

## RESEARCH PAPER

### Title

Landscape composition and life-history traits influence bat movement and space use: analysis of 30 years of published telemetry data

### Running head

Bat movement and space use patterns

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## **Biosketch**

Alexis Laforge is a conservation ecologist with particular interest on bat ecology at both species and community level. He is involved in several bat research programs, including bioacoustic sampling, home range selection, individual movements, functional traits, landscape ecology and responses to human disturbances such as forest fragmentation, light pollution and road mortality.

## **Author contributions**

A.L., F.A. and L.B. conceived the study, A.L., F.A., A.C., C.S., J.F., N.G., K.B., CR., F.C., C.K. and L.B. contributed to read the literature and to extract the dataset, A.L. performed the data analyses with support from F.A., S.L. and H.M. computed the GIS data, A.L. led the writing and all authors contributed to edit the final version of the manuscript.

## **Abstract**

**Aim:** Animal movement determines home range patterns, which in turn affect individual fitness, population dynamics and ecosystem functioning. Using temperate bats, a group of particular conservation concern, we investigated how morphological traits, habitat specialization and environmental variables affect home range sizes and daily foraging movements, using a compilation of 30 years of published bat telemetry data.

**Location:** Northern America and Europe.

**Time period:** 1988 – 2016.

**Major taxa studied:** Bats.

**Methods:** We compiled data on home range size and mean daily distance between roosts and foraging areas at both colony and individual levels from 166 studies of 3,129 radiotracked individuals of 49 bat species. We calculated multi-scale habitat composition and configuration in the surrounding landscapes of the 165 studied roosts. Using mixed models, we examined the effects of habitat availability and spatial arrangement on bat movements, while accounting for body mass, aspect ratio, wing loading and habitat specialization.

**Results:** We found a significant effect of landscape composition on home range size and mean daily distance at both colony and individual levels. On average, home ranges were up to 42% smaller in the most habitat-diversified landscapes while mean daily distances were up to 30% shorter in the most forested landscapes. Bat home range size significantly increased with body mass, wing aspect ratio and wing loading, and decreased with habitat specialization.

**Main conclusions:** Promoting bat movements through the landscape surrounding roosts at large spatial scales is crucial for bat conservation. Forest loss and overall landscape homogenization lead temperate bats to fly farther to meet their ecological requirements, by increasing home range sizes

and daily foraging distances. Both processes might be more detrimental for smaller, habitat-specialized bats, less able to travel increasingly longer distances to meet their diverse needs.

## **KEYWORDS**

Animal movement, Chiroptera, central place forager, home range, landscape complementation, mammals, Minimum Convex Polygon, spatial behaviour, radiotracking

## **1. INTRODUCTION**

With approximately 50 to 70% of Earth's land surface currently modified by human activities (Barnosky *et al.*, 2012), the expanding human footprint (e.g., urban cover, road density, cropland) is expected to be associated with reduced animal movements (Tucker *et al.*, 2018). This may be due to a barrier effect to movements and/or to a food resource concentration effect (Tucker *et al.*, 2018). Previous studies have shown the severe effects of reduced movement on these processes such as threatened individual fitness and population viability (Hanski & Ovaskainen, 2000; Allan *et al.*, 2003). Among the various ecological processes that are deeply affected by movement ability of individual animals, species turnover and survival at the landscape scale, role of species in ecosystem functions and macro-scale diversity patterns are particularly important for conservation biogeography (Nathan *et al.*, 2008; Jeltsch *et al.*, 2013). Animal movement influences biotic interactions (e.g., predator-prey dynamics, competition for resources), including those with conspecifics (e.g., social facilitation), as well as ecological functions fulfilled by species in ecosystems according to their life traits (e.g., pest regulation, seed dispersal, disease dynamics and gene flow) (Lundberg & Moberg, 2003; Bauer & Hoye, 2014).

The quest for resources is one of the most important drivers of animal movements (Almenar *et al.*, 2011), including both trophic and breeding requirements. Typically, home range, or the area used by an animal to achieve its ecological requirements in a given time lapse, decreases with increasing amount of resources (Anthony & Kunz, 1977). The spatial arrangement of resources and the interspersed habitats containing vital resources (i.e., increasing landscape complementation) also affect animal movements (Fahrig, 2017). It is expected that individuals travel shorter daily

distances in heterogeneous than in homogeneous landscapes to obtain complementary resources, because the former provides more diverse resources within a smaller area (Tucker *et al.*, 2019).

Two main types of life-history traits drive species responses to landscape modification: morphology and specialization to diet and habitat (Keinath *et al.*, 2017). For instance, previous studies have shown that larger non-flying mammals have larger home range sizes (Tucker *et al.*, 2014) and that larger birds usually fly farther (Tucker *et al.*, 2019). Based on allometric relationships, larger species have higher absolute energetic demands and need to travel farther to gain the resources needed to meet those demands (McNab, 1963). It is also expected that habitat specialists would travel shorter distances than generalists, because the cost of moving through the landscape mosaic would be higher for specialists than for generalists. Long distance movements are overall described to increase the risk of moving in a different, less favorable habitat and thus decrease the benefits of specialization (Baguette & Van Dyck, 2007; Poisot *et al.*, 2011). However, this also depends on the scarcity of the resource and how it is distributed in the landscape (Davidson-Watts & Jones, 2006; Samways & Lu, 2007).

Despite the large body of work on the physiological and ecological variables that might affect animal movement and home range size, knowledge gaps remain in our understanding of which combination of factors actually drive them (Tucker *et al.*, 2014). Furthermore, to date, empirical studies on this topic have been biased towards birds and non-flying mammals, most often excluding bats. Moreover, previous research on the link between bat movement and landscapes has largely focused on single populations (Knight, 2006; Reiter *et al.*, 2013), with less attention on how home range size and daily movement distance are impacted by habitat distribution for multiple species in relation to their life-history traits.

As central-place foragers, bats are highly mobile between roosts and foraging sites (Voigt *et al.*, 2017). Their individual home ranges are generally heterogeneous areas because they use multiple habitat patches to meet their needs within the landscape (Presley *et al.*, 2019). Furthermore, bats are highly dependent on forest habitat either to roost, commute or forage, making them very sensitive to forest amount and configuration in the landscape (Ethier & Fahrig, 2011). Consequently, we expected an increase in forest patch number, overall forest amount or landscape heterogeneity to be associated with reduced bat movements by facilitating landscape complementation process (i.e., increased access to different types of non-substitutable resources) at shorter mean distances (Dunning *et al.* 1992; Ethier & Fahrig, 2011). We also expected landscape

anthropization to be associated with reduced bat mobility by an increased barrier effect to daily movements, natural habitats being more fragmented by roads and urban areas in more anthropized mosaics. Urbanization may also produce a potential additional effect of food resource concentration, for instance by artificial lighting at night attracting insects (Russo & Ancillotto, 2015).

For life history traits, we predicted that: (i) home range size and daily movement distance increase with body mass according to allometric scaling; (ii) species with larger aspect ratio and wing loading travel longer daily distances and have therefore larger home ranges, because a higher wing aspect ratio reduces the wing inertia and the flight cost while a higher wing loading induces a faster flight (Norberg & Rayner, 1987). We also explored potential relationships between habitat specialization and bat movement/space use.

## **2. MATERIALS AND METHODS**

### *2.1. Telemetry data*

We compiled telemetry data from 166 published studies between 1988 and 2019 (see Appendix 1 for a full list of the data sources) for 3,129 individuals of 49 temperate bat species across 22 countries and two continents (119 in Europe and 47 in North America). Our data represent 78% of all European bat species (32 out of 41) and 46% of all North Americans (17 out of 37 species; see Appendix S2). Studies were identified from the literature using a rigorous, transparent and repeatable protocol (Pullin & Stewart, 2006; see details in Appendix S3).

### *2.2. Movement and space use metrics*

We extracted from each study, when available: (i) the Minimum Convex Polygon (MCP), as a metric of bat space use and the most frequently used method to estimate home range size (Harris *et al.*, 1990); and (ii) daily distance travelled between roosts and foraging areas as a metric of bat movement (summary statistics of the data included in the analyses are in Appendix S4). We then built four different response variables: home range size and daily foraging movement distance at colony level (i.e., mean from all the radio-tracked individuals at each roost) and at individual level. As studies did not systematically report data at both colony and individual levels, it was relevant

to evaluate the consistency of our results through these two levels using different data subsets. Data at the colony level included the majority of studies (85%) and species (100%) because authors often documented mean values at that level, while data at the individual level were included in only 59% of the studies and 82% of the species. Sample size (i.e., number of radio-tagged individuals) was reported for each data at colony level. For each home range and distance data, we reported the sex, age and reproductive status of the radio-tracked bats when available. Due to differential energetic requirements, these variables are expected to influence bat movement and space use (Henry *et al.*, 2002; Flaquer *et al.*, 2008; Istvanko *et al.*, 2016). Complementary details on data acquisition are listed in Table S5.1 (Appendix S5).

### *2.3. Landscape-level variables*

To test our hypothesis that landscape structure influences space use and daily bat movements, we first reported the approximate location of 165 colony roosts from 118 studies (out of 166; Figure 1) because some studies did not provide enough information to properly locate their studied roosts (see Table S6.1 in Appendix S6). We then created four buffers (1, 5, 10 and 20 km radii) around each relocated roost to identify the strongest biologically relevant ‘scale of effect’ (Jackson & Fahrig, 2012). At each spatial scale, we measured the following landscape variables: (i) the Shannon diversity index as a proxy of landscape compositional heterogeneity computed for all types of land covers in a given buffer; (ii) the proportion of forests as a proxy of overall forest amount; (iii) the number of forest patches as a proxy of forest configuration; (iv) the road density; and (v) the mean Human Footprint Index (HFI), an index with a global extent that combines multiple factors of human influence, as a proxy of landscape anthropization (details on the landscape variables are in the Appendix S6). All these steps were conducted using ArcGis 10.5.1 (ESRI, Redlands, CA).

### *2.4. Life-history traits*

To test our hypotheses that (i) body mass, (ii) aspect ratio (the square of the wingspan divided by wing area) and (iii) wing loading (body mass divided by wing area) are positively associated with daily distance and home range size, while (iv) habitat specialization is negatively related to movement and space use, we calculated these four different life-history traits and used them as

explanatory variables (Appendix S7). Species mean body mass was obtained from Dietz et al. (2009) for European species and from Harvey et al. (2011) for North American species. Aspect ratio and wing loading (two metrics widely used for estimating bat mobility) were obtained from Norberg and Rayner (1987).

For European species we used the ‘Species habitat Specialization Index’ (SSI), an index estimated as the coefficient of variation of the number of acoustic bat passes across habitats (Kerbiriou *et al.*, 2018; Barbaro *et al.*, 2019). This index was calculated from a large-scale acoustic survey of bat communities (5,595 nights of survey over 1,158 sites) performed during nine years across France (<http://www.vigienature.fr/fr/chauves-souris>). Although the analysis of the effect of this habitat specialization index on bat movements was restricted to European species only, we argue that this is the most relevant and accurate method to test our prediction in comparison with other methods based on expert-opinion or on coarse information (e.g., IUCN Red List and Pantheria database).

## 2.5. Statistical analyses

We tested the effect of landscape structure and life-history traits on bat home range size and daily movement distance at both colony and individual levels, using linear mixed-effect models with a Gaussian error distribution. All analyses were conducted in R version 3.4.3 (R Core Team, 2017) and details on the R packages used in the analyses can be found in the Supplementary Information (Appendix S8). We log-transformed home range size and daily distance values as response variables to make our data approximately normal distributed, as confirmed with calculation of skewness (values ranged between -0.6 and 0.4) and kurtosis (values ranged between 1.3 and 3.2). For each model, we further checked the residuals for normality (i.e., Q–Q plots). All continuous variables used as fixed effects were scaled to correct for skewness (with a mean of 0 and a standard deviation of 1), to make associated regression coefficients comparable in magnitude and to interpret their effects biologically (Schielzeth, 2010). We checked for the absence of collinearity among predictors with the Spearman’s correlation coefficient and the variance inflation factors (VIFs) and we found  $|r| \leq 0.66$  and  $VIFs < 3.0$  for all variable pairs. We examined the goodness-of-fit for each model using the marginal  $R^2$  (variance explained by the fixed effects) and conditional  $R^2$  (variance explained by both fixed and random factors) values (Nakagawa & Schielzeth, 2013).

The amount of information varied considerably among studies. As a result, the data set contained a number of missing values (e.g., some roosts could not be properly located to calculate landscape variables). To deal with this issue, rather than restricting the analyses to the subset of data with all informed explanatory variables, we used a multistep process to construct a ‘best-supported model’ (see Figures S9.1 and S9.2 in Appendix S9), an approach that has been successfully used in other studies with many possible explanatory variables (Yamashita *et al.*, 2007; Keinath *et al.*, 2017). At each step, the best-supported model (i.e. best combination of variables) was identified from forward selection based on AICc (i.e. lowest AICc value). All candidate models at each step contained different subsets of variables except ‘study ID’ and ‘species’ (both as random factors) which were included in all models to control for both inter-study and inter-species variations.

#### 2.5.1. Colony level

The number of individuals used to calculate the MCP and distance means was added as a covariate in the base model (i.e. in all candidate models at each step; see Appendix S9).

Step 1.1: First, we compared models including morphological traits only (as fixed effects) using the most extensive part of the data (‘trait subset’). This step was not used for selection of the most important morphological trait but rather to evaluate the robustness of those relationships with the ‘landscape subset’ which is a more restrictive data subset, as not all study sites could be located to calculate landscape variables (see Tables S10.1 to 4 in Appendix S10).

Step 1.2: Second, we identified the best combination of landscape variables by comparing models that differed only in their combinations of landscape metrics as fixed effects with the ‘landscape subset’ (traits not included in the models at this stage). The best model of this step (i.e. ‘best model landscape’) is not presented in the results because the data subset (i.e. ‘landscape subset’) did not differ between this step and the next one (i.e. step 2). This step was used to reduce the number of landscape variables to include alongside trait variables, and hence limit the risk of over-parametrization.

Step 2: forward selection was used to select the best-supported models of the effect of morphological and landscape variables on home range size and daily distance, including the three morphological traits and important landscape variables previously identified (i.e., from the ‘best model trait’ and ‘best model landscape’ from steps 1.1 and 1.2 respectively). This procedure (step 1.2 + step 2) was repeated for the four different spatial scales (i.e., 1, 5, 10 and 20 km radii). The

best spatial scale was identified according to the highest marginal  $R^2$  among the four best-supported models obtained (one per scale).

Step 3: To evaluate the robustness of effects identified within best-supported models at the best spatial scale (i.e. from step 2), we first applied the Bonferroni test (Simes, 1986) to identify outliers having a significant impact on model fitting (i.e., no studentized residuals with Bonferroni p-value < 0.05). Second, we used Cook's distance as a measure of sensitivity (Cook, 1977) by identifying the most potential influential observations (i.e., a large value of Cook's distance) on the covariate patterns (i.e., high leverage values). We then removed these previously identified observations (from both tests) from the dataset (i.e., from the 'landscape subset'), re-fitted the best-supported model (i.e. from step 2) and checked if the removal process caused substantial changes in coefficient estimates (see Appendix S10).

Step 4: To test our prediction that movement of a given bat species is likely to decrease with the species' niche width, we reproduced step 2 by adding SSI as a covariate with a subset of the European species data ('Europe subset') alongside morphological and landscape variables, only at the best spatial scale previously identified. Besides testing our prediction, this step allowed us to assess whether the models better fitted the data with or without the inclusion of SSI, and to re-evaluate the consistency of other predictors.

### 2.5.2. Individual level

Analyses at the individual level aimed at improving the accuracy of our models, by including, whenever data was available, the intra-colony variance around the means through the individual variations in each colony. Furthermore, analyses at the individual level also permitted to test the effects of biological status (age, i.e. adults / juveniles; sex; reproductive status of the females, i.e. gestating / lactating / post-lactating) on home range size and daily movement distance. The analytical procedure described above at the colony level was repeated using 2,072 individual data. To do so, the number of individuals (fixed effect) was removed from the base model while 'roost ID' was added as a random effect to account for the likely correlation between observations on individual bats from the same roost (pseudo-replication). Sex, age and reproductive status as well as the three morphological traits and landscape variables were included as fixed effects during the forward model selection (see Appendix S9).

### 2.5.3. Potential biases exploration

Important methodological information such as the number of fixes used to calculate home-range size, the number of nights of telemetry survey and the transmitter weight tagged on individual bats were unfortunately too scarce among the collected studies to be included in our main analyses. We therefore conducted complementary analyses on the most restrictive dataset ('sampling subset') by including consecutively those information as predictors (fixed effects) in our best-supported models and compared to the results of the original models (see Tables S11.1 and 2 in Appendix S11). Bat movement data were obtained from studies carried out between 1988 and 2016 and the sampling years did not necessarily coincide with that of the land cover data used to calculate landscape predictors. We thus re-ran our best models with a data subset in which this difference does not exceed 10 years and compared results (see Figures S12.1 and 2 and Table S12.1 in Appendix S12). In addition, we have chosen to use different land cover data for each continent in order to optimise the spatial resolution and habitat classification details of our data. For this reason, we explored the effect of the factorial variable 'continent' and its interaction with our landscape predictors selected in our best models (see Figure S13.1 and Table S13.1 in Appendix S13). We compared all those 'alternative models' results with our best-supported models of the step 2.

### 2.5.4. Accounting for phylogenetic relatedness

We finally re-tested the relationships between landscape metrics, life-history traits and bat movement/space use obtained from our best linear mixed-effect models within an explicit phylogenetic framework. We used Bayesian generalized linear mixed models (MCMCglmms) to check if not incorporating information on the phylogenetic relatedness among species in our best models did not inflate Type I error rates, i.e. showing significant relationships that may not actually exist (Stone *et al.*, 2011). We obtained phylogeny for our 49 focal species from the PHYLACINE project ([https://megapast2future.github.io/PHYLACINE\\_1.2](https://megapast2future.github.io/PHYLACINE_1.2)), an open access global database of mammals (Faurby *et al.*, 2018 ; see Figure S14.1 in Appendix S14). For each best linear mixed-effects models (i.e. for both MCP and daily movement distance as response variables at both colony and individual levels), we ran an alternative MCMCglmm model with a Gaussian distribution and the same set of fixed and random effects (see Tables S14.1 and 2 in Appendix S14 for details on model parametrization and evaluation).

### 3. RESULTS

We found a significant negative effect of landscape compositional heterogeneity on bat home range size and a negative effect of forest proportion on daily distance from roosts to foraging areas (Table 1, Figure 2). The results were similar at both colony and individual levels (Tables 1 and 2, Figure 2). Landscape heterogeneity had the most significant effect on home range size when measured within a 20 km radius, while forest proportion had the most significant effect on mean daily distance a 5 km radius. On average, home range size was reduced by up to 42% within the most heterogeneous landscapes and daily distance by up to 30% within the most forested landscapes (Figure 2). The Human Footprint index (HFI) had a negative effect on daily distance although the relationship was only robust at individual level (see Figure S15.1. in Appendix S15). These results remained unchanged when accounting for phylogenetic relatedness (Appendix S14).

Body mass was the morphological trait most often selected across different models and data subsets. We found a positive effect of body mass on both home range size and daily distance (Tables 1 and 2, Figure 3), although the latter was not consistent at the individual level (Table 2). Also, when accounting for phylogeny in the models (i.e. MCMCglmm), the effect of body mass on home range size became marginally significant at the individual level (estimate = 1.449; 95% CI: -0.079, +3.157;  $P_{\text{MCMC}} = 0.057$ ; Appendix S14). We also detected a positive effect of aspect ratio on home range size (Tables 1 and 2), although it also became marginally significant when accounting for phylogeny at colony level (estimate = 0.615; 95% CI: -0.096, +1.294;  $P_{\text{MCMC}} = 0.089$ ; Appendix S14). The positive effect of wing loading on home range size was only significant for the European species (Tables 1 & 2, Appendix S14). Home range size decreased with species habitat specialization (SSI), both at the colony and individual levels (see Tables 1 and 2, Figure 3 and Appendix S14).

At the individual level, juveniles tended to have larger home ranges than adults, irrespective of species identity, while their mean daily movements tended to be shorter than those of adults (Table 2 and Appendix S14). We did not find any significant effect of number of individuals, road density, number of forest patches, sex and reproductive status on home range size and daily distance.

The best mixed models including both landscape and trait variables (i.e., step 2) explained 60–98% of the variation in bat home range size and daily foraging distance at colony and individual levels (both random and fixed effects included). The best models still explained 19–35% of the variation when accounting for fixed effects alone (Tables 1 and 2).

The addition of covariates such as the number of fixes, the number of nights or the transmitter weight in the models did not change the significance of landscape predictors (Tables S11.1 and S11.2 in Appendix S11). Only the number of fixes had a significant positive effect on home-range size at individual level (Table S11.2). However, by adding one of these covariates, the effects of some morphological traits were no longer significant (Tables S11.1 and S11.2). The effects of these three landscape predictors were consistent between the two continents and did not depend on the ‘continent’ effect (Appendix S13). Finally, the results were similar when using only data with less than 10-years’ time-lags between bat surveys and land cover maps. Full results from complementary analyses can be found in the Supplementary Information (Appendices S11, S12, and S13).

#### **4. DISCUSSION**

By re-analyzing 30 years of bat telemetry data from 22 temperate countries across Northern America and Europe, our study highlights the close relationships existing between animal movements, their life-history traits and their environments (Tucker *et al.*, 2014, 2018). In particular, we validated our hypotheses that landscape compositional heterogeneity, forest amount or Species Specialization Index (SSI) were negatively related either to home range size or to daily distance travelled between roosts and foraging areas. We also confirmed that larger temperate bats generally have greater home ranges and travel longer distances daily. Despite high methodological variation between studies, we found evidence for bats being highly sensitive to landscape composition and spatial distribution of resources (Presley *et al.*, 2019). The high variability among radio-tracking studies did not allow us testing simultaneously all predictors on the entire dataset, which advocate for more consistency in the methodologies used and mandatory information to be provided in publications from future telemetry studies. Such heterogeneity in the data led us to apply a step-by-step analytical approach, to some extent analogous to multiple sensitivity tests with different subsets, at both colony and individual levels, in order to quantify the robustness of our results.

Estimates of home range size are known to be very sensitive to sampling effort and methodological choices (Laver & Kelly, 2008). However, we did not find an effect of the number of individuals within a given colony on its home range size. In our case, home range size varied

much among bat species (x10,000 between *Nyctalus noctula* and several *Myotis* spp., Appendix S4), which may mask slight differences and possible biases in methodological options used to estimate MCPs (Nilsen *et al.*, 2008). Moreover, most of the telemetry studies only provide MCP values when the asymptote between the number of fixes and home range size is reached (i.e., plateaued), thus minoring potential statistical issues by using MCP values from different studies. Providing such information has become a methodological requirement following recommendations made by Harris *et al.* (1990).

We neither studied seasonal variation in bat movements, nor the effect of colony size, because this information was too scarce. Yet, bats are known to adapt their movements to seasonal variations in food availability (Law, 1993) and intra- and interspecific interactions are often seen as a main driver in shaping bat movements, as a trade-off between social information transfer and food competition cost (Roeleke *et al.*, 2018; Salinas-Ramos *et al.*, 2019). We detected a robust effect of HFI only at the individual level. Tracking bats in the most urbanized areas may be less attractive to conservationists, leading to an unbalanced data from urban landscapes compared to more natural ones. Furthermore, HFI index may be too coarse for proper home range estimates, combining multiple proxies of human influence with a large resolution (1 km). While we did not detect a robust or significant negative effect of HFI and road density using this data set, several studies have shown that bats are very sensitive to urbanization (Russo & Ancillotto, 2015) and roads (Claireau *et al.*, 2019), so that we cannot formally exclude that increased HFI and road density would actually reduce bat movements. We used a data set that was unbalanced in favor of European data and towards the unique family of *Vespertilionidae* and the genus *Myotis*, highlighting the need for more North American studies on bat movement of species belonging to less diversified and studied clades, to better predict temperate bats' response to human-induced landscape change at a macro-spatial scale.

We showed that the magnitude and spatial extent of bat movements depended on landscape composition. Home range size was on average 42% smaller in the most heterogeneous landscapes (Shannon diversity index equals to 1.8) compared to the most homogeneous landscapes (Shannon diversity index 0.2) and mean daily distance was on average 30% shorter within the most forested landscapes (forest amount of 95%) compared to the least forested landscapes (1%). Interestingly, the strongest negative relationships between landscape heterogeneity and home range size, and between forest proportion and daily movement distance consistently occurred at different spatial

scales, 20 and 5 km respectively. Estimates of mean daily distance account more for ‘routine’ behaviour while MCP method account more for more ‘unusual’ – exploratory behaviour (i.e., peripheral fixes) as this method is generally calculated from all fixes obtained without taking into account the spatial density of the fixes (Harris *et al.*, 1990). Our results may thus reveal that forest habitats close to roosts are important to facilitate commuting and foraging behaviour of short mean daily distance, while landscape compositional heterogeneity at larger scale may reduce the maximum daily distance needed to reach secondary foraging areas when food availability is scarce (Dunning *et al.*, 1992).

Many of the studies used in our analyses showed that temperate insectivorous bats (i) tend to forage in a wide range of habitats and (ii) most often roost outside their preferential foraging areas (Dietz *et al.*, 2009). We argue that bats have smaller home-range sizes in more heterogeneous landscapes, where the spatial arrangement of foraging and commuting habitats is more interspersed, so that bats can access multiple and diverse foraging habitats while reducing distance costs from roosts (Dunning *et al.*, 1992). As it is the case for birds, bat movements are strongly influenced by landscape heterogeneity, so that it is crucial to improve landscape complementarity of habitat patches in human-modified areas where heterogeneous landscapes (i.e., diversified) are most often converted into homogeneous landscapes (i.e. dominated by impervious surfaces and croplands) (Monck-Whipp *et al.*, 2018; Tucker *et al.*, 2019).

Forests are well-known key habitats for most temperate bats. Forest edges, forest interiors and tree canopies can altogether act either as a navigational reference (i.e. commuting), a source of insect prey (i.e. foraging), a shelter from wind, a preferential roost, or as protection from predators, depending on bat species (Dietz *et al.*, 2009). Large wooded patches may provide a higher spatial heterogeneity in stand structure and forest management, clearings, logging-tracks, and potentially more tree micro-habitats and deadwoods (i.e., food availability and diversity) than small patches. Forest tree composition and microhabitat diversity, as well as deadwood amount, are all known to have a positive effect on bats (Paillet *et al.*, 2018; Barbaro *et al.*, 2019; Langridge *et al.*, 2019). As a result, forest loss may trigger enhanced bat movements needed to achieve their different daily requirements found in other habitats of the mosaic (i.e., through resource complementation), especially in more anthropized landscapes.

In addition, the quality of foraging habitats surrounding roosts plays a decisive role in roost choice for temperate bats (Boughey *et al.*, 2011) but also in the temporal dynamics of the colony size

(Froidevaux *et al.*, 2017). Thus, because bats are highly dependent on the availability of appropriate and sustainable structures to roost in the landscape, finding such roosts in an optimal landscape structure may often be difficult (Popa-Lisseanu *et al.*, 2009). Promoting bat movements through the landscape surrounding roosts at large spatial scales is therefore crucial for bat conservation.

When morphological traits were selected in our best-supported models, they were always positively associated with bat home range size and daily movement distances, and often significantly. These results support our predictions that heavier bat species may fly farther owing to higher energy efficiency (higher aspect ratio), increased flight speeds (higher wing loading) and increased resource requirements (Norberg & Rayner, 1987). However, we note that some morphological relationships became non-significant by including the number of fixes or the phylogenetic relatedness in our models (Tables S11.2, S14.1 & S14.2).

We found that the most habitat-specialized species had on average smaller home range size. Specialist species may perceive a given landscape as more fragmented and hostile than generalist bats, and their longest distance movements may be more costly (Baguette & Van Dyck, 2007; Poisot *et al.*, 2011). However, species specialization can be further quantified from a variety of resources and niche dimensions (e.g., diet, suitable day roost, hibernacula and mating sites) and these different components of specialization may respond differently to landscape modification. For instance, it could also be argued that some specialists are more mobile than their more generalist counterparts because the resources they rely on are spatially and temporally rarer at the landscape scale (Samways & Lu, 2007). Another hypothesis is that competition processes (e.g., competitive exclusion) may also contribute to explain this result. Generalist bat species may be less competitive than generally more agile specialist bat species, which have a more accurate sonar, but may have a better ability to switch between habitat types and alternative prey. This may allow them to also exploit lower-quality, suboptimal habitats, both from a prey abundance or a distance to travel perspectives, by offering refuges from interspecific competition (Roeleke *et al.*, 2018).

Contrary to our expectations, we did not find a significant effect of sex and reproductive status on bat space use and daily movement distances. Within bat telemetry studies, differences of space use and movement patterns between males and females and between individual reproductive status are not always significant in the literature (Henry *et al.*, 2002; Almenar *et al.*, 2011; Istvanko *et al.*, 2016). When authors found significant differences, they were also supported by differences in habitat selection suggesting that resource availability (i.e., landscape composition) outweighs the

roles of biological individual status (e.g., sex and reproductive status) to explain bat intraspecific variability in home range size and daily movement distance (Henry *et al.*, 2002; Popa-Lisseanu *et al.*, 2009; Almenar *et al.*, 2011). Our multi-continent analysis showed that juveniles tended to have larger home ranges, while their daily mean distances between roosts and foraging areas were reduced in comparison with adults. Juveniles may most often prefer to forage closer to the roost to improve flight maneuverability and foraging success in the most productive and safest habitats (Flaquer *et al.*, 2008) but may have a rarer but bolder behavior in exploring their new territories than adults (Goiti *et al.*, 2006). However, age of bat individuals was very unbalanced in our dataset, irrespective of the species ID (i.e., 90% of tracked individuals were adults against 10% of juveniles). Yet, including age improved the overall predictive power of our models without changing the effects of the other predictors, so that this result should be cautiously interpreted. Our results are also consistent with the co-evolution hypothesis of morphological traits, habitat specialization and movements (Tucker *et al.*, 2014; Keinath *et al.*, 2017). It is important to notice that morphological traits seem to better explain home range size (MCP) than mean daily distance variations. The ability of bats to modulate their maximum travel distances (i.e., peripheral fixes of the MCP), to compensate for a local and temporary food depletion in proximity to the roost for instance, seems to be more driven by morphological constraints while the mean daily distance is probably more driven by habitat specialization. This study alerts once again on the homogenization of bat communities with the expansion of human-modified landscapes favoring larger and generalist species at the expense of smaller habitat specialists (Russo & Ancillotto, 2015; Monck-Whipp *et al.*, 2018). However, promoting protected natural areas with more forested and diversified landscape mosaics could counteract this potential trend by favouring the most specialized bat communities (Kerbioui *et al.*, 2018).

## CONFLICT OF INTEREST

The authors declare no competing financial interests.

## DATA ACCESSIBILITY STATEMENT

The data sets supporting this article are available via an open-access repository (<https://doi.org/10.5061/dryad.qnk98sfhh>).

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## Appendix 1 – Data Sources

Exhaustive list of the 166 studies compiled from which data were used.

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## Table captions

**Table 1** Model coefficients,  $p$ -values,  $R^2$  and sample sizes of linear mixed-effects models predicting the log-transformed mean home range size (logMCP) and mean daily distance between roosts and foraging areas (logDist) at the colony level. Predictor variables included fixed effects for the Shannon diversity index of habitats in the landscape measured at 20 km ('Shannon index20'), forest proportion and Human Footprint Index (HFI) both measured at 5 km ('Forest proportion5' and 'HFI5'). All models also included 'study ID' and 'species ID' as random effects. Studies: number of studies; Species: number of species; Data: number of colonies (several MCP and distance values could be available from the same study).

logMCP				logDist			
Step 2: Best-supported model obtained with the 'landscape subset'							
	Estimates	SE	$p$		Estimates	SE	$p$
n individual	-0.056	0.134	.677	n individual	-0.098	0.105	.355
<b>Body mass</b>	<b>0.760</b>	<b>0.282</b>	<b>.016</b>	<b>Body mass</b>	<b>0.330</b>	<b>0.142</b>	<b>.027</b>
<b>Aspect ratio</b>	<b>0.684</b>	<b>0.320</b>	<b>.047</b>	<b>Forest proportion5</b>	<b>-0.489</b>	<b>0.106</b>	<b>.000</b>
<b>Shannon index20</b>	<b>-0.482</b>	<b>0.182</b>	<b>.009</b>	<b>HFI5</b>	<b>-0.252</b>	<b>0.111</b>	<b>.028</b>
<i>R<sup>2</sup> marginal</i>	.257				.345		
<i>R<sup>2</sup> conditional</i>	.858				.979		
Studies	64				44		
Species	31				30		
Data	91				55		
Step 4: Best-supported model obtained with the 'europe subset' to add the Species Specialization Index (SSI) as covariate in model selection							
	Estimates	SE	$p$		Estimates	SE	$p$
n individual	0.242	0.175	.173	n individual	-0.015	0.102	.883
<b>SSI</b>	<b>-0.706</b>	<b>0.236</b>	<b>.013</b>	<b>Forest proportion5</b>	<b>-0.401</b>	<b>0.119</b>	<b>.002</b>
<b>Wing loading</b>	<b>0.688</b>	<b>0.235</b>	<b>.009</b>	<b>HFI5</b>	<b>-0.237</b>	<b>0.116</b>	<b>.048</b>
<i>R<sup>2</sup> marginal</i>	.253				.192		
<i>R<sup>2</sup> conditional</i>	.918				.971		
Studies	57				36		
Species	25				22		
Data	81				46		

**Table 2** Model coefficients,  $p$ -values,  $R^2$  and sample sizes of linear mixed-effects models predicting the log-transformed mean home range size (logMCP) and mean daily distance between roosts and foraging areas (logDist) at individual level. Predictor variables included fixed effects for the Shannon diversity index of habitats in the landscape measured at 20 km ('Shannon index20'), forest proportion and Human Footprint Index (HFI) both measured at 5 km ('Forest proportion5' and 'HFI5'. The model also included 'study ID', 'roost ID' and 'species ID' as random effects. Bat movement of adult individuals were used as the reference (i.e., intercept). Studies: number of studies; Species: number of species; Data: number of individuals (several MCP and distance values could be available from the same study).

logMCP				logDist			
Step 2: Best-supported model obtained with the 'landscape subset'							
	Estimates	SE	$p$		Estimates	SE	$p$
Wing loading	-1.064	0.673	.130	<b>Age</b>	<b>-0.685</b>	<b>0.228</b>	<b>.003</b>
<b>Body mass</b>	<b>1.823</b>	<b>0.794</b>	<b>.035</b>	<b>Forest proportion5</b>	<b>-0.446</b>	<b>0.124</b>	<b>.003</b>
Aspect ratio	1.036	0.519	.059	<b>HFI5</b>	<b>-0.480</b>	<b>0.147</b>	<b>.006</b>
<b>Age</b>	<b>0.636</b>	<b>0.188</b>	<b>.001</b>	-	-	-	-
<b>Shannon index20</b>	<b>-0.698</b>	<b>0.232</b>	<b>.004</b>	-	-	-	-
<i>R<sup>2</sup> marginal</i>	.278			<i>R<sup>2</sup> marginal</i>			
<i>R<sup>2</sup> conditional</i>	.790			<i>R<sup>2</sup> conditional</i>			
Studies	46			19			
Species	23			9			
Data	655			235			
Step 4: Best-supported model obtained with the 'europe subset' to add the Species Specialization Index (SSI) as covariate in the model selection							
	Estimates	SE	$p$		Estimates	SE	$p$
<b>SSI</b>	<b>-0.995</b>	<b>0.252</b>	<b>.000</b>	SSI	-0.374	0.221	.137
<b>Wing loading</b>	<b>0.316</b>	<b>0.147</b>	<b>.032</b>	<b>Age</b>	<b>-0.689</b>	<b>0.228</b>	<b>.003</b>
Age	0.371	0.229	.106	<b>Forest proportion5</b>	<b>-0.472</b>	<b>0.129</b>	<b>.003</b>
<b>Shannon index20</b>	<b>-0.673</b>	<b>0.274</b>	<b>.020</b>	<b>HFI5</b>	<b>-0.540</b>	<b>0.149</b>	<b>.003</b>
<i>R<sup>2</sup> marginal</i>	.279			<i>R<sup>2</sup> marginal</i>			
<i>R<sup>2</sup> conditional</i>	.727			<i>R<sup>2</sup> conditional</i>			
Studies	38			18			
Species	17			8			
Data	527			230			

## Figure captions

**Figure 1** Location of the 165 roosts (light blue points) from telemetry studies in Northern America (n = 47) and Europe (n = 118) from 118 studies providing sufficient location details of their studied roosts and from which we calculated landscape variables.

**Figure 2** Bat home range size at the colony level (i.e., mean; A) and individual level (B) with increasing Shannon diversity index of habitats in the landscape (on the x axis, low values means homogeneous landscapes and high values means heterogeneous landscapes) calculated at 20 km radius scale; and bat daily distance between roosts and foraging areas at the colony level (i.e., mean; A) and individual level (B) with increasing forest proportion (%) within a 5 km radius from the colony. Results from the ‘best-supported model’ obtained at step 2 (‘landscape subset’). Plots include regression lines from the linear mixed-effects models (solid lines) and associated 95% confidence intervals (bands).

**Figure 3** Bat home range size at the colony level (i.e., mean; A) and individual level (B) with increasing 1) body mass (g), 2) aspect ratio and 3) habitat specialization index (i.e. SSI; most habitat specialized species are on the right). Results from the ‘best-supported model’ obtained at step 2 (‘landscape subset’) for body mass and aspect ratio; at step 4 for SSI (‘Europe subset’). Plots include regression lines from the linear mixed-effects models (solid lines) and associated 95% confidence intervals (bands).

## List and captions of supplementary figures

**Figure S9.1** Procedure of the statistical analyses performed at the colony level for each response variable ('resp.var' in the scheme): the log-transformed MCP and the log-transformed daily movement distance between roost and foraging areas.

**Figure S9.2** Procedure of the statistical analyses performed at the individual level for each response variable ('resp.var' in the scheme): the log-transformed MCP and the log-transformed daily movement distance between roost and foraging areas.

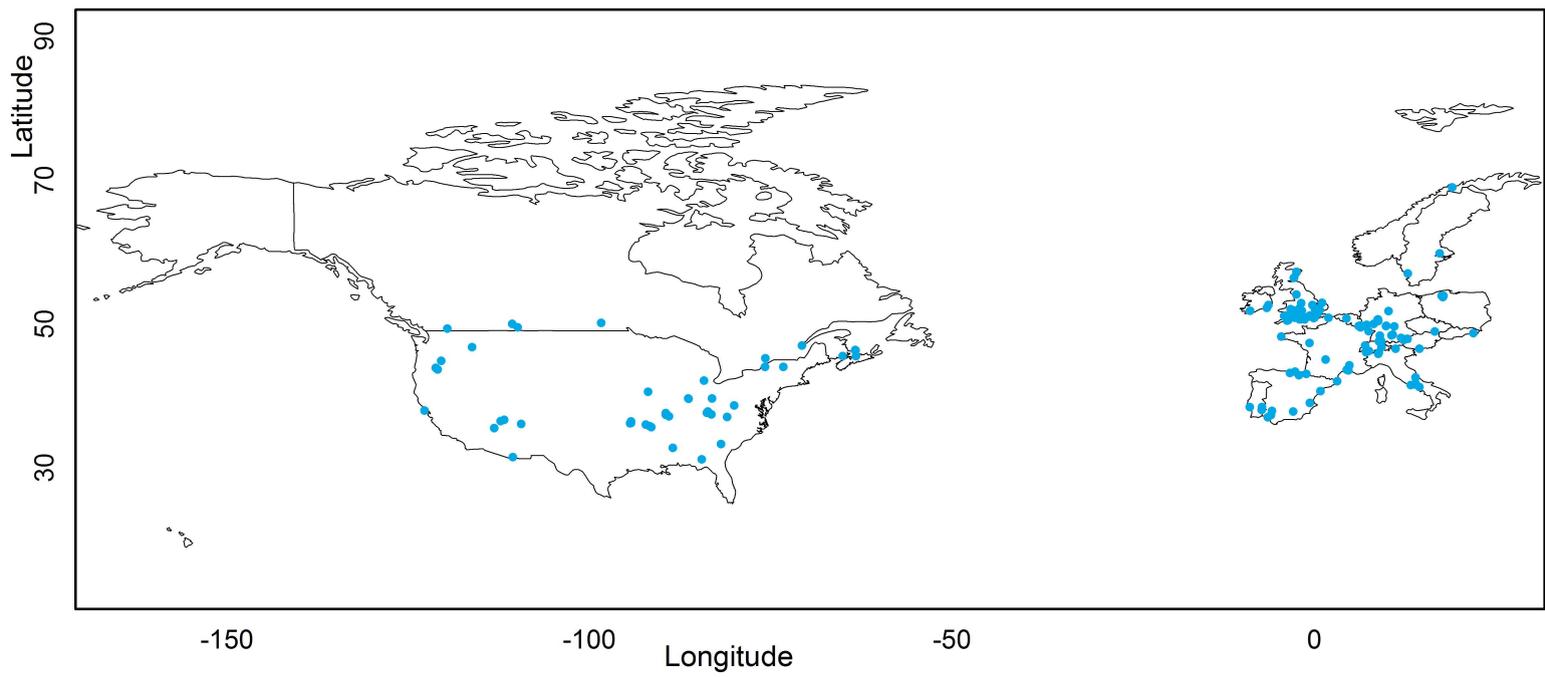
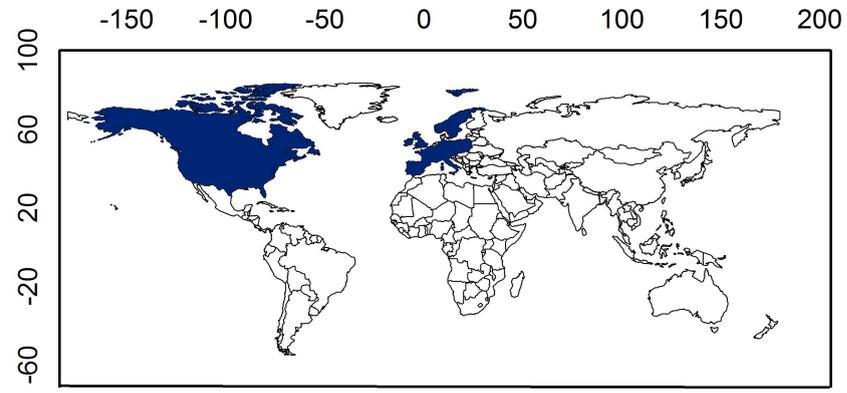
**Figure S12.1.** Histogram showing the relative frequency of the number of radio-tracking studies per year among our data (n studies = 166). The two orange bars represent the two acquisition years of the global Human Footprint Index (HFI; 1993 and 2009).

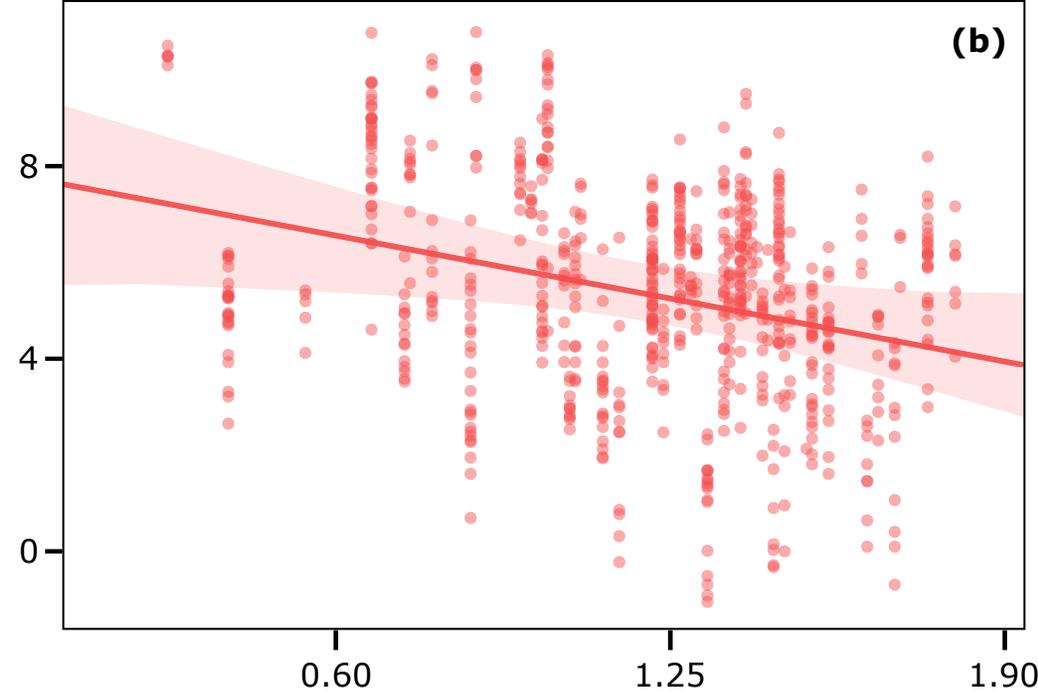
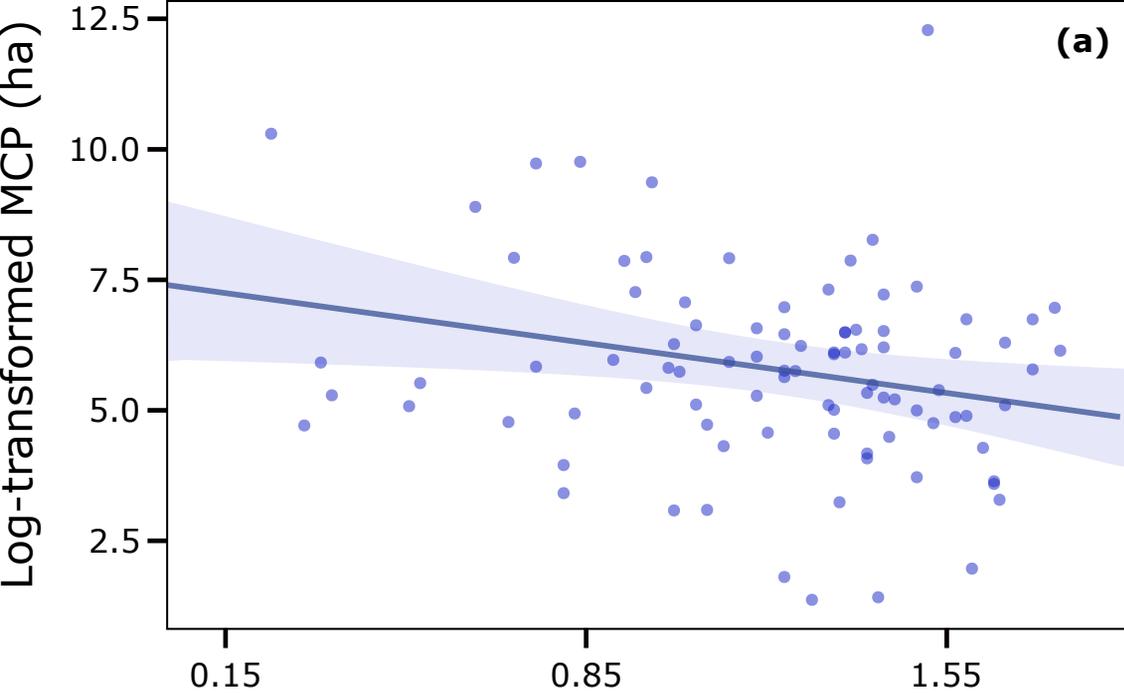
**Figure S12.2.** Histogram showing the relative frequency of the number of years between bat surveys' year and (the timely closest) HFI data acquisition year among our data (n studies = 166).

**Figure S13.1** Bat home range size and daily distance movement at the colony level (i.e., mean; A) and individual level (B) with increasing 1) Shannon diversity index of habitats in the landscape (on the x axis, low values means homogeneous landscapes and high values means heterogeneous landscapes) calculated at 20 km radius scale; 2) forest proportion and 3) Human Footprint Index (HFI), both calculated at 5 km radius scale. Result from the alternative models, i.e. best supported-models (from step 2) in which we included as fixed effects the factorial variable "Continent" as well as its interaction with selected landscape variables. Scatterplots include regression lines from the linear mixed-effects models (solid and dashed lines) for European data (blue) and North American data (orange).

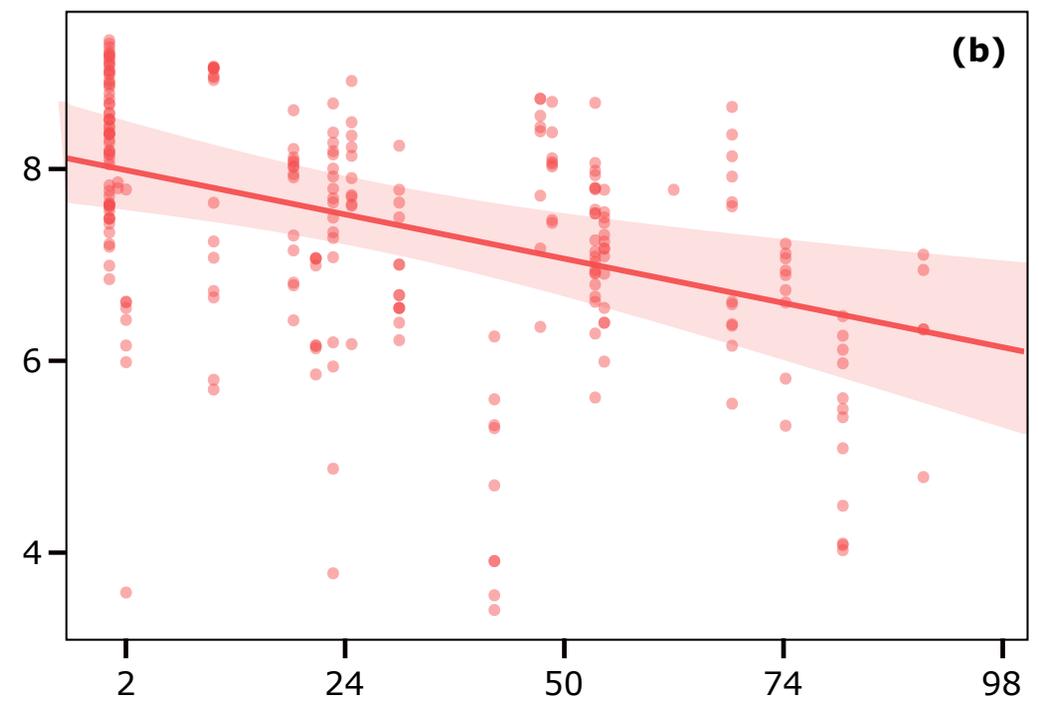
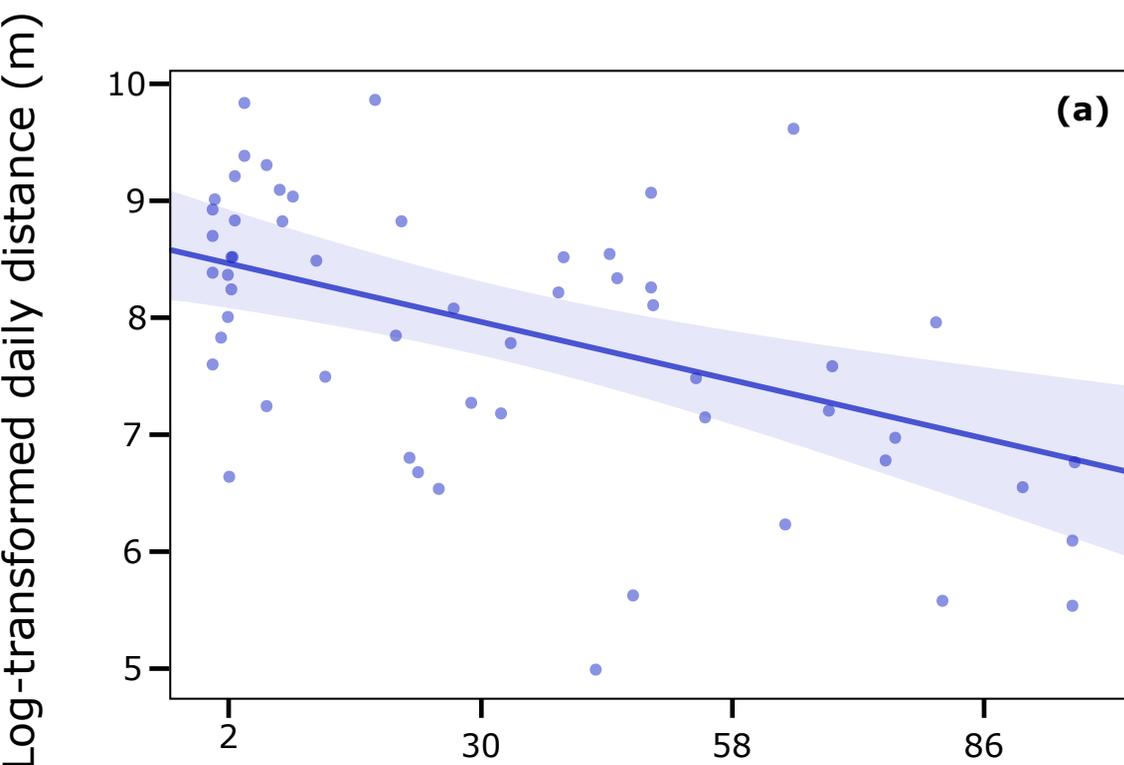
**Figure S14.1** Maximum clade credibility tree for our 49 focal species.

**Figure S15.1.** Log-transformed bat daily distance between roosts and foraging areas at colony level (i.e., mean; A) and individual level (B) with increasing Human Footprint Index (HFI) in the landscape (on the x axis, low values means low-anthropized landscapes and high values means high-anthropized landscapes) within a 5 km radius from the colony. Results from the 'best-supported model' obtained at step 2 ('landscape subset'). Plots include regression lines from the linear mixed-effects models (solid lines) and associated 95% confidence intervals (bands).





Landscape compositional heterogeneity (Shannon diversity index) at 20 km scale



Forest proportion (%) at 5 km scale

