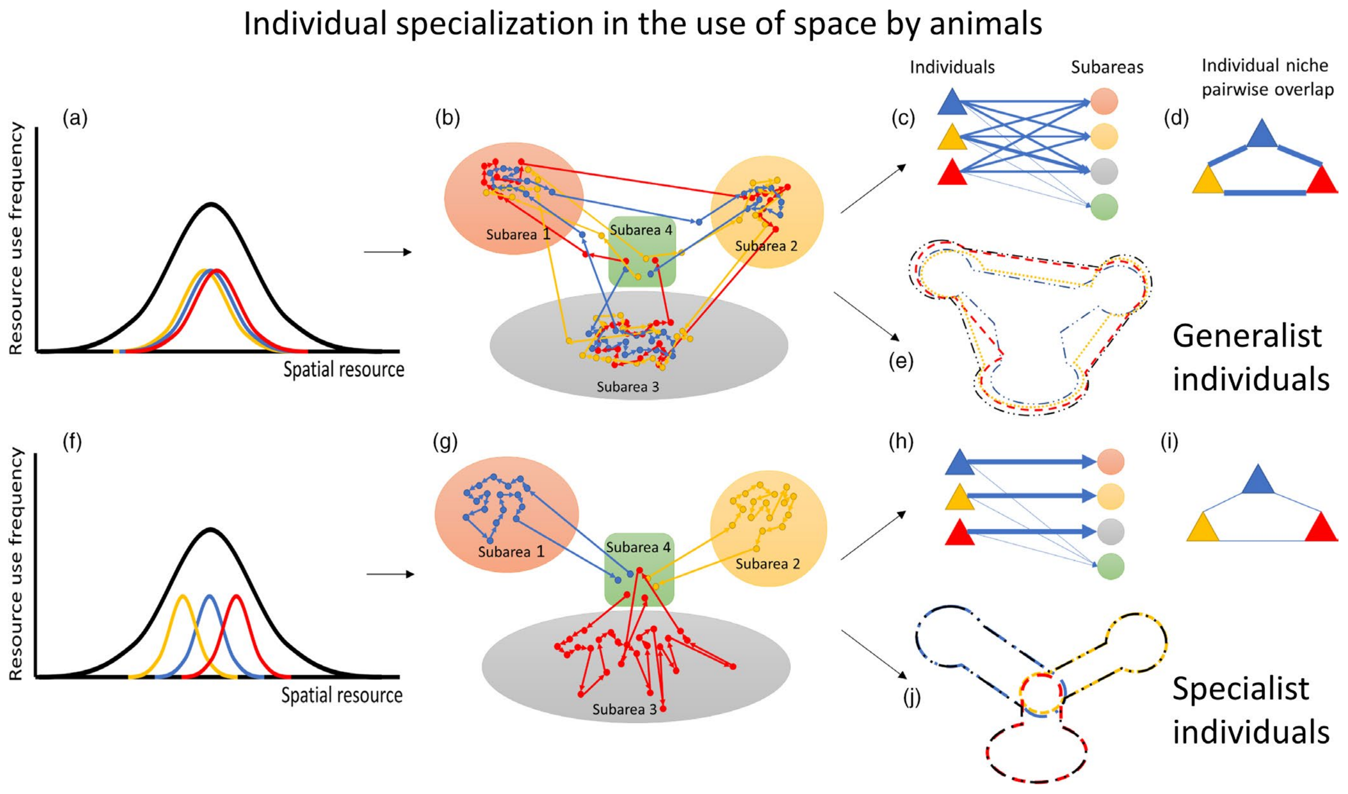

FIGURE 1 Conceptual framework linking individual specialization to movement ecology. (a) and (f) show how different individuals (coloured thin curves) share the population's niche (thick black curve; adapted from Bolnick et al., 2003). The width of the spatial niche is represented in the *x* axis and the frequency of use in the *y* axis. (a) Represents a generalist population composed of generalist individuals, while (f) represents a generalist population composed of specialist individuals. (b) and (g) show predicted movement patterns for the two hypothetical populations: (b) individual generalization and (g) individual specialization. (c) and (h) represent hypothetical bipartite networks formed by individual bats and the subareas visited by them in the two hypothetical populations. The thickness of the links between individuals and subareas represent their frequency of use. (d) and (i) show another network representation where the nodes are individuals and the thickness of the links represents the overlap in the use of subareas. In (d) there is high overlap between individuals, while in (i) the overlap is low. (e) and (j) show hypothetical areas of activity used by individual bats (coloured lines) and the whole population (black line), represented by the 95% kernel density estimator isopleth (95% KDE). In (e) there is individual generalization, while in (j) there is individual specialization

specialization (reviewed by Carneiro, Bonnet-Lebrun, Manica, Staniland, & Phillips, 2017).

This connection between individual specialization and movement might be efficiently studied using bats (Mammalia: Chiroptera) as a model, since they have high flight capacity and move over different habitats (Trevelin, Silveira, Port-Carvalho, Homem, & Cruz-Neto, 2013). The movement ecology of bats has been put recently into the context of the movement ecology framework, which facilitates unveiling patterns and processes, and deriving testable predictions (Voigt et al., 2017). In this study, we used as a model the yellow-shouldered bat *Sturnira lilium* (E. Geoffroy, 1810; Phyllostomidae: Stenodermatinae), an important seed disperser in the Neotropics because of its broad frugivorous diet (Lobova, Geiselman, & Mori, 2009), large foraging areas (Mello, Kalko, & Silva, 2008) and legitimate seed dispersal behaviour (Fleming & Sosa, 1994). Interindividual variations in fruit preferences have been observed in the same *S. lilium* population investigated in this study, under experimental conditions (Muylaert, Matos, & Mello, 2014), but it remains unknown whether those interindividual variations in diet are linked to foraging movements and space use. Therefore, the aim of our study was to fill this gap by assessing individual specialization in the space use of *S. lilium* bats and linking it to the heterogeneous spatial availability of their preferred food items.

The link between space use and diet may be a result of the interplay between fruit availability, an external factor, and individual preference, an internal factor. As the main fruits consumed by *S. lilium* are patchily distributed and grow in different habitats, and as individual specialization in diet was observed for these bats (Muylaert, Matos, et al., 2014), we expected variation in diet between individuals to be reflected on their space use. This led to two predictions. First, we expected that, if individuals of the same population were diet specialists, each individual would forage mainly where its favourite fruits were more abundant, resulting in high individual specialization in space use. Second, we expected little overlap in the areas used by different individuals, as a consequence of the use of these different habitats (Figure 1). Other factors, such as predation risk (Lima & O'Keefe, 2013) and environmental conditions (Thies, Kalko, & Schnitzler, 2006), can also affect foraging behaviour in frugivorous bats. Nevertheless, as predation risk is still poorly known in the Neotropics (Lima & O'Keefe, 2013) and environmental conditions were the same for all individuals of the studied population, we did not assess those factors.

2 | MATERIALS AND METHODS

2.1 | Approach

To test the hypothesis of a link between individual specialization, diet and space use, we adapted tools from the literature and proposed new methods to integrate data. We extended the concept of individual specialization from diet to space use by considering spatial elements as resources. In this context, spatial elements may be landscape elements (e.g. habitat or land cover polygons) or the geographical space itself (e.g. geographical locations within the landscape). By doing that, we may compare which spatial resources were used by different individuals and the population as a whole, and in which frequency, to assess individual specialization in space use (Figure 1a,f). As a consequence, individuals may be classified into specialists and generalists: at one extreme, all individuals in a population may use the same habitat types or locations, so that there is a large overlap in their space use patterns and low individual specialization (Figure 1a–e). At the other extreme, individuals in a population may use totally different resource patches or locations, leading to low spatial overlap and high individual specialization (Figure 1f–J).

We developed three approaches to classify spatial elements as resources: the land cover approach (‘*Land cover*’), in which habitat polygons correspond to resources; the land cover and foraging areas approach (‘*Foraging*’), in which spatial resources are defined by the intersection between habitat type and foraging areas used by animals; and the space as resource approach (‘*Space*’), where geographical locations are considered as resources. For *Land cover* and *Foraging* we applied network science analysis and in *Space* we proposed two indices of individual specialization based on the spatial overlap between individual utilization distributions (Figure 1). Finally, we also compared food availability between foraging sites to test its role as a driver of interindividual variation in space use.

2.2 | Study site

Our study was carried out in a protected area of Cerrado (Brazilian savanna) in São Carlos, state of São Paulo, southeastern Brazil, within the campus of the Federal University of São Carlos (UFSCar: 21°58'S, 47°52'W; Figure 2).

The area comprises a mosaic of natural vegetation, plantations and anthropogenic areas, with 124.68 ha of Cerrado, 5 ha of gallery forests, 93.84 ha of *Eucalyptus* plantations with Cerrado understorey, 171 ha of *Eucalyptus* plantations with cleared understorey, 8.39 ha of *Pinus* plantations and 83.67 ha of trails and abandoned fields (Muylaert, Teixeira, et al., 2014). The study site was mapped using QGIS (QGIS Development Team, 2015) and classified into six land cover classes: forest, Cerrado, forestry, open forest, pasture with scattered trees and matrix (pasture without trees, crops, water and urban areas).

The regional climate is classified as Cwa (tropical climate of altitude) in the Köppen system (Center of Weather Research—CEPAGRI – UNICAMP, 2017) with two well-defined seasons: a rainy season from October to March and a dry season from April to September.

2.3 | Radiotracking

In order to study the movements of *S. lilium* bats we radiotracked them during the dry season from 25 June to 10 August 2009, and

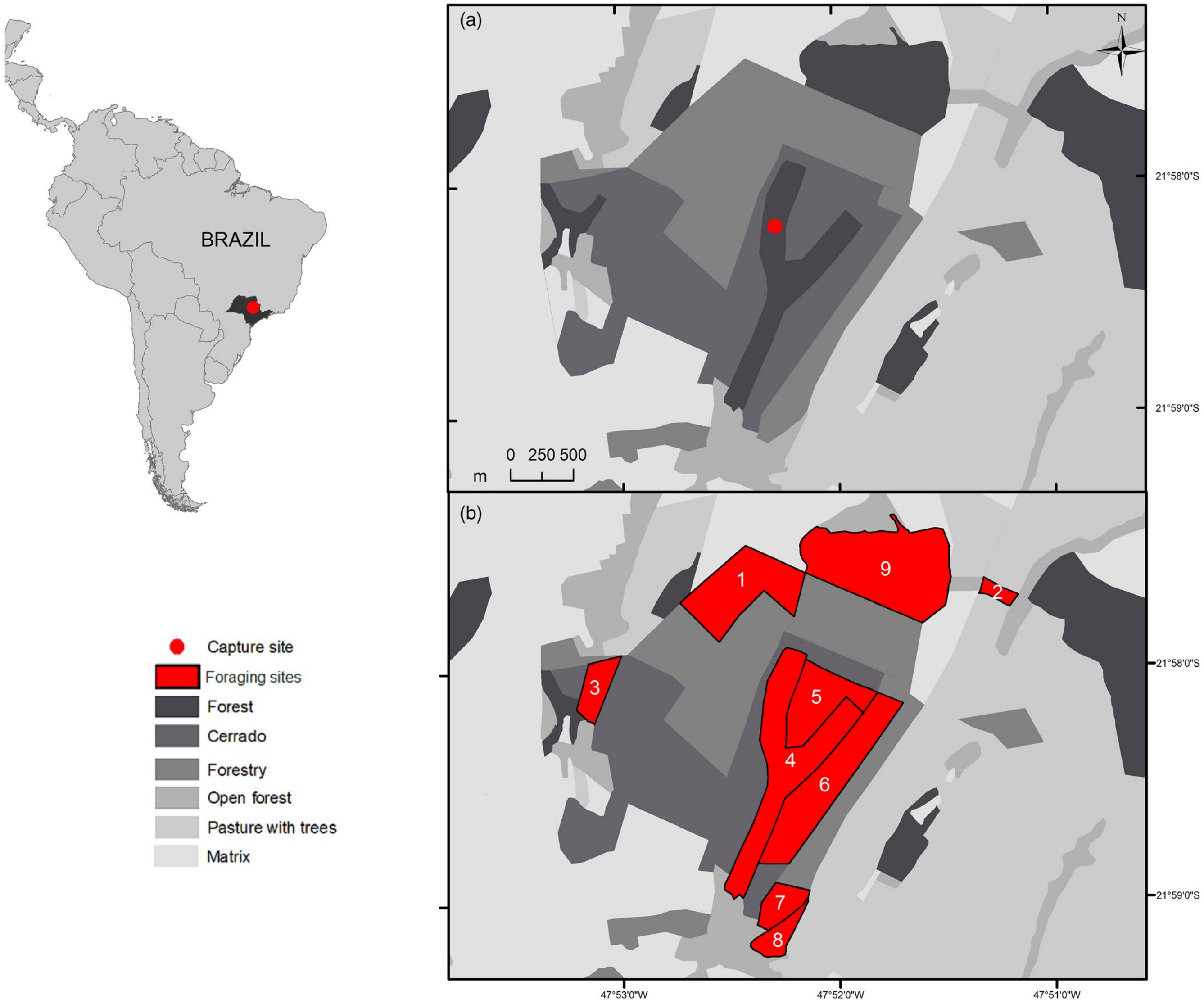

FIGURE 2 Study area in São Carlos, state of São Paulo, southeastern Brazil, which we classified into six vegetation types: forest, Cerrado, forestry, open forest, pasture with scattered trees and matrix (pasture without trees, crops, water and urban areas). (a) In the *Land cover* approach, we classified each polygon detected in the landscape according to habitat type (vegetation). (b) In the *Foraging* approach, foraging sites (red polygons) were defined based on the bats' core areas of activity (50% KDE) and the main habitat type used: 1—forestry, 2—open forest, 3—forest, 4—forest, 5—Cerrado, 6—Cerrado, 7—forestry, 8—open forest and 9—forest. The red dot in (a) corresponds to the location where the *Sturnira lilium* bats were captured

from 25 June to 10 August 2010, to avoid the rainy season and standardize the sampling. Bat handling followed the guidelines established by the American Society of Mammalogy (Sikes, 2016). In each sampling period, we carried out 10 nights of capture, followed by approximately 2 weeks of radiotracking. Bats were captured with mist nets (nylon, model 716/7P, 7 × 2.5 m; denier 70/2, 16 × 16 mm mesh; Ecotone Inc.) in a gallery forest (Figure 2a).

A miniature radiotransmitter (Model BD–2N, Holohil Systems) was attached to the back of each bat using veterinary glue (Vetbond™, 3M). Only the first adults captured on each night were selected for radiotracking, so we could infer that their day roosts were located near the capture site, which was confirmed with the posterior radiotracking. In addition, individuals were marked with split aluminium forearm rings (A.C. Hughes, Inc.).

Two radio-receivers (model Yaesu VR500, Wagener Telemetrieanlagen) coupled to 2 two-element H antennas were used to locate the day roosts and monitor the nocturnal activity of the bats. To locate the day roosts, we used the 'homing in on the animal' technique (Fenton et al., 2000). Nocturnal activity was assessed through triangulation, with two teams working simultaneously in the field, each one with a radio-receiver and a HT radio for communication (model EP450), and a handheld GPS (model GPS Map60 CX, Garmin Inc.).

Each bat was radiotracked for a week, from 30 min before sunset to 6 hr after, as frugivorous bats tend to be more active in the first half of the night (Thies et al., 2006). Therefore, we assumed that half a night was sufficient to detect interindividual differences in movements. Field tests indicated an average error (± *SD*) of 19.7 ± 1.56 m ($n = 5$) for triangulation made with a non-moving transmitter in an open Cerrado. Radiotracking data were first corrected by magnetic declination in GeoMag 3.0 and then processed in the software LOAS 4.0. Finally, the data were analysed together with a satellite image (Quickbird, spatial resolution of 60 cm) in ArcView 9.3, using the extension Hawth's Analysis (Beyer, 2004).

In total, 20 individuals of *S. lilium* were radiotracked. Nevertheless, seven individuals were not detected again after being tagged and released, and three were excluded from the analysis because of insufficient sampling (the number of radiotracked nights was not enough for reaching stability in the accumulation curves for their areas of use, using the 95% minimum convex polygon; Figure S1). Therefore, 10 individuals (seven females and three males) provided us with data that could be used in the analyses. Four individuals were tracked in 2009 and six in 2010.

2.4 | Individual specialization analysis

2.4.1 | Utilization distribution and kernel density estimates

To describe space use by animals, we used the concepts of utilization distribution (UD) and kernel density estimation. The UD is a probability density function that represents the intensity of space use at each location within an animal's home range or study area (Anderson, 1982; Worton, 1989). Kernel density estimators (KDE) are nonparametric methods used to estimate the utilization distribution by placing a probability density (a kernel) function over each observation point and averaging the densities at each location (Seaman & Powell, 1996). While the UD volume is a direct measure of probability of space use, it may also be sliced to produce contours that encompass the areas with higher intensity of use, which are helpful to quantify animal space use. Here we use 'X% KDE' to mean the area that encompasses the central X% of the UD volume (Anderson, 1982). We set $X = 95$ for determining the approximate extent of a home range and $X = 50$ for the core areas of activity (Anderson, 1982; Fieberg & Kochanny, 2005). We estimated the UD using a bivariate Gaussian kernel and the smoothing parameter h was defined as the reference value, h_{ref}, according to Worton (1989).

2.4.2 | Landscape as resource: *Land cover* and *Foraging* approaches

In *Land cover* we classified each polygon detected in the landscape according to habitat type using the previously mentioned land cover categories, and we considered each polygon as a potential resource unit used by bats. Resource units were then classified a priori, before movement data collection. Polygons of the same habitat type that were contiguous, with no physical boundaries other than trails or rivers between them, were considered as a single homogeneous spatial resource unit (Figure 2a).

In *Foraging* we used a combination of a land cover classification (as in *Land cover*) and an estimation of animal space use through the UD. First, we estimated the UD and calculated the core area of activity (50% KDE), to consider only the nuclear area of activity of each individual. Second, we defined foraging sites as the habitat polygons that overlapped with the core area of activity. Different habitat polygons overlapped by the core area of the same individual corresponded to different foraging sites. Therefore, in *Foraging* these foraging sites were considered as resource units and their definition was made a posteriori, after movement data collection and kernel density estimation (Figure 2b; Figure S2). We excluded from the analysis all foraging sites that corresponded to degraded areas without food resources for bats, such as pastures without fruiting trees or shrubs and forestry areas with no understorey.

2.4.3 | Confounding factors

We tested for an influence of the main intrinsic factors that lead to interindividual variations in natural populations: age, sex and body mass (Bolnick et al., 2003). Only adults were used to control for age. Because *S. lilium* bats do not present different morphotypes (Gannon, Willig, & Jones, 1989), this factor was excluded. To test whether sex and body mass influenced space use, we fit a generalized linear model with binomial response and logit link function to both *Land cover* and *Foraging*, considering as the response variable the proportion of activity points recorded for each individual in each habitat type (or foraging site), and the additive effect of sex and body mass as predictor variables, according to Warton and Hui (2011). Random intercepts for individuals and habitat polygons (or foraging sites) were added to account for overdispersion in the data (Warton & Hui, 2011):

$$\text{proportion of activity points}_{ij} \sim \text{Binomial}\left(N_i,\, p_{ij}\right),$$

$$\text{logit}(p_{ij}) = \log\left(\frac{p_{ij}}{1-p_{ij}}\right) = \alpha_0 + \alpha_1 \cdot \text{sex}_i + \alpha_2 \cdot \text{body mass}_i + \beta_i + \gamma_j,$$

$$\beta_i \sim \text{Gaussian}\left(0,\, \sigma^2_{\beta_i}\right),$$

$$\gamma_j \sim \text{Gaussian}\left(0,\, \sigma^2_{\gamma_j}\right),$$

where i denotes each individual and j denotes each habitat polygon or foraging site. N_i is the number of activity points by individual i, p_{ij} is the probability that individual i visits polygon j, and β_i and γ_j are the random intercepts for individuals and habitat (foraging site) polygons. The proportion of activity points is the ratio of the number of points of activity of an individual in a given polygon and the total number of locations for that individual. We also generated a no effect model that only included the random intercepts and compared the models through AIC. Models were considered equally plausible if ΔAIC between them was smaller than 2.

2.4.4 | Network analysis

Based on *Land cover* and *Foraging* approaches we assessed individual specialization using network science tools.

First, we calculated individual specialization in space use based on the individual niche overlap network (*E* index; Araújo et al., 2008): the nodes of the network represent individual animals, and the links represent dietary overlap between individuals. A score w_{ij} of dietary overlap, varying from 0 to 1, was associated to each link between individuals *i* and *j*, with 0 indicating no dietary overlap (when individual *i* and individual *j* do not consume any resource in common) and 1 indicating full dietary overlap (when individual *i* consumes the same resources in the same proportion as individual *j*).

At the network level, interindividual differences in diet can be quantified as the individual specialization index $= 1 - \overline{w}_{ij}$, where $\overline{w}_{ij}$ is the score of dietary overlap averaged over all pairs of individuals of the population. Therefore, in the absence of interindividual niche variation, *E* is zero, and it increases towards 1 with the increase of interindividual variation (Appendix S1; Araújo et al., 2008).

Furthermore, this analysis allows one to quantify the degree of clustering among vertices using the index C_{ws}, which is a combined measure of the number and weight of the edges of the whole population relative to the average number of connections in the network (see Appendix S1 for a precise definition). C_{ws} varies from −1 to +1. When C_{ws} is −1, each individual uses a specific resource arrangement, different from the other individuals (overdispersion of niches). When it is +1, there are well-defined groupings of individuals sharing the same resources and little overlap between groups (complete clustering). $C_{ws} \sim 0$ is a network with no clusters or overdispersion.

For adapting these indices to study space use, we considered that in our network the nodes represent individual bats and the links between them represent niche overlap (Figure 1d,i). As the resources correspond to landscape elements (habitat polygons or foraging sites), the niche overlap is based on the use of these resources and the index *E* varied from 0 (low specialization, full overlap in the use of landscape elements) to 1 (high specialization, use of different landscape elements by the individuals).

The indices of individual specialization (*E*) and clustering (C_{ws}) were calculated in the software DIETA1 (Araújo et al., 2008). To verify the existence of individual specialization (*E*) and clustering (C_{ws}), we performed 1,000 permutations in which each individual was assigned a number of points of activity equal to the observed one, but they were randomly assigned to the different spatial resource units, with no preference or variation among individuals. For each permutation, the values of *E* and C_{ws} were recalculated; *E* and C_{ws} were then compared to the values from randomized datasets through a one- and two-tailed comparison, respectively, using a significance level $\alpha = 0.05$ (for more details see Appendix S1; Araújo et al., 2008).

Second, in order to test for specialization from another perspective, we also used the H_2' index (Blüthgen, Menzel, & Blüthgen, 2006). The calculation of this index requires the representation of interactions as a bipartite network, where one node class contains individual bats and the other node class contains the spatial resource units used by them (Figure 1c,h). In this network, the index H_2' measures how much the nodes differ from each other in terms of weighted connection patterns. Values of H_2' range from 0 (all individuals use the same set of space units in the same frequency) to 1 (each individual uses a different set of space units). H_2' is estimated based on the two-dimensional Shannon entropy (termed H_2) and standardized on a scale between its maximum and minimum value. To test whether H_2 was higher than expected if individuals chose spatial resource units at random, first, the individual-resource network was randomized by keeping constant the total number of visits of each individual and the total number of visits each spatial resource unit received. Then, a new value of H_2 was calculated for this randomized network and this procedure was repeated 10,000 times. The significance of H_2 was estimated as the proportion of times the observed H_2 was greater than the randomized H_2, using a significance level $\alpha = 0.05$ (for more details see Appendix S2; Blüthgen et al., 2006).

2.4.5 | Space as resource: Space approach – Spatial individual specialization index (*SpatIS*)

To consider the Space as Resource (*Space*) we developed two novel metrics, the spatial individual specialization index (*SpatIS*) and the spatial individual complementary specialization index (*SpatICS*). The *SpatIS* measures specialization based on the overlap of intensity use functions or areas of activity between each individual and the population, regardless of the spatial heterogeneity in the availability of food items or habitat types, and is an analogy to the Individual Specialization (*IS*) index proposed by Bolnick, Yang, Fordyce, Davis, and Svanbäck (2002; Figure 1). The *SpatICS* is similar but compares the overlap in space use between each individual and the rest of the population, i.e. all individuals but the one being analysed. This means that *SpatICS* represents how complementary the space use of this individual is in relation to the rest of the population. The general definition of *SpatIS* and *SpatICS* is

$$SpatIS_{i,\mathrm{pop}} = 1 - \mathrm{Overlap\ Index}_{i,\mathrm{pop}},$$

$$SpatICS_{i,\mathrm{rest}} = 1 - \mathrm{Overlap\ Index}_{i,\mathrm{rest}},$$

where the overlap in space use is assessed between each individual *i* and the whole population pop for *SpatIS* (Overlap $\mathrm{Index}_{i,\mathrm{pop}}$) and between each individual *i* and the rest of the population for *SpatICS* (Overlap $\mathrm{Index}_{i,\mathrm{rest}}$). The default overlap index to calculate *SpatIS* and *SpatICS* is the volume intersection ('VI') method, which estimates the intersection between two utilization distribution volumes (Fieberg & Kochanny, 2005). To calculate *SpatIS* and *SpatICS*, we first calculated the UD for each individual bat (UD_i) and the whole population (UD_{pop}, for *SpatIS*) or the rest of the population (UD_{rest}, for *SpatICS*). The individual *SpatIS* (*SpatICS*) value was defined as the volume of the individual UD_i that did not overlap with UD_{pop} (UD_{rest}),

$$SpatIS_{i,\,pop} = 1 - \int_{\Omega} \min\left[UD_i(x, y),\; UD_{pop}(x, y)\right] dxdy,$$

$$SpatICS_{i,\,rest} = 1 - \int_{\Omega} \min\left[UD_i(x, y),\; UD_{rest}(x, y)\right] dxdy,$$

where Ω is the study area. The population *SpatIS* (*SpatICS*) was calculated as the individual *SpatIS* (*SpatICS*) value averaged over all individuals of the population (Appendix S3). This is an adaptation from Fieberg and Kochanny (2005).

SpatIS (*SpatICS*) is 0 when there is full overlap between the individual animal UD and the UD of the (rest of the) population. As the overlap decreases toward zero, the *SpatIS* (*SpatICS*) tends to 1. *SpatICS* is generally higher than *SpatIS*, since the focal individual is omitted from the population and the overlap in space use decreases. To check the significance of *SpatIS* and *SpatICS*, we tested if the observed individual specialization indices remained the same if individuals moved randomly, i.e. with no spatial bias or space use pattern. The alternative hypothesis was that the observed *SpatIS* (or *SpatICS*) was higher than what is expected at random. To operationalize the test, the recorded bat locations were randomized between individuals, with no replacement, keeping the locations of each individual which refer to the day roost. This procedure was repeated 1,000 times. *SpatIS* (*SpatICS*) was calculated for both the randomized and observed scenarios, and p was calculated through a one-sided t test between the distributions of observed and randomized individual *SpatIS* (*SpatICS*) values (pooling all randomizations in a single distribution), using a significance level $\alpha = 0.05$. To test for sufficiency in the number of individuals sampled, we calculated statistical power as the proportion of times when we found a significant result ($p < \alpha$) in the t test used to compare the observed and randomized distributions of *SpatIS* (*SpatICS*) values.

SpatIS and *SpatICS* may be used to compare populations regarding specialization in their space use, but also to characterize how individuals use the space differently within a population. Individuals may differ in their core activity areas, in their degree of site fidelity to these areas or in both, what may create different levels of individual specialization. Plotting individual and population UDs and analysing the individual values of these indices shows how individual specialization in space use occurs within a population. See Appendix S5 for further details.

Utilization distributions were calculated using the *kernelUD* function of the ADEHABITATHR package for R (Calenge, 2006), using the reference value h_{ref} as smoothing parameter (Worton, 1989), grid parameter = 100 and extent = 1.5. The overlap between UDs in *SpatIS* was assessed through the *kerneloverlap* function of the same package, using the method 'VI', that calculates the intersection between UD volumes. However, *SpatIS* and *SpatICS* were also defined in terms of other methods to assess overlap in space use, according to Fieberg and Kochanny (2005; methods 'HR', 'PHR', 'BA', and 'UDOI'; see definitions and a comparison among the methods in Appendix S4). The utilization distribution and *SpatIS*/*SpatICS* analyses were performed in R 3.3.1 (R Core Team, 2017). Further information may be found in the Appendices S3, S4 and S5.

2.4.6 | Food-plant availability

For *Foraging*, we estimated the food-plant availability and assessed the relationship between the use of foraging sites and food-plant availability. For each foraging site, the density of the main plant genera present in *S. lilium* diet, *Solanum* (Solanaceae), *Piper* (Piperaceae) and *Cecropia* (Urticaceae; Andrade, Thies, Rogeri, Kalko, & Mello, 2013), was measured using 10 random plots of 25 m^2, counting plant individuals and estimating plant density in an area of 250 m^2. For each individual bat and each of the plant genera, we fit a linear regression separately with the total number of activity points located in each foraging site as the response variable and the food-plant availability as the predictor variable, considering each site as an independent observation (n = 8 because we did not get a sampling permit for site 9):

$$\text{number of activity points} \sim N\left(\mu_k, \sigma^2\right),$$

$$\mu_k = \alpha \cdot \text{plant genera density}_k + \beta,$$

where α, β and σ^2 are parameters and k may refer to three genera, *Solanum*, *Piper* and *Cecropia*.

3 | RESULTS

The core areas (50% KDE) used by each individual bat during the 7 days of monitoring ranged from 1.46 to 241.07 ha (mean ± *SD* = 73.83 ± 76.69, n = 10; Table S1; Figure S2b). The maximum linear distance moved between two locations by the same individual ranged from 1.6 to 4.29 km (2.7 ± 0.99 km, n = 10), and the maximum commuting distance (between the day roost and the farthest foraging point) ranged from 0.31 to 3.37 km (1.97 ± 0.94 km, n = 10; Table S1). Individual body mass varied from 20 to 22 g (21.1 ± 0.78 g, n = 10) and their proportion of use of sites was averaged 0.14 (*SD* = 0.22, n = 10) for *Land cover* and 0.33 (*SD* = 0.34, n = 10) for *Foraging*.

Individual bats used different habitats as their core foraging areas (Figure S2b). Some used more than one core area (individuals 1 and 9), whereas others used only one. The interindividual variations observed in the use of the landscape were not explained by sex (for *Land cover*: estimate [*SE*] = 0.12 [0.52], z = 0.22, p = 0.82; for *Foraging*: −0.26 [1.91], z = 0.14, p = 0.89) or body mass (for *Land cover*: estimate [*SE*] = −0.12 [0.32], z = −0.38, p = 0.71; for *Foraging*: −1.48 [1.22], z = −1.21, p = 0.22; Figures S3 and S4; Table S2).

TABLE 1 Population level-trends in individual specialization for *Sturnira lilium* bats for the *Land cover*, *Foraging* and *Space* approaches. All indices vary between 0 and 1, where 0 represents no individual specialization and 1 represents high individual specialization

Index of individual specialization	Observed *Land cover*	Observed *Foraging*	SpatIS value *Space*
E[a]	0.82	0.79	–
$H_2{}'$[b]	0.65	0.72	–
SpatIS[c]	–	–	0.69
SpatICS[d]	–	–	0.75

[a] E—Individual specialization index, measures specialization based on individual niche overlap network (Appendix S1; Araújo et al., 2008).

[b] $H_2{}'$—Complementarity specialization index based on a bipartite network formed by individuals and areas visited (Appendix S2; Blüthgen et al., 2006).

[c] SpatIS—Spatial individual specialization index, measures the overlap between the utilization distributions of individuals and the population (Appendix S3).

[d] SpatICS—Spatial individual complementary specialization index, measures the overlap between the utilization distributions of each individual and the rest of the population (Appendix S3).

All individual specialization metrics pointed to individual specialization in *S. lilium* (Table 1; Figure 3). The results were similar for both *Land cover* ($E = 0.82$, $p < 0.001$; $H_2{}' = 0.65$, $p < 0.001$; Figure 3b,c) and *Foraging* ($E = 0.79$, $p < 0.001$; $H_2{}' = 0.72$; $p < 0.001$; Figure 3d,e), without formation of clusters (*Land cover*: $C_{ws} = -0.12$, $p = 1$; *Foraging*: $C_{ws} = -0.12$, $p = 1$). This means that, for both classifications of landscape elements as resources, we found low overlap in the areas used by individual bats. High individual specialization was also detected by the spatial individual specialization (*SpatIS* = 0.69, compared to 0.27 after location randomization; $t = 8.45$, $df = 9$, $p < 0.001$; power = 1.0) and spatial individual complementary specialization indices (*SpatICS* = 0.76, compared to 0.20 after location randomization; $t = 12.14$, $df = 9$, $p < 0.001$; power = 1.0; Table 1; Figure 3a; Figures S5 and S6). *SpatIS* and *SpatICS* were also higher than expected by chance when the other methods to assess these indices were used (Appendix S4).

Site use by different individuals was associated with food-plant density. Individuals 4 and 5 had higher activity in foraging sites with higher density of *Solanum* plants (respectively: $R^2 = 0.88$, $df = 6$, $p < 0.001$; $R^2 = 0.90$, $df = 6$, $p < 0.001$). Individuals 1, 3, 8 and 9 had higher activity in sites with higher density of *Piper* plants (respectively: $R^2 = 0.62$, $df = 6$, $p = 0.01$; $R^2 = 0.87$, $df = 6$, $p < 0.001$; $R^2 = 0.91$, $df = 6$, $p < 0.001$; $R^2 = 0.58$, $df = 6$, $p = 0.02$), and individual 6 had higher activity in sites with higher density of *Cecropia* plants ($R^2 = 0.80$, $df = 6$, $p < 0.001$; Table 2; Table S3). The locations of individuals 2 and 10 were not correlated with food-plant density. The effect of food-plant density on the use of foraging sites by individual 7 could not be assessed, since most of its visits were to the foraging area 9, where plant density could not be estimated.

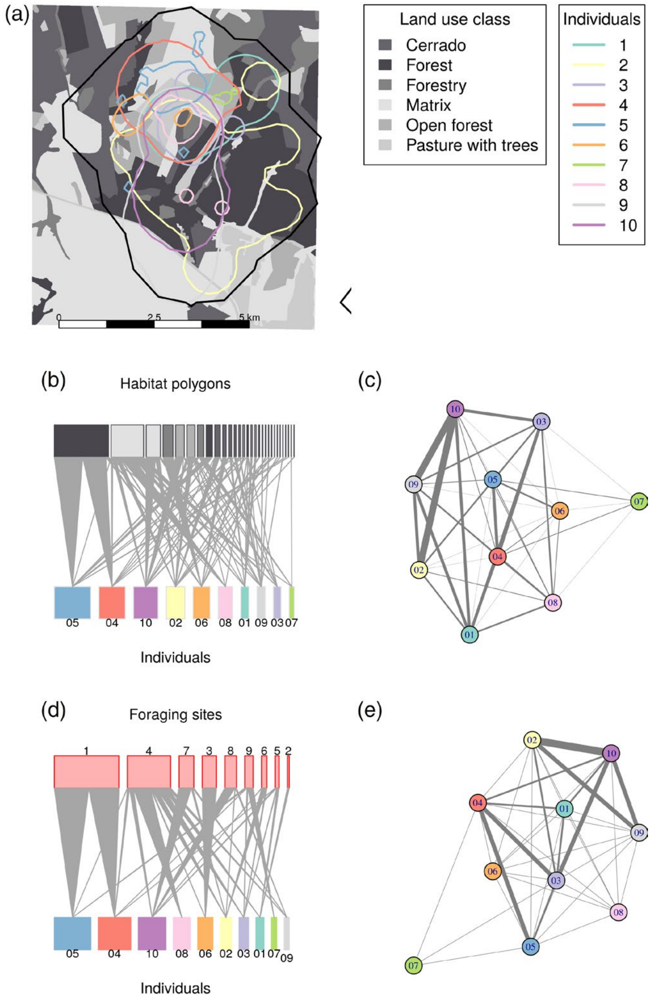

FIGURE 3 Individual specialization in the use of space by *Sturnira lilium* bats according to the following approaches: *Space* (a), *Land cover* (b, c), and *Foraging* (d, e). (a) Overlap in the utilization distributions of different individuals (colours) and the whole population (black), which was the basis for defining the Spatial Individual Specialization index, *SpatIS*. To aid the illustration of several individuals and avoid contours or three-dimensional representations with different colours, we presented here the 95% KDE, but it is important to note that *SpatIS* was based on the overlap of the utilization distribution volume of each individual and the population. (b) and (d) represent a bipartite spatial network formed by individual bats (below) and landscape resources (polygons or foraging sites, above) and the link width represents the frequency of use of landscape resource by each bat. (c) and (e) represent individual niche overlap network with individual bats as nodes and the link width representing the overlap in the use of landscape resources for each pair of individuals

4 | DISCUSSION

Studies on individual specialization mostly addressed aspects related to diet in their beginning. Lately, the development of more efficient and precise tracking devices and analytical tools, in addition to isotope analysis, have allowed movement ecology to understand patterns of individual variation (Carneiro et al., 2017).

TABLE 2 Coefficient of determination and significance of linear regression between the proportion of activity points of each individual bat at each foraging site and the availability of different food-plant genera in these sites ($df = 6$). Foraging site 9 was excluded from the analysis as permission to enter was not granted. Significant results ($p < 0.05$) are presented in boldface

	Solanum		*Piper*		*Cecropia*		Favourite subareas (Figure 2)
Id	R^2	p	R^2	p	R^2	p	
1	0.15	0.33	**0.62**	**0.01**	0.10	0.43	2, 4, 5
2	0.18	0.28	0.43	0.07	0.00	0.96	4, 6, 7, 8
3	0.11	0.41	**0.87**	**<0.01**	0.02	0.68	4, 5
4	**0.88**	**<0.01**	0.01	0.76	0.05	0.56	1
5	**0.90**	**<0.01**	0.03	0.67	0.06	0.58	1
6	0.03	0.88	0.04	0.61	**0.8**	**<0.0 1**	3
7	NA	NA	NA	NA	NA	NA	9
8	0.07	0.51	**0.91**	**<0.01**	0.03	0.66	4, 5
9	0.07	0.49	**0.58**	**0.02**	0.12	0.39	4, 5, 7, 8
10	0.01	0.74	0.00	0.90	0.15	0.34	4, 7, 8

Individual specialization in the use of space has been associated with multiple concepts, such as site fidelity, spatial and environmental consistency, consistency or repeatability of movement trips (e.g. in distance, duration, range or direction) and overlap in areas of use, utilization distributions or environmental niches between individuals (e.g. Bonnet-Lebrun, Phillips, Manica, & Rodrigues, 2018; Dehnhard et al., 2019; Harris et al., 2020; Wakefield et al., 2015). Individuals move for multiple reasons (e.g. search for food, mates, shelter, nesting or calving sites) and may specialize in the movement during these different behaviours, both in the selection and use of sites as well as in the timing to move, the selection of the routes to reach these places and the navigational cues used to move. Here we strengthened the connection between individual specialization and movement ecology by adapting available analytical tools and by developing new indices of individual specialization in space use. Our approach was also rooted in the concepts of site fidelity and overlap in areas of use and are a direct analogy to the indices developed in dietary studies (Araújo et al., 2008; Bolnick et al., 2002).

In this study, we present strong evidence of individual specialization in space use by frugivorous bats of the species *S. lilium*. Different individual bats foraged more often in different geographical locations and types of habitat, which had different availability of food–plants of the genera *Cecropia*, *Piper* and *Solanum*. This is consistent with a previous study on interindividual variations in diet carried out with the same population (Muylaert, Matos, et al., 2014). A diversified tool set combining network science and spatial statistics led to convergent results in our study. Below we highlight the meaning of each approach and discuss the causes and consequences of individual specialization in space use.

First, we considered landscape elements as resources. It was difficult to determine the boundaries between spatial resources. On the one hand, if they were determined a priori (*Land cover* approach), based on the habitat types found in the landscape, we might include noise related to habitat types that could not be used by the model species. On the other hand, if spatial resources were determined based on their use by bats as foraging sites (*Foraging* approach), this might be viewed as an error of circularity. Therefore, we decided to use those two approaches in parallel and test their consistency. Both led to similar results and pointed to individual specialization in space use. As an additional line of evidence, we proposed two indices that assess the overlap between the utilization distribution of each individual bat and that of the population as a whole, regardless of landscape information. We found again high individual specialization, which corroborates the hypothesis that individual bats differ in their space use.

Other studies also found individual specialization in space use using analogous methods (Carneiro et al., 2017), most of them using marine birds as model species. Wakefield et al. (2015) measured individual consistency in foraging sites (site fidelity) in gannets using overlap in utilization distributions between individuals, but with a definition different from *SpatIS*. Bonnet-Lebrun et al. (2018) developed the multidimensional individual specialization index (MISI) to quantify individual foraging site fidelity considering the volume of environmental and spatial niche, but not based on utilization distributions. Our approach is complementary to theirs; we adapted our definition of *SpatIS* directly from Bolnick's individual specialization index and we can also measure how complementary each individual space use is in relation to the rest of the population using *SpatICS*.

Ecological niche theory predicts that, to avoid competition, individuals should segregate in their use of resources in space, time, or diet. In this context, population level generalist strategies should be selected for in heterogeneous and unpredictable environments, while specialization would be favoured in spatio-temporally stable environments (Dehnhard et al., 2019). Dehnhard et al. (2019) showed that three fulmarine petrel species breeding in a highly variable and unpredictable area behave as generalists in their space use, even though this increased the potential for competition within and among these sympatric species. We found high individual specialization in space use. Even though these are opposite results, they support the same hypothesis, since the studied bats foraged in a predictable environment. Furthermore, it is important to notice that some individuals (2 and 10) showed an activity pattern that was not related to food-plant availability, which suggests that the level of specialization in space use varied between individuals of the same population (Bolnick et al., 2003).

Site fidelity and repeatability in movements in a marine predator bird was recently reported by Harris et al. (2020), but patterns were not linked to the spatial segregation of resources. Instead, they were a result of the behavioural difference between individuals, since bolder individuals presented higher site fidelity. This means individual specialization is also present at longer time scales and may arise from the interplay between environmental conditions, habitat availability and individual personality.

We discuss two possible explanations for the link between individual specialization in diet and space use in *S. lilium* bats. The first mechanism involves intraspecific competition for fruits. *S. lilium* bats show strong preference for fruits of the genus *Solanum* (Andrade et al., 2013; Muylaert, Matos, et al., 2014). Nevertheless, *S. lilium* bats have high digestive capacity and can use both high- and low-quality fruits (fruits of *Solanum* and *Piper* contain higher percentages of carbohydrates and proteins than do *Cecropia* fruits; Saldaña-Vázquez, Ruiz-Sanchez, Herrera-Alsina, & Schondube, 2015). In fact, individual bats of the same population studied here are able to feed on other fruits and so differ in their secondary preferences (Muylaert, Matos, et al., 2014). In addition, as observed in our study, plants of those three genera are not uniformly distributed in the landscape. Therefore, we conclude that the large and very common populations formed by *S. lilium* (Muylaert et al., 2017) are maintained by ecological plasticity with individual bats segregating their dietary and spatial niches at a local scale.

An alternative to niche segregation, learned behaviour can be viewed as a second mechanism driving individual specialization. Individual bats can learn foraging habitats and favourite fruits from their parents (Geipel, Kalko, Wallmeyer, & Knörnschild, 2013). Furthermore, preferences related to habitat and diet might emerge from the social group through information transfer, as *S. lilium* is a social species with strong within-colony interactions (ter Hofstede & Fenton, 2005) and some of the studied individuals were found in very close roosts. Day roosts might also be limiting factors. *Sturnira lilium* bats roost mainly in tree cavities (Garbino & Tavares, 2018) and all roosts were found in riparian forests in our study. This type of habitat represents a small proportion of the study area, which is consistent with the hypothesis that these bats have specific roosting requirements.

Regardless of the mechanism behind it, individual specialization in space use might have implications for seed dispersal. The success of a seed depends on several factors, such as its distance from the parent plant (Connell, 1971; Janzen, 1970) and its likelihood of reaching safe places for germination and establishment (Howe & Smallwood, 1982). In our study, individual bats moved different distances and used areas of different sizes. It means that the fate of a seed depends on the individual movement pattern of its disperser bat. In addition, if different individuals take the seeds to different sites, it increases the diversity of habitats where they are deposited, which increases their likelihood of reaching a safe site (Zwolak, 2018).

In conclusion, the connection made in our study between individual specialization and movement ecology was only possible by reinterpreting metrics and methods from the literature. The classification of spatial resources (*Land cover*, *Foraging* and *Space* approaches) and tool set (*SpatIS* and *SpatICS*) created in our study may be applied to other species, ecosystems and types of movement data. Although *SpatIS* and *SpatICS* used traditional space use functions and estimators, they could be also adapted to other kinds of utilization distribution and kernel density estimators, such as Brownian Bridge models (Horne, Garton, Krone, & Lewis, 2007) or continuous-time movement models and autocorrelated kernel density estimators (Fleming & Calabrese, 2017), that explicitly consider movement between locations.

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AUTHORS' CONTRIBUTIONS

P.K.-R. conceived and designed the study, collected field data and carried out the statistical analysis; B.B.N. carried out the statistical analysis and developed the R code; R.L.M. collected field data and carried out the statistical analysis. M.A.R.M. acquired funding, collected field data and conceived and designed the study. All authors wrote the manuscript and gave final approval for publication.

CONFLICT OF INTERESTS

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

All data and code used in this manuscript are available on the GitHub repository https://github.com/LEEClab/SpatIS, including scripts to calculate SpatIS and SpatICS http://doi.org/10.5281/zenodo.3969084 (Niebuhr, Kerches-Rogeri, Muylaert, & Mello, 2020).

To ease the accessibility of the data in a standard format for movement ecology studies, we also archived the bat movement data on MoveBank (https://www.movebank.org, study name: 'Individual specialization in the use of space by frugivorous bats').

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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