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Going beyond species richness and abundance: robustness of community specialisation measures in short acoustic surveys

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Abstract

Passive Acoustic Monitoring offers promising opportunities for biodiversity assessments and species conservation and is still in development. The robustness of community metrics depends on sampling effort, and acoustic surveys should be adjusted for cost-effectiveness. Using a large-scale acoustic survey of bat assemblages conducted along 5,487 survey nights across France, we assessed the effect of sampling duration on the level of confidence of four community metrics (total bat activity, species of conservation concern activity, species richness, and community specialisation index). We further investigated this effect varied across habitat and seasons. Overall, a high level of confidence (i.e., 95% similarity between consecutive survey nights) was reached after 2 to >20 sampling nights, depending on the community metric, the habitat and the season considered. CSI required the lowest sampling duration. A higher sampling duration was required in three-dimensionally structured habitats (e.g., forests) and habitats unfavourable to bats (e.g., intensive farmlands), while a high degree of confidence was reached earlier in more favourable habitats and non-intensive farmlands, and during the season of higher activity. Beyond providing recommendations for the design of context-dependent minimum sampling duration in acoustic surveys, we show that weighted community indices such as the CSI are efficient summary measures, and advocate for their use when monitoring resources are limited.

Key words: Bat activity, Bioacoustics, Community Specialisation Index, Ecological indicators, Sampling effort, Species of conservation concern.

Introduction

Robust biodiversity assessments are of utmost importance for successful conservation, which often relies on cost-effective survey effort specification (Richardson et al 2019). With the recent progress in data storing capacity, the decrease in the cost of acoustic devices and the improvement of species detection and identification, the use of passive acoustic monitoring (PAM) offers promising opportunities in biodiversity assessments, especially for elusive and/or nocturnal taxa (Barré et al., 2019; Gibb, Browning, Glover-Kapfer, & Jones, 2019). PAMs offer a wide range of applications to policy makers and environmental consultant firms (Adams, Jantzen, Hamilton, & Fenton, 2012; Claireau et al., 2019) as well as to academic researchers in studies of vocal species such as amphibians (Rosa et al., 2012), birds (Gregory et al 2004), cetaceans (Nowacek, Christiansen, Bejder, Goldbogen, & Friedlaender, 2016), nocturnal arthropods (Jeliazkov et al 2016) and echolocating bats (Stahlschmidt & Brühl, 2012). Beyond providing support for inventories, PAMs enable studies of species habitat use (Russo and Jones 2003) and assessment of anthropogenic pressure (e.g. agricultural intensification: Wickramasinghe et al., 2004; disturbance of commuting and migration routes: Barré, Le Viol, Bas, Julliard, & Kerbiriou, 2018; light pollution: Azam et al., 2016; road-zone effects: Claireau, Bas, Pauwels, et al., 2019). PAM schemes are under development in most countries (e.g., UK, Russ et al. 2008; Barlow et al., 2015; USA and Canada, Hertzog & Britzke 2009; Loeb et al., 2015; France, Kerbiriou et al. 2010; Penone et al., 2013; Ireland, Roche et al. 2011; Australia, Wimmer, Towsey, Roe, Grace, & Williamson, 2012 ; Germany, Stahlschmidt & Brühl, 2012; Switzerland, Obrist & Giavi, 2016). A recurrent issue in PAM design is the trade-off between observer investment (number of replicates) and the robustness of the biological indicators produced. Hence, there is an urgent need to assess how local surveys could be further optimised in terms of sampling duration allocated.

Optimising sampling duration is not straightforward, because of the non-linear (logarithmic) relationship between the sampling duration allocated to PAM and the level of confidence of occurrence predictions, abundance and richness estimations (Skalak, Sherwin, & Brigham, 2012; Froidevaux, Zellweger, Bollmann, & Obrist, 2014; Richardson, Lintott, Hosken, & Mathews, 2019). In many taxa, acoustic activity shows considerable daily, as well as seasonal variation. For instance, bat activity exhibits considerable night-to-night variation because it is narrowly linked to weather conditions and insect availability (Hayes, 1997; Kusch & Idelberger, 2005; Fischer, Stott, Law, Adams, & Forrester, 2009). Consequently, too short duration (i.e., number of survey nights) in PAM schemes may fail to detect periods of highest bat activity (Richardson et al 2019), which may induce uncertainty in community assessments. Studies focussing on the sampling duration needed to produce robust ecological assessments are recent (e.g., Skalak et al., 2012; Froidevaux et al., 2014; Banner et al., 2019; Richardson et al., 2019), and many aspects remain to be explored such as spatial (e.g., habitat) and temporal (e.g., season) specificities. Specifically, there is a need to provide context-dependent guidelines for the design of effective acoustic surveys in terms of minimal sampling duration.

Biodiversity assessments rely on the estimation of ecological indicators such as total abundance (i.e., all species pooled) or species richness (Gotelli and Colwell, 2001; Gregory et al., 2007; Voříšek et al., 2010). The level of confidence of these metrics can be influenced by sampling duration (Skalak et al 2012; Richardson et al 2019). Total abundance (or total activity when the number of individuals is hard to measure; e.g., Dubos et al 2020) can be used as a simple summary index to monitor average trends, but obscures the identities of species driving the trend (Siriwardena et al 2019). Species richness describes a quantitative aspect of an assemblage while ignoring species composition and structure (Mouillot et al 2013). The use of ecological indices that are sensitive to changes in these aspects has been recently advocated for the assessment of ecosystem health (Siriwardena, Henderson, Noble, & Fuller, 2019; Tuneu-Corral et al., 2019). For instance, indices of habitat specialisation (e.g. Community Specialisation Index; CSI) were used to detect worldwide declines in specialist species, representing a significant form of biotic homogenisation at the global scale (Clavel et al 2011). Community-level specialisation accounts for changes in species composition and species-specific relative abundance. It has been proposed as an indicator of species assemblage response to the combined effect of habitat and climatic disturbance, applicable at both local and global scales (Devictor, Julliard, Clavel, et al., 2008; Clavel et al., 2011). An additional aspect of a community that is of interest to conservation practitioners is the abundance of species of conservation concern (hereafter, SCC; Razgour et al., 2011). These species are generally rarer, and their temporal variability in abundance is expected to differ from the most common species and overall trends/responses (Inger et al 2015). Until recently, trait-based approaches have been seldom tested on bat assemblages, due to a lack of large-scale data on community composition and species traits (Regnery, Couvet, Kubarek, Julien, & Kerbiriou, 2013; Kerbiriou, Azam, et al., 2018a; Kerbiriou, Parisot-Laprun, & Julien, 2018c; Lacoeuilhe, Machon, Julien, & Kerbiriou, 2018). So far, recent studies focusing on the effect of sampling duration on bat assemblages were either based on species richness (Skalak et al., 2012; Froidevaux et al., 2014), occupancy/presence-absence (Banner et al., 2019; Froidevaux et al., 2020) or activity (Fischer, Stott, Law, Adams, & Forrester, 2009; Richardson et al., 2019). Species richness, abundance or activity, and community indices respond differently to environmental drivers through time and space (Devictor, Julliard, Clavel, et al., 2008; Kerbiriou, et al., 2018a; Kerbiriou, Parisot-Laprun, & Julien, 2018c). Therefore, there is a need to simultaneously assess the variation in these community metrics between temporal replicates (e.g., consecutive survey nights in bats) and determine whether a given community metric is more demanding than another in terms of sampling duration.

Species abundance and composition vary across habitat types and management regimes, mostly due to contrasting resource availability such as insect abundance for bats from temperate regions (Azam et al., 2016; Kerbiriou, Parisot-Laprun, et al., 2018c; Froidevaux et al., 2019). Dynamics in prey abundance can differ between habitat types (Ciechanowski et al 2007). In addition, the devices' ability to detect echolocation calls can be affected by the spatial structure of a given habitat (Brigham et al 1997). It is therefore crucial to assess whether habitat can influence the level of confidence in bat community metrics across broad environmental gradients in order to adjust the sampling duration required.

Seasonal changes in environmental conditions, as well as daily weather fluctuations at a given site may also affect species activity and estimations of species composition (Hayes 1997; O'Donnell 2000). In temperate bats, intra-annual changes in activity measures mostly occur with migration or hibernation, but also due to variation in energetic demands (which increase during the reproductive season and before hibernation). PAM schemes need to account for intra-annual changes in species activity to provide robust ecological assessments.

Using data from a French citizen science programme of bat PAM, we examined how the level of confidence (i.e., the similarity between consecutive nights) in the estimation of four community metrics was affected by sampling duration (i.e., the number of sampling nights). We predicted that the longest sampling duration is needed for bat activity, because of the larger amplitude due to between-night variability in activity, especially for species of conservation concern. The community specialisation index (hereafter, CSI) should be the most consistent through sampling nights, since its calculation (i) is based on count proportions that are less fluctuating than activity per se, and (ii) is less sensitive to taxonomic turnover between assemblages. We further assessed how variation in the level of confidence differed between seasons and along habitat gradients. Longer sampling duration should be required during periods of the lowest activity (e.g., April-May), and in unfavourable habitats (e.g. intensive agricultural and urban areas) because resources are expected to be less abundant/predictable, inducing more daily variation in activity We expected the opposite response in more favourable habitats (e.g. forests or semi-natural open habitats such as scrublands), because bat activity should be less variable through time and space with more abundant resources (e.g. Adams, Law, & French, 2005)..

Material and Methods

Bat survey

We used data from the French Bat Monitoring Programme (FBMP; http://vigie-nature.mnhn.fr/page/vigie-chiro), carried out by trained volunteers between 2011 and 2019. We excluded sites that were monitored only during one night, resulting in 1,715 replicates (site-year combinations) for a total of 5,487 survey nights. Replicates were distributed within 1,158 sites across France (Fig. 1), which were monitored between 1 and 4 years (mean: 1.17 years). The closest study sites were distant from less than

1km from each other (maximum = 1340 km, mean = 398 km). Each year, sites were monitored during 2 to 20 consecutive nights (mean: 3.3 nights; Fig. S1). Volunteers set stationary recording devices, recording all sounds between 8 and 192 kHz throughout the entire night, from 30 min before sunset to 30 min after sunrise. Bat calls were recorded during key activity periods between April and September, which encompass the gestation period (April-May, characterised by important population movements), the lactation period (June-July, with important foraging activity; Racey & Swift, 1981; Dietz, Nill, Von Helversen, Lina, & Hutson, 2007) and the post-breeding period (August-September, with juveniles dispersal, mating and fat deposition for hibernation; Arévalo, Burgos, del Hoyo, & López-Luna, 1990). Observers used a variety of acoustic ultrasound recorders, mainly Song Meter SM2Bat+, SM3Bat and SM4Bat (Wildlife Acoustics Inc., Concord, MA, USA) and Batlogger (Elekon), all responding to the FBMP criteria with standardised trigger setting to limit heterogeneity in detectability. Sampling sessions occurred only when weather conditions were favourable, i.e. no rain, temperature above seasonal normal and avoiding strong winds (<30 km.h^{-1}). Recordings were treated with the Tadarida software (https://github.com/YvesBas/Tadarida-C/; Bas, Bas, & Julien, 2017). This software automatically detects and extracts sound parameters of recorded echolocation calls and classifies them into known classes (i.e bat taxa) according to a confidence index value using a random forest algorithm (Breiman 2001). Species (n = 26; Table S1) were identified with Tadarida software (Bas et al 2017) and filtered according to a minimum of 90% success probability (see Barré et al. 2019 for more details). We assumed that this conservative approach would be sufficiently accurate to compute reliable community metrics despite the small proportion of errors. With the filtering, some *Myotis* are strongly underrepresented in our dataset such as *M.*

bechsteinii which obtained such low error risk across only 34 nights. However, we are confident that in the best conditions, all *Myotis* except *M. brandtii*, *M. myotis* and *M. blythii* (the latter 2 being grouped in our dataset) can be identified with certainty on the basis of acoustic records. For instance, *M. capaccinii* and *M. daubentonii* overlap only partially, and particularly little on their longest calls (open/commuting behaviour; see Barataud, 2015 and unpublished internal report at http://www.spektrogram.chiroptera.se/wp-content/uploads/2015/11/VisualDeterminationOfMyotis.pdf). We therefore assume that the proportion of detection errors should not affect our conclusions.

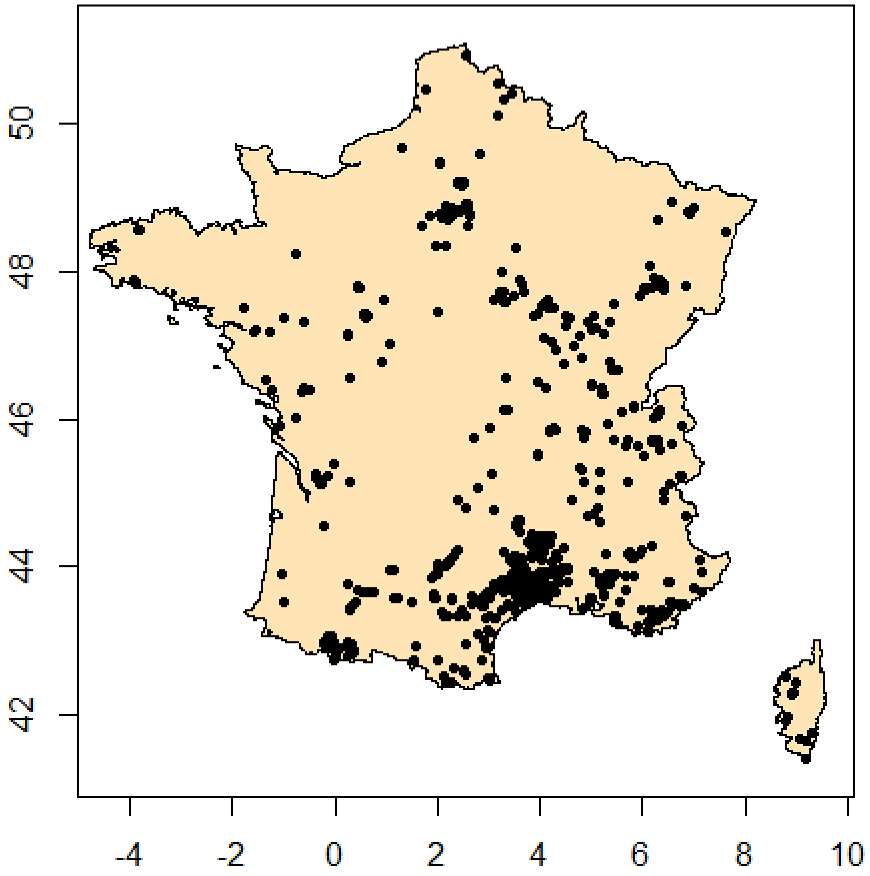

Fig. 1 Distribution of the 1158 study sites across France sampled between 2011 and 2019. We show the longitude and latitude (WGS84).

Computing community metrics

Total activity – We considered the number of bat passes recorded during one night as a measure of activity (Hundt, 2012; Mimet, Kerbiriou, Simon, Julien, & Raymond, 2020). One bat pass is recorded when a bat pulse is detected within a five-second interval, i.e. the mean duration of bat species passes according to commonly accepted standards in France and Europe (Stahlschmidt and Brühl, 2012; Barataud, 2015; Millon, Julien, Julliard, & Kerbiriou, 2015; Kerbiriou et al., 2018b). We considered total activity as the sum of bat passes, all species included. Overall, the average total activity per site was 521 bat passes ± 853 SD (see Table 1 for habitat- and season-specific statistics, Fig. S4 for distribution frequencies).

Activity of species of conservation concern (SCC) – This metric was computed as the total activity of all species that are listed in Annex II of the EU Habitats Directive 92/43/EEC (EEC, 1992; Table S1). The list considered here included *Barbastella barbastellus*, *Miniopterus schreibersii, Myotis bechsteinii, Myotis capaccinii, Myotis emarginatus, Myotis myotis*, *Rhinolophus euryale*, *Rhinolophus ferrumequinum* and *Rhinolophus hipposideros*. Mean SCC activity was 24.9 bat passes ± 106.4 SD (Fig. S3).

Species richness – Species richness was computed as the total number of species recorded during one sampling night. We considered 27 of the 34 species recorded in

France (Table S1). Across all sites, mean species richness was 8 ± 3.25 SD (Fig. S3).

Community specialisation (CSI) – We first computed for each species a ‘Species habitat Specialisation Index’ (SSI; Julliard, Clavel, Devictor, Jiguet, and Couvet, 2006). The SSI was computed by totalising the number of bat passes of the species recorded within 20 habitat classes across France (i.e. categories for which ≥ 10 pixels were represented in the final data; Table S2) and computing the coefficient of variation of those 20 counts. This performance of this index has been assessed and is assumed to fairly represent the degree of habitat specialisation in bats (Kerbiriou et al 2010). The higher the coefficient, the more specialised the species is with respect to habitat. Habitat type data were extracted from Copernicus (Corine Land Cover 2012, resolution 100m x 100m; https://land.copernicus.eu/pan-european/corine-land-cover) and associated with each study site at their corresponding pixel. To integrate the different habitats used by our study species as comprehensively as possible, SSIs were computed for every site of the full FBMP dataset (*N* = 3,596; i.e., we included the sites that were monitored only one night). We eventually computed a Community Specialisation Index (CSI) for each study site, as the average SSI of all individuals (here bat passes) recorded at the site (Julliard et al. 2006). The average CSI across study sites was 1.23 ± 0.33 SD (Fig. S3).

Table 1. Distribution of the 1,715 study site-years across habitat types (proportion of Corine Land Cover habitat types represented within 200m buffers) and seasons in France between 2011 and 2018. We show mean ± standard deviation (*SD*) of total activity, species of conservation concern (SCC) activity, species richness and community specialisation index (CSI) per dominating habitat type and season.

Main habitat type	Proportion represented (%)	Number of sites	Mean bat activity	Mean SCC activity	Mean species Richness	Mean CSI
Non-intensive farmland	28.0	480	557 ± 823	16 ± 78	8.3 ± 3.0	1.25 ± 0.29
Intensive farmland	13.3	228	201 ± 340	12 ± 27	6.8 ± 3.1	1.18 ± 0.23
Scrub/Herbaceous	12.1	208	500 ± 983	40 ± 181	8.8 ± 3.3	1.31 ± 0.39
Urban	15.0	258	620 ± 814	22 ± 104	7.0 ± 2.9	1.14 ± 0.27
Forest	31.5	541	583 ± 959	34 ± 110	8.4 ± 3.4	1.24 ± 0.38
Season						
April-May	20.3	348	454 ± 893	21 ± 129	8.1 ± 3.3	1.28 ± 0.37
June-July	50.5	866	595 ± 898	15 ± 53	7.8 ± 3.2	1.17 ± 0.29
August-September	29.2	501	490 ± 807	44 ± 148	8.3 ± 3.3	1.30 ± 0.35

Statistical analyses

Assessing the sensitivity of community metrics to sampling duration – We first assessed how the four aforementioned community metrics (i.e. total bat activity, SCC activity, bat species richness and CSI) varied along a range of temporal sampling duration. Community metrics (CMs) were computed for a varying number of survey nights. We computed CMs at each site, for *n* nights of monitoring (*n* being the number of nights included in the calculation, ranging between 1 and the maximum number of monitored night available at each site). Specifically, total activity and activity of SCC were the mean number of nightly bat passes (respectively for all species included and for SCC only) across *n* nights (i.e., average activity per night), species richness was computed as the total number of cumulated species detected across *n* nights, and CSI as the mean CSI across *n* nights. We calculated an index of similarity between consecutive nights, as the ratio between a metric computed on the basis of *n* nights and the same metric computed with *n+1* nights, which we interpret as a level of confidence/robustness in CM estimations. We chose to use ratios instead of differences to provide a relative measure of CM confidence independent of the magnitude of the indices. To estimate the level of confidence in community metric estimations, regardless of the direction of the dissimilarity (i.e. overestimation or underestimation), we considered the 'absolute value' of this ratio. Therefore, we assumed Similarity index = CM_n / CM_{n+1} when $CM_n < CM_{n+1}$; otherwise, we assumed Similarity index = CM_{n+1} / CM_n. This enabled us to obtained indices of similarity ranging between 0 and 1, with 1 representing a high level of confidence. We chose to report the number of nights needed to reach a 95% of similarity as a conservative level of confidence in CM estimations.

To assess the effect of sampling duration, we modelled the response of Similarity indices to the number of nights using Generalised Linear Models assuming a beta distribution (GLM; glmmTMB R package; Brooks et al., 2019). This technique enables to produce beta regressions, and produced the same results when using the betareg R package (Cribari-neto and Gruen, 2020; see Fig. S2 for the equivalent of the predicted values presented in Fig. 2). We accounted for habitat, seasonal and site effects as follows:

Habitat effect – We considered the proportion of five habitat types that were represented within a 200m buffer around the recording device (corresponding approximately to the maximal detection range for bats). To characterise habitat types, we pooled the Corine Land Cover categories into five main classes (intensive farmland, non-intensive farmland, forest, scrubland/herbaceous and urban; Table 1).

Proportions were extracted from buffer zones using the raster R package (Hijmans 2018). We did not include wetlands in our analyses because they were poorly represented in our dataset (Table S2). We added four continuous variables, representing the proportion of a given habitat type (respectively intensive farmland, non-intensive farmland, forest, and scrubland/herbaceous; see below for more details) as continuous fixed variables (additive effects). We chose not to include the effect of urbanised areas because these were the most represented in our study area (31.5%; Table 1). Therefore, the effect of urbanised areas was represented at the intercept and predicted when setting the proportion of the remaining four habitat variables to zero.

Seasonal effect – We used a three-level season factor, representing each key study period of the year: pre-breeding (April-May), lactation (June-July) and post-breeding periods (August-September). The season was added to the model as an additive categorical fixed effect.

Residual site and year effects – we quantified the residual variation between sites and year using random terms (therefore, switching to Generalised linear mixed models using the same modelling technique and error distribution). The model assessing the effect of each additional survey night on community metrics resulted in the following formula:

m0. Similarity index$_{ts}$ ~ α_s . + β_n . Number of nights +
β_i . Intensive farmland + β_{ni} . Non-intensive farmland + β_{sh} . Scrubland +
β_f . Forested + $\varepsilon_{\text{site}} + \varepsilon_{\text{year}} + \varepsilon$

where α is the intercept for a season s (corresponding to the mean certainty after 1 day of sampling), β_t, β_i, β_u, β_s, β_f and β_s are respectively the slope estimates of the fixed effect of the number of nights *n*, the proportion of intensive farmland *i*, non-intensive farmland *ni*, scrubland-herbaceous *sh* and forested areas *f*, ε_{site} and $_{year}$ are the unexplained variance between site and year respectively, and ε is the residual variance.

We accounted for spatial autocorrelation by including a spatial autocovariate in our models, which was computed using the spdep R package version 0.6-13 (Learnbayes 2017). Since its inclusion did not affect our results, we reported the resulting estimates in supporting information (Table S3).

Assessing habitat and seasonal effects – We tested whether the sensitivity of similarity indices to sampling duration differed between habitats and seasons. In other terms, we assessed whether community metrics needed longer or shorter sampling periods in a given habitat or season to reach an equivalent level of confidence. We included to the model *m0* an interaction term between the number of nights and the proportion of habitat classes, and between the number of nights and season. This resulted in the following model:

m1. Similarity index.$_{ns}$ ~ α_{s} . + $\beta_{n.s}$. Number of nights + β_{i} . Intensive farmland +
β_{ni} . Non-intensive farmland + β_{sh} . Scrubland + β_{f} . Forested +
$\beta_{n.i}$. Intensive farmland + $\beta_{n.ni}$. Non-intensive farmland + $\beta_{n.sh}$. Scrubland +
$\beta_{n.f}$. Forested + ε_{site} + ε_{year} + ε

where $\beta_{t.s}$ is the season-specific slope for effect number of nights *n*, $\beta_{n.i}$, $\beta_{n.ni}$, $\beta_{n.sh}$ and $\beta_{n.f}$ are respectively the slopes for the interactions between the number of nights *n* and the proportion of intensive farmland *i*, non-intensive farmland area *ni*, scrubland-herbaceous *sh* and forested areas *f*.

Results

Sensitivity to sampling duration

The ‘level of confidence” is inferred from an index of similarity between estimations based on *n* survey nights and estimations based on *n*+1 survey nights. For practical purposes, the x-axis is represented as the number of nights included in the estimation (a value of 2 represents the ratio between estimations based on 1 and 2 nights). Predicted values were obtained from univariate beta regressions (shaded areas represent 95% confidence intervals).

Species of Conservation concern activity required the highest sampling duration to obtain similar estimations between *n* and *n*+1 survey nights, and a 95% level of similarity was not reached after 20 nights. An average 95% of similarity was reached after 13.8 ± 0.7 nights for total bat activity. Species richness required 8.6 ± 0.4 nights to reach the same level of similarity. For CSI, a mean similarity > 95% was already reached after 2 nights of monitoring (Fig. 2).

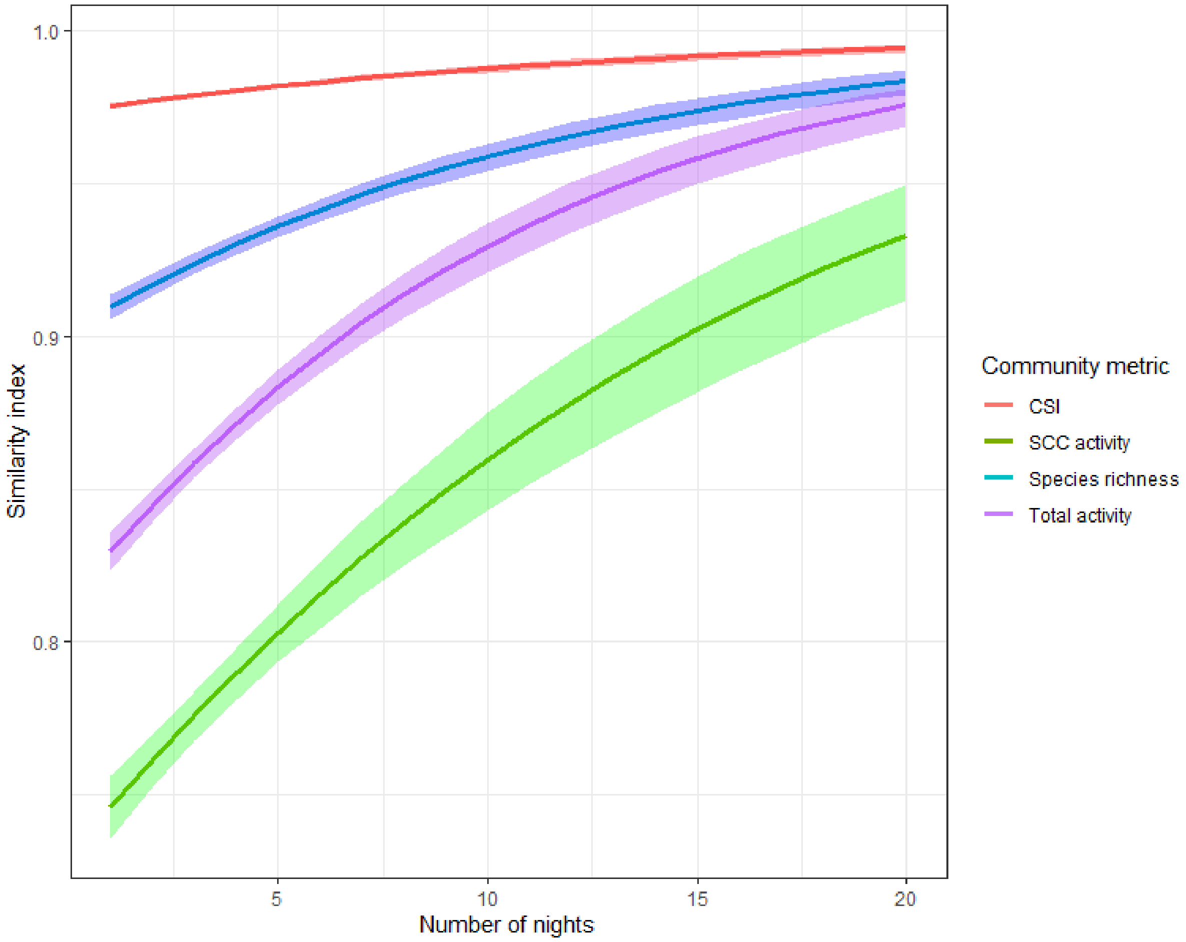

Fig. 2 Variation in the level of confidence in community metric estimations (total bat activity, species of conservation concern activity, species richness, Community Specialisation Index) along a gradient of sampling effort (number of survey nights).

Habitat effect

Overall, CM estimations were the most uncertain in forests, intensive farmland and urbanised areas (Table 2), requiring the highest sampling duration in these habitats. CMs were the most similar between *n* and *n*+1 survey nights in semi-natural open habitats (scrubland/herbaceous) and non-intensive farmlands overall. Compared to semi-natural open habitats, intensive farmlands approximately required 9 (total bat activity), 10 (SCC activity), 8 (species richness) and 0 (CSI) additional sampling nights to reach a 95% level of similarity, respectively (Fig. 3).

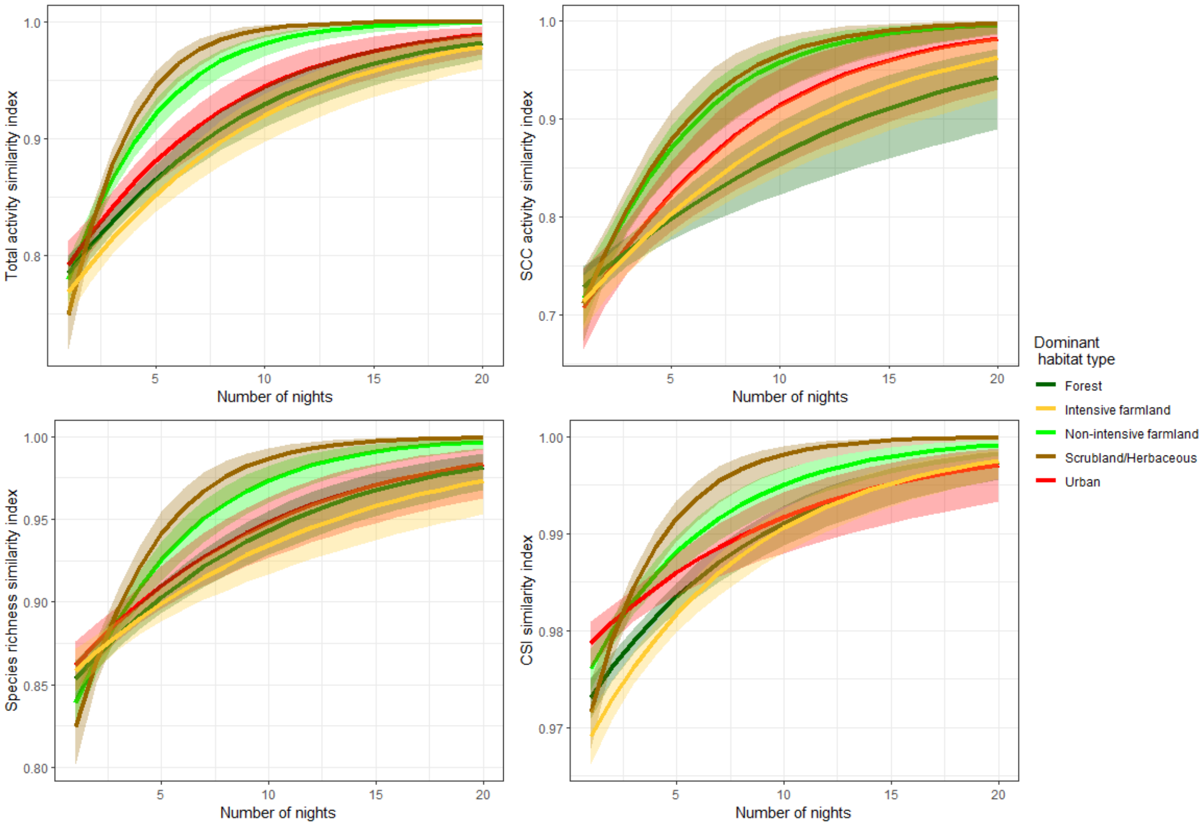

Fig. 3 Effect of habitat type on the variations in the level of confidence in four community metrics (total bat activity, species of conservation concern activity, species richness, and Community Specialisation Index) along a gradient of sampling effort. Predicted values were obtained from beta regressions (shaded areas represent 95% confidence intervals). Habitat effects are treated as continuous variables (proportion represented within 200m buffer zones). Each curve represents the prediction for a value of 1 of the corresponding variable (i.e. corresponding habitat type covering 100% of the surrounding 200m), and 0 for the remaining variables.

Seasonal effect

The level of confidence of CM estimations was the lowest during the period of April-May, the highest during the lactation period (June-July), and intermediate during the post-breeding periods (August-September; Fig. 4). During the April-May period, average values of total bat activity, SCC activity, species richness and CSI estimations required approximately 6, >6, 3 and 0 additional sampling days to reach a 95% similarity compared to the June-July period, respectively. However, the seasonal effect was robust to model selection uncertainty only for SCC activity (Table 2).

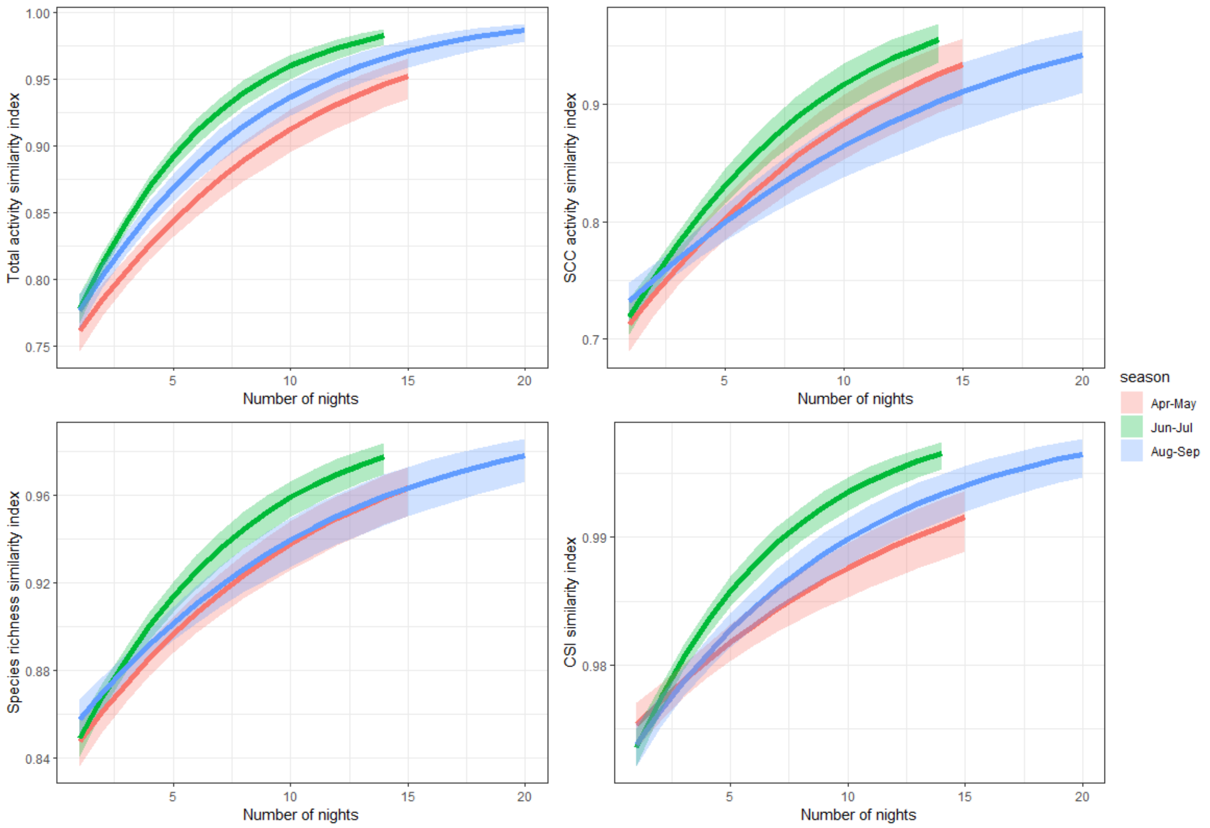

Fig. 4 Effect of the season on variation in the level of confidence in four community metrics (total bat activity, species of conservation concern activity, species richness and community specialisation index) along a gradient of sampling effort. Predicted values were obtained from beta regressions (shaded areas represent 95% confidence intervals). The season is treated as a categorical variable.

Table 2. Parameter estimates for the effect of habitat and season on the level of confidence in four community metrics (total bat activity, species of conservation concern SCC activity, species richness, and community specialisation index CSI) along a sampling effort gradient (number of consecutive survey nights). The level of confidence is inferred from the similarity between estimates based on *n* and *n*+1 survey nights. Estimates were obtained from mixed beta regression and included site and year random effects. The intercept represents the April-May season for a 100% proportion of forested area. The tested variables with a significant effect are shown in bold. The site and year variances were respectively of 0.05 and 0.001 (Bat activity), 0.005 and 0.006 (SCC activity), $1.5.10^{-9}$ and $2.6.10^{-16}$ (Species richness), 0.01 and 0.001 (CSI).

Bat activity similarity index	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	1.450	0.073	19.749	<0.001
Number of nights	0.076	0.018	4.128	0.001
Intensive agriculture	-0.148	0.089	-1.655	0.019
Non-intensive agriculture	-0.127	0.097	-1.320	0.055
Urban	-0.029	0.108	-0.267	0.789
Scrub/Herbaceous	-0.484	0.137	-3.762	<0.001
Season (Jun-Jul)	-0.109	0.071	-1.604	0.094
Season (Aug-Sep)	-0.031	0.065	-1.672	0.655
Number of nights:Intensive agriculture	**0.045**	**0.022**	**1.999**	**0.046**
Number of nights:Non-intensive agriculture	**0.183**	**0.035**	**5.248**	**<0.001**
Number of nights:Urban	**0.073**	**0.034**	**2.139**	**0.032**
Number of nights:Scrub/Herbaceous	**0.310**	**0.050**	**6.109**	**<0.001**
Number of nights:Season (Jun-Jul)	**0.117**	**0.019**	**6.254**	**<0.001**
Number of nights:Season (Aug – Sep)	**0.055**	**0.019**	**2.998**	**<0.001**

SCC activity similarity index	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	0.977	0.091	10.727	<0.001
Number of nights	0.049	0.020	2.461	0.013
Intensive agriculture	-0.099	0.099	-1.000	0.317
Non-intensive agriculture	-0.176	0.113	-1.560	0.118
Urban	-0.218	0.154	-1.414	0.157
Scrub/Herbaceous	-0.232	0.144	-1.604	0.104
Season (Jun-Jul)	0.038	0.082	-0.460	0.645
Season (Aug-Sep)	-0.138	0.085	1.627	0.103
Number of nights:Intensive agriculture	0.042	0.026	-0.663	0.096

Number of nights:Non-intensive agriculture	**0.160**	**0.052**	**3.049**	**0.002**
Number of nights:Urban	**0.097**	**0.049**	**1.971**	**0.048**
Number of nights:Scrub/Herbaceous	**0.162**	**0.046**	**3.493**	**<0.001**
Number of nights:Season (Jun-Jul)	**0.051**	**0.023**	**2.214**	**0.026**
Number of nights:Season (Aug – Sep)	-0.023	0.021	-1.133	0.257

Species Richness similarity index	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	2.227	0.073	29.511	<0.001
Number of nights	0.066	0.014	4.660	<0.001
Intensive agriculture	0.033	0.082	0.557	0.577
Non-intensive agriculture	-0.121	0.095	-2.149	0.032
Urban	0.102	0.103	0.870	0.384
Scrub/Herbaceous	-0.377	0.135	-4.112	<0.001
Season (Jun-Jul)	-0.107	0.067	-2.450	0.014
Season (Aug-Sep)	0.03	0.070	0.317	0.751
Number of nights:Intensive agriculture	-0.014	0.017	-0.858	0.391
Number of nights:Non-intensive agriculture	**0.085**	**0.024**	**3.560**	**<0.001**
Number of nights:Urban	0.006	0.029	0.210	0.831
Number of nights:Scrub/Herbaceous	**0.187**	**0.037**	**4.981**	**<0.001**
Number of nights:Season (Jun-Jul)	**0.064**	**0.016**	**4.242**	**<0.001**
Number of nights:Season (Aug – Sep)	0.003	0.016	0.359	0.763

CSI similarity index	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	3.604	0.062	58.24	<0.001
Number of nights	0.052	0.015	3.42	<0.001
Intensive agriculture	-0.130	0.072	-1.81	0.070
Non-intensive agriculture	0.060	0.079	0.76	0.447
Urban	0.257	0.087	2.98	0.003
Scrub/Herbaceous	-0.237	0.108	-2.20	0.028
Season (Jun-Jul)	-0.161	0.056	-2.88	0.004
Season (Aug-Sep)	-0.087	0.059	-1.48	0.138
Number of nights:Intensive agriculture	0.021	0.019	1.14	0.254
Number of nights:Non-intensive agriculture	**0.061**	**0.029**	**2.12**	**0.034**
Number of nights:Urban	-0.013	0.026	-0.48	0.634
Number of nights:Scrub/Herbaceous	**0.186**	**0.042**	**4.35**	**<0.001**
Number of nights:Season (Jun-Jul)	**0.084**	**0.016**	**5.22**	**<0.001**
Number of nights:Season (Aug – Sep)	**0.031**	**0.015**	**2.03**	**0.042**

Discussion

Differential sensitivity to sampling duration between community metrics

Amongst the four tested community metrics, the index of mean habitat specialisation of bat assemblages (CSI) showed the highest similarity between each additional survey night. Its apparent low between-night variability was not related to a lack of spatial (Fig. S3) nor temporal (Fig. S4) variance. The higher consistency of CSI between consecutive survey nights may instead be due to the use of proportions of count data between species, enabling this metric to remain consistent despite large variations in the number of bat passes—unlike abundance/activity, and despite occasional detection of new species—unlike species richness.

A high level of confidence in species richness estimation was reached earlier than activity, presumably due to a smaller overall magnitude for this metric (Table 1; Fig. S3). Nightly variation may be related to transient individuals, which are more frequent during the pre-breeding period (Fig. 4). Temporal shifts in species richness may be related to variability in density between species differing in home range size (e.g., Boughey, Lake, Haysom, & Dolman, 2011). Species with larger home ranges are expected to be less easily detected than species that are concentrated in smaller areas. Species-specific variation may be also due to differential sensitivity to weather between species of different foraging strategies (e.g. Ciechanowski, Zając, Biłas, & Dunajski, 2007; Meyer et al., 2011). We found that 7 to 15 nights were required to reach a threshold of 95 % similarity in species richness, mostly depending on the habitat. The magnitude of our results is consistent with Skalak, Sherwin, and Brigham (2012), whose study found that 2 to 5 nights of monitoring were needed to detect 80% of the most common species in a North American bat assemblage. These authors also suggested that more extended sampling periods (> 45 nights) were necessary to detect the rarest species, which is also consistent with our findings regarding species of conservation concern.

Being the last metrics to reach a 95% level of similarity between estimations based on *n* and *n*+1 nights, total bat activity and species of conservation concern activity (i.e. the number of bat passes), were the most sensitive to sampling duration amongst the investigated metrics. This was expected since bat activity strongly depends on weather-driven insect activity (Kusch and Idelberger 2005), which generates a high between-day variation in detection. Bat activity can be influenced by weather also through effects on reproduction (e.g. temperature effect on mating calls; Kusch & Idelberger, 2005), or foraging (e.g. the fog which could absorb echolocation calls; Ciechanowski et al., 2007). The degree of confidence in this metric may also be limited by differences in detection range between species. The confidence levels established for bat activity were similar to those found in a previous study performed in the UK (Richardson et al 2019).

Estimations of SCC activity were the least similar between consecutive survey nights. Those species are generally rarer. Hence, the number of nights with no activity detected is likely to be greater, which may cause more substantial between-day variation compared to total bat activity. This result can also be affected to higher chances of detection errors for some species. However, the high level of data filtering (90% of success probability; Barré et al., 2019) should minimise this impact.

Sensitivity to habitat

The lowest level of confidence in CM estimations was found in forested areas, intensive agricultural landscapes and urbanised areas. This was expected for intensive farmlands (Azam et al 2016). A lower proportion of foraging *versus* commuting behaviours is likely to increase with the level of agricultural intensification in the surrounding landscape, due to a lower prey availability driven by the use of agrochemicals and the loss of semi-natural structural elements such as hedgerows, grassland patches or herbaceous strips along with crops (Frey-Ehrenbold, Bontadina, Arlettaz, & Obrist, 2013; Azam et al., 2016; Cleary, Waits, & Finegan, 2016). The lower frequency of foraging behaviour in unfavourable matrix habitat increase individual home range sizes and probably contributed to a higher variability in bat detection in intensive farmland.

Higher sampling durations are also needed in forested and urbanised areas, presumably because of the structural complexity of these habitats (Gehrt and Chelsvig, 2003; Froidevaux et al., 2016, 2014). A three-dimensionally structured habitat would induce more complex fly paths (Brigham et al 1997), which would tend to increase the variability of echolocation call records and hence the level similarity in community metrics between survey nights.

Semi-natural open habitats (i.e. scrubland and herbaceous areas) were associated with the highest level of confidence in the estimation of bat community metrics. This was expected because grasslands and scrublands are supposedly favourable to bat activity due to a higher presence of structural elements (e.g., hedgerows) that promote insect abundance (Evans, Wilson, & Bradbury, 2007; Boughey et al., 2011; Azam et al., 2016; Kerbiriou et al., 2018a, b). These elements would induce a higher proportion of foraging behaviour, resulting in lower variation in activity between consecutive nights.

Sensitivity to season

The season with the most consistent measures between survey nights corresponds to the reproduction period (June-July). Individuals, especially females, tend to forage closer to their roost during this period (Racey and Swift 1985). Moreover, foraging activity is expected to be more constant for females during June-July as a result of a higher metabolic demand during lactation (Racey & Swift, 1985). The tested community metrics were the least consistent during April-May, which was expected given the lower bat activity and subsequent higher nightly variation during this period. All metrics showed a slightly lower level of confidence during August-September compared to the June-July period, presumably due to higher dispersal rates and juvenile activity. The temporal variability in dispersal events would have translated in more variable bat detections subsequent to a decreased density.

Limitations

Using acoustic detectors suggests a bias in the detection of some species: low frequency and higher intensity echolocation calls are more easily detectable than high frequency and low intensity echolocation pulses. This led to a relative underestimation of the activity of some species. Moreover, the variety of detector types may have induced a variability in species detection, despite the standardisation of triggering criteria. However, we believe that the influence of these potential biases on our results may be limited in our study due to the large number of replicates (1715 replicates).

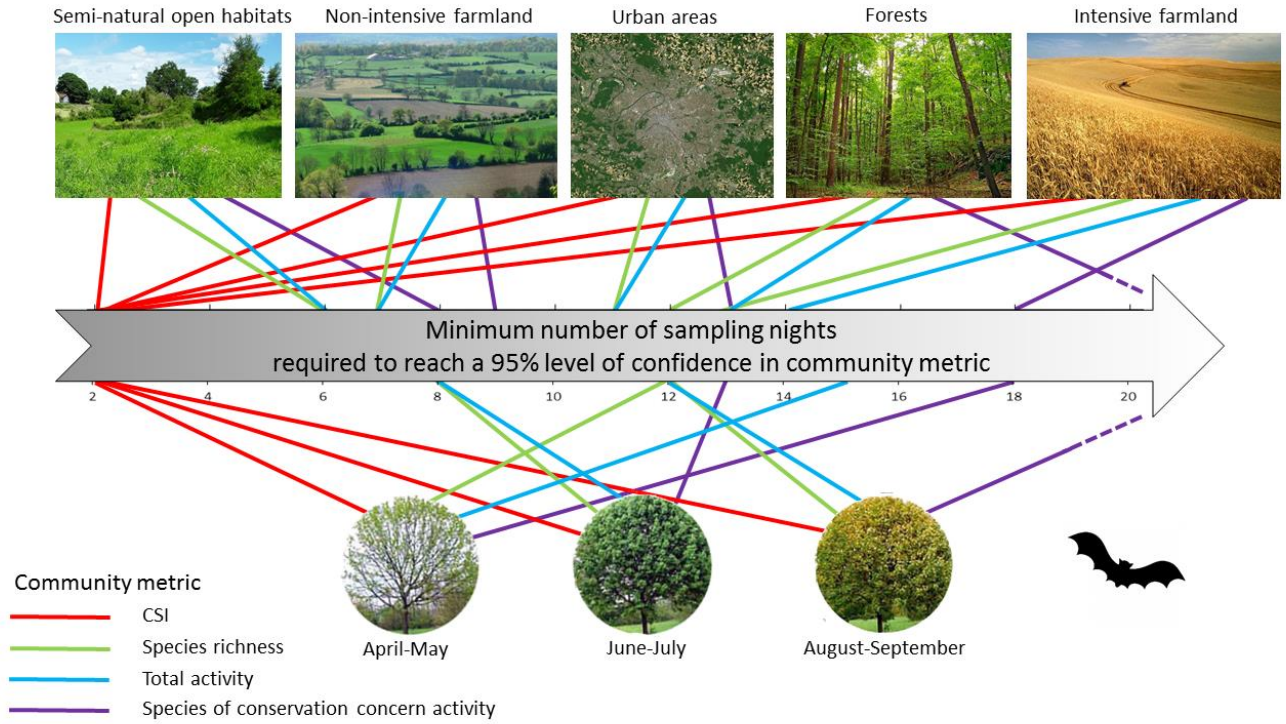

Fig. 5 Practical framework representing habitat- and season-specific mean sampling duration required to obtain a 95% similarity between four community metrics computed on the basis of *n* and *n*+1 survey nights.

Conclusions

The present study provides guidelines for the implementation of cost-effective bat surveys that would avoid the most common methodological pitfalls in community-level assessments. In practice, we provide recommendations for a conservative, minimum number of sampling nights according to the mean values found to reach a high degree of confidence in specific metrics (Fig. 5). We identified that longer sampling duration is needed in unfavourable habitats, and habitats that are structurally complex for comprehensive assessments of the many facets of species assemblages. Adjusting sampling duration according to the ecological context will enable relevant comparison between sites, with a similar level of confidence in community metrics. Our results also support that community indices such as the community habitat specialisation index (CSI), being less demanding than other community metrics in terms of sampling duration, can be efficient summary metrics for biodiversity assessment in case of limited resources. Provided they are used in complementarity with other biological indicators, the advantage of weighted community metrics can be extended to a broader range of taxa, and to other indices such as the Community Openness Index (COI; Tuneu-Corral et al., 2019), the Community Thermal Index (CTI; Devictor, Julliard, Couvet, & Jiguet, 2008), the Community Precipitation Index (CPI; Tuneu-Corral et al., 2019), the Community Functional Index (CFI; Godet et al., 2014; Barbaro et al 2019), and the diversity profile (Siriwardena et al 2019). With the recent development of automated species identification (Barré et al 2019) and the decreasing cost of acoustic devices (Whytock and Christie 2017; Hill et al 2018; Sethi et al 2018), increasing the number of spatial replicates will become more and more accessible, which will also give room for temporal optimisation of sampling effort. Passive acoustic monitoring schemes represent powerful tools for reliable assessments of potential trends in biodiversity metrics. The improvement of their cost-effectiveness should contribute to their development, along with a better understanding of biodiversity response to global changes and more effective conservation practices.

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Author contributions

ND and YB designed methodology; data were collected by volunteers; JFJ CK and YB coordinated the national monitoring scheme, ND analysed the data, wrote the first draft and led the writing of the manuscript. All authors critically contributed to the idea conceptions and drafts, and gave their final approval for publication.

Declarations

All authors consent to participate and publish, and declare no conflict of interest.

Data accessibility

The data used in this study is provided as an R object in the supporting information. Raw acoustic data are archived and available via the French citizen science programme "Vigie-Chiro" (http://vigienature.mnhn.fr/page/participer-vigie-chiro), at the portal http://vigiechiro.herokuapp.com/.

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