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Common bats are more abundant within Natura 2000 areas

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Abstract

The Natura 2000 network is the largest conservation effort in Europe. However, despite the known importance of conserving common and widespread biodiversity, criteria used to designate a Natura 2000 site are oriented toward rare and/or emblematic biodiversity. In this study, we took advantage of the fact that the management of Natura 2000 is just beginning to assess whether the five most common bat (Chiroptera) species and one genus in France exhibit a greater relative abundance within rather than outside Natura 2000 boundaries, and three bats communities index: total relative abundance, species richness, Community Habitat specialization index. We model the relative abundance of each taxa and indices using data from a nationwide volunteer-based acoustic survey. We found that three of the six taxa studied exhibit greater relative abundance within Natura 2000 sites (this increase is noteworthy for *E. serotinus* (x 2.1) and *Myotis* ssp (x 3.6)). We also provide evidence that total relative abundance of bat activity and richness are globally higher in Natura 2000 sites (respectively +24% and + 14%) and on average communities are more specialized within Natura 2000 sites. In addition, when the effect of Natura 2000 is adjusted to the main land use types, a significant positive effect of Natura 2000 remains for most metrics. The positive Natura 2000 effect appears relatively small compared to the main land use pressure: intensive agriculture and artificial light at night. However, Natura 2000 has a comparable sized effect as habitat widely recognized as having a positive impact on bats, such as streams.

Keywords: bats relative abundance, common biodiversity, Natura 2000; mean trait community,

Introduction

Among the approaches employed to preserve biodiversity, the establishment and management of statutory protected areas are widely regarded as key strategies (Jackson *et al.*, 2007). This classic protection approach is based on the principle that the designation of areas affords the protection of habitats, species and/or populations that are threatened elsewhere (Gaston *et al.*, 2008). In addition to National Nature Reserves, National Parks and Regional Parks that are designated by state members, the European Union (EU) has coordinated the Natura 2000 network. This network, which is the most important coordinated supra-national conservation effort at the world level (Evans, 2012), aims at maintaining remarkable biodiversity through the sustainable use of natural resources by establishing a network of areas that must maintain a range of habitat types and wildlife species in a “favorable conservation status” (European Commission, 2000). Over the last 25 years, the EU has built a vast network that represents 18% of the EU’s land area (see Supplementary Material S1). In France, this network represents 12.5% of the continental territory. The main objectives of conservation and restoration are stated at the local scale in the Natura 2000 management plan and the French Natura 2000 areas are mainly managed through contracts between land owners and the state. Agri-Environmental Schemes (Caps) are applied in agricultural land, whereas ones in non-agricultural land may receive incentives for measures that favor conservation of biodiversity. Although such actions are defined in each management plan, the field management of Natura 2000 has only recently begun (by 2005 only 20% of Natura 2000 sites had endorsed their management plan (Maresca *et al.* 2006) and by 2012 nearly 73%, and establishment of new plan has been slow since 2005, Debain, 2011).

Identification of the Natura 2000 areas is now broadly completed (Note however, that Member States can regularly add new sites), and attention is turning toward assessing whether

the Natura 2000 network effectively protects species and habitats (Martínez *et al.*, 2006). As Kliejn & van Zuijlen (2004) stated, the observed differences between protected and non-protected areas may result from either the initial state of biodiversity ('designation effect', assessed through a comparison of the biodiversity inside and outside the N2000 sites) or from the protection efficiency *per se* ('protection effect', which involve the comparison of the state of biodiversity before and after the designation of N2000 sites). Thus, the French case provides a good opportunity to assess the first of these effects ('designation effect'), *i.e.*, differences in the initial biodiversity state between areas inside and outside the Natura 2000 network, because within the studied period half of Natura 2000 sites had just endorsed their management plan and thus, management actions were too recent to already have an effect on the state of the biodiversity.

A growing number of studies have been carried out to evaluate the effectiveness of the Natura 2000 network for threatened species (Trochet & Schmeller, 2013) or species or habitats targeted by Natura 2000 (*i.e.* listed under priority Annex, vegetation: Rosati *et al.*, 2008, bats: Lisón *et al.*, 2015). Some studies like Donald *et al.*, (2007) have found a strong positive correlation between Member States' percentage land cover of Natura 2000 and population trends of species targeted by the EU Birds Directive (EC79/409).

Common biodiversity is of particular importance in ecosystem functioning (Smith & Knapp, 2003; Solan *et al.*, 2004), but there are few protection measures directed toward common species. While some common species are legally protected (common bats are listed in Annex IV Habitat Directive), there are no protected areas designated specifically at the benefice of these species, as protected areas are not considered as the appropriate tool for these kinds of species (Gaston 2011). Surprisingly, few studies (Devictor *et al.*, 2007, Pellissier *et al.*, 2013) have assessed the importance of classical protection measures on common bird biodiversity,

showing that common bird species have actually benefited from protection measures directed toward other target species.

In addition, among the studies focused on the evaluation of the designation effectiveness of the Natura 2000 network, the overwhelming majority of them were gap analyses based on species distribution (vertebrates: Kukkala *et al.*, 2016, invertebrates: Sánchez-Fernández *et al.*, 2013, amphibians and reptiles: Abellán & Sánchez-Fernández, 2015, Bat: Lisón *et al.*, 2013, 2015, all vertebrates: Kukkala *et al.*, 2016, all taxa: Trochet & Schmeller, 2013), while ecosystem functioning also requires the consideration of species abundance and community scale (Loreau *et al.*, 2001). In addition, a review of studies dealing with Natura 2000 performed by Orlikowska *et al.*, (2016) concluded that a majority of studies were performed in single Natura 2000 site, and suggest that more studies will need to encompass large spatial scale. Monitoring based on skilled volunteers counting common species (birds, amphibians and reptiles, mammals, butterflies and plants) has already provided reliable abundance data and unbiased results (Genet & Sargent, 2003; Schmeller *et al.*, 2009) regarding the effects of climate change (Julliard *et al.*, 2004) or the effectiveness of protection measures (Devictor *et al.*, 2007; Jiguet, 2011). Using volunteer bat-workers, the French National History Museum initiated a bat monitoring program (Vigie Nature 2011) to assess the current state and trends of common bat population in France (Kerbiriou *et al.*, 2010). Most of the European bat populations, including common species, have experienced dramatic declines in the last century (Voigt & Kingston, 2016) mostly because of the habitat loss and fragmentation induced by agricultural intensification (Wickramasinghe *et al.*, 2004, Azam *et al.*, 2016), urbanization (Kurta & Teramino, 1992; Azam *et al.*, 2016) and intensive forest management (O'Donnell, 2000)

Using the French bat monitoring data, we tested, mostly on non-target species, whether the relative abundance of species or community metrics (total relative abundance, richness and

habitat community specialization) were influenced by the Natura 2000 network. This test of Natura 2000 designation effect was achieved through two analyses, one comparing bat activities within and outside Natura 2000 sites and a second approach, in which we assessed the influence of Natura 2000 areas controlling for the main land uses and at different landscape scales. Higher relative abundance within Natura 2000 is expected if the Natura 2000 areas exhibit a ‘designation effect’, *i.e.*, the Natura 2000 areas are high-value areas for common species.

MATERIAL AND METHODS

Car transect survey

The data were provided by the French bat monitoring program (FBMP) (<http://vigienature.mnhn.fr/page/vigie-chiro>), a citizen-science program running since 2006 and coordinated by the French National Museum of Natural History (NMNH). Volunteers recorded bat activity while driving at a constant low-speed (25 ± 5 km/h) along a 30 km road circuit within a 10 km buffer around their home. Surveyors were asked to design their road circuit so that it proportionally crossed, as much as possible, the different land-cover types and it remained on low-traffic roads for security reasons. After final validation of the circuit outline, program coordinators randomly selected the starting point of the survey. Each circuit was then divided into 10 road transects (length of transect 2 km) where bats were recorded, separated by 1 km road portions where recording was not carried out (Supplementary Material 1). Such a sampling design resulted in a survey of habitats that are quite representative of French land cover (see Supplementary Material 1). We used data from surveys carried out every year from the 15th of June to the 31st of July, corresponding to a seasonal peak in bat activity, a period during which bat females typically give birth to and feed their offspring. Surveys started 30 min after sunset and lasted approximately 1.5 h during

the period of bat activity, and were only carried out when weather conditions were favorable (*i.e.*, no rain, low wind speed of <7 m/s, temperature >12 °C). This sampling design is quite similar to that used by many European bat monitoring schemes (Roche *et al.*, 2011). At total of 160 different car-based circuits were surveyed during the study period (2006 to 2013) (Supplementary Material 1), corresponding to 1608 independent 2-km transects, and each circuit was sampled an average of 2.4 ± 0.04 times.

Biological data

Along transects, volunteer surveyors recorded bat echolocation calls with ultrasound detectors connected to digital recorder (See Supplementary Material 1 for more details about technical points). Once the recording was performed, the observers were asked to identify the species detected in each transect using Syrinx software version 2.6 (Burt, 2006) and spectrogram analyses. The majority of volunteers involved in the bat monitoring participated in training courses organized by the MNHN, allowing a high level of homogeneity of the identification criteria. In a second step, the identifications were validated by MNHN experts. Bat calls were identified at the species level except for species of the *Myotis* genus. Due to the lack of general consensus on the acoustic criteria to distinguish some *Myotis* species and some overlap between their acoustic repertoires, it was not possible to assign the exact species with certainty for all calls; thus, we constructed a *Myotis spp* group (see Supplementary Material S1). Note that according to their foraging trait, bat species of the genus *Myotis* within the study area could be considered as a group of slow-flying species including mainly “narrow space gleaning foragers” and “trawling bat” compared to the group of the fast-flying species including mainly “open or space aerial foragers” (*i.e.* *Pipistrellus spp*, *Eptesicus serotinus* and *Nyctalus spp*) species that mainly hunt for airborne prey in open space or in edge space (Dezinger & Schnitzler, 2013). Indeed, an analysis based on a group composed of species of

the same genus (i.e. *Myotis spp*) could lead to non-significant results due to opposite effects among species included such a group. However, when significant effects are detected, this involves that at least one species of this group was enough sensitive to the variable tested. As it is impossible to distinguish individual bats from echolocation calls. For this reason, we produced for each 2-km road transect sampled, and for each year, a bat activity index (name hereafter “relative abundance”) defined as a number of bat pass per species (a bat pass corresponds to a trigger of the bat detector in time expansion, see Supplementary Material 1). The response variables were (i) species relative abundance (i.e. number of bat passes); (ii) total relative abundance (this measure was corrected by species distance of detection (Barataud 2015), species bat activity was weighted by the multiplicative inverse of the distance of detection squared, thus a species with a great distance of detection contributes less for total relative abundance than a species with a small distance of detection; (iii) species richness, (iv) Community Habitat specialization index (CSI). CSI is a mean trait community index based on weighted average of habitat specialization of each species present in the community, for more detail on CSI calculation see Supplementary Material 2. The recorded species are all protected species listed in annex IV of the Habitats Directive but they are not target species of the Natura 2000 network (non annex II species, except within the group *Myotis spp* which may include some species included in annex II but mainly in very slight proportion in our data collection see Supplementary Material 1, Table S1-6).

Landscape and Natura 2000 data

Around each of the 1608 transects (i.e. the 2-km road portions), we generated a set of landscape variables using QGIS 2.2. Because the landscape effect on bat activity could change according to the spatial scale considered (Grindal & Brigham, 1999; Lacoëuilhe *et al.*, 2016) we calculated these variables at 4 different buffers of 200, 500, 700 and 1000 m. At

1000 m landscape scale, there was 25 % overlap between nearby transects belonging to a same road circuit. However, this still allowed the measurement of variation in landscape characteristics within the same road circuit. However, we could not extend the analyses into larger landscape scales, because the overlapping rate between transect buffers would exceed 50 %. We assessed the proportion of the Natura 2000 areas included in each buffer (shapes were provided by the Muséum national d'Histoire naturelle (<http://inpn.mnhn.fr>, see Supplementary Material 3). Sites designated for birds (Special Protection Areas, SPA) and/or Habitats directive (Sites of Community Importance, SCI) were considered together as the evaluation deals with the whole network designation effect on non-target bat biodiversity. Note that analyses at the level of each directive (SCI and SPA) did not reveal any obvious difference with the analysis performed at the level of Natura 2000 sites (both together), see Supplementary Material 5, Table S5-3 & S5-4.

We also calculated seven land use variables within each buffer, (i) the proportion of intensive agriculture (*Inten. Agri.*, Code 2.1; CORINE Land Cover, including irrigated and non-irrigated arable land such as cereals, leguminous and forage crops.) within each buffer because they represent a major land use pressure for bats (Azam *et al.*, 2016); (ii) the proportion of heterogeneous agriculture (*Heter. agri.*), defined as areas with a complex mosaic of annual and permanent cultures and semi-natural habitats (Code 2.4; CORINE Land Cover); (iii) the proportion of deciduous and mixed forests (*Forests*, Code 3.1; CORINE Land Cover) as they were commonly represented in our buffers and were known to influence bat activity at a landscape scale (Boughey *et al.*, 2011; Frey-Ehrenbold *et al.*, 2013); (iv) the proportion of open habitat (*Open habitat*, code 231 and 32 CORINE Land Cover; (v) the total length of streams and water sources (*Streams*, IGN/2012) because numerous studies have identified aquatic habitat as a favorable where abundance of bat is high (Rainho & Palmeirim 2011; Russo & Jones 2003, Salvarina 2016); (vi) the total length of roads (*Roads*, IGN/2012)

within each buffer because effect of road network can be considered as a land use pressure, especially regarding landscape connectivity. However, this pressure could not accurately be tested in our study because transects were mostly located in areas with secondary low-traffic roads, therefore, we only took into account the total length of roads as a potential confounding factor of the urbanization. In addition, roads often included hedgerows, which could have a positive effect on bat activity (Verboom & Huitema, 1997; Lacoëuilhe *et al.*, 2016); and (vii) artificial light at night (*ALAN*) defined as the radiant flux (i.e., radiant power) reflected or emitted by a given surface., (see supplementary material 4 for details on the computation of this variable). We used light pollution data as a proxy of the urbanization process as it encompasses both the effects of impervious surfaces and urban-induced pollution that propagates beyond urban areas (Azam *et al.* 2016)

Representativeness of habitats and land uses sampled in the French bat monitoring program

This survey protocol resulted in the collection of data along roads chosen by volunteers, which may introduce a bias in the habitat sampling. Preliminary analysis have underlined that the choice of the circuit performed by volunteers plus the randomization introduced by the MNHN limited the bias in habitat representativeness at local and national scales (see Supplementary Material S1, Table S1-1). Because buildings tend to be concentrated along road networks, the main bias observed was with regard to urban areas and, in particular, impervious areas, which comprises 5% of France. However, our survey included 11% at a 200 m landscape scale, but note that this bias decreases when landscape scale take into account increase (6% of impervious areas in buffer of 1000 m size). We did not detect any bias for the representativeness of Natura 2000 regardless of the spatial scale considered (see Supplementary Material S1, Table S1-1)

A second expected type of bias concerns the presence of hedgerows or forest edges along the roads, which could result in an overall increase in insect availability, as aerial insects tend to concentrate on the lee side of hedgerows (*e.g.*, Lewis & Stephenson, 1966). Therefore, the observation of an over-representation of linear elements in the Natura 2000 areas could indicate a biased prediction of bat activity. Indeed, some bat species tend to forage along these linear elements (Verboom & Huitema, 1997) and fly along such features when commuting from roosts to foraging areas (Limpens & Kapteyn, 1991). Surprisingly, we detected a slight trend for there to be fewer hedgerows within the Natura 2000 area (See Supplementary Material 1, table S1-2, table S1-3). In general, habitats along roads are not a random subset of all the available habitats in the wider countryside. In fact, some rare habitats are most likely underrepresented; in addition, with such road sampling, we mainly sampled edge habitats instead of core habitats, which could result in a bias for some *Myotis* species that preferentially forage in closed environments (see Russo & Jones, 2003; Rainho, 2007) but is most likely to not a major problem for the five other species studied here, which do not select closed environments (Russ & Montgomery, 2002; Rainho, 2007).

Statistical analyses

Model building

Initially, we assessed if bat activity measures along transects differ from site to site within or outside a Natura 2000 site (*Natura 2000_PA*, a binomial variable) using Generalized Linear Mixed Model (GLMM). The response variable was either species relative abundance (n=6 taxa) or bat community metrics (total relative abundance, richness or CSI). We add as co-variables *the date of survey, the wind speed, the time elapsed after sunset* and *the temperature* because we assumed that bat activity might be affected by weather conditions (Ciechanowski *et al.*, 2007). Note however, that the protocol is performed only when weather conditions are

generally favorable (see Supplementary Material 1, Table S1-1). As these co-variables might have non-linear effects on these co-variables, we included quadratic form terms for the variables (see Supplementary Material 5, S5-1). According to the hierarchical structure of our sampling design (same sites were sampled year to year), we treated *site* and *year* as random effects (Zuur *et al.*, 2009). Thus, our models were structured in the following way:

$$[\text{bat activity}] \sim \text{Natura 2000_PA} + \text{date of survey} + \text{wind speed} + \text{minutes after sunset} + \text{temperature} + 1|\text{year} + 1|\text{site}$$

Check of assumptions of GLMM

Before performing our models, we systematically evaluated the correlations among explanatory variables using Spearman's rho for quantitative variables (Crawley, 2009) to detect obvious correlation (See Supplementary Material 5). Secondly, we performed variance-inflation factors (VIF) on each model (Fox & Monette 1992); all variables had $VIF < 2$ indicating no problem of multicollinearity in the explanatory variables of our models. Close points (even if they differ from habitat) are likely to have a similar bat population density due to similar climatic conditions or large-scale landscape compositions and could therefore imply spatial autocorrelation. Thus, we performed a variogram to observe if correlation between neighbors falls off with distance. When we detected such patterns in our data, we added in our GLMM an autocovariate (i.e., a distance-weighted function of neighboring response values; Dormann *et al.* 2007) with the autocov dist function in R (package spdep, Bivand R. *et al.* 2011) to account for spatial autocorrelation.

In a second step, using the same approach and same model validation (check of spatial autocorrelation, multicollinearity), we assessed the effect of the proportion of Natura 2000

areas at a landscape scale on bat activity taking into account the main land uses. Thus, in addition to Natura 2000 areas, we included seven other landscape variables as fixed effects. These analyses were performed at four scales: 200, 500, 700 and 1000 m. The fixed effects were centered and standardized so that the regression coefficients were comparable in magnitude and their effects were biologically interpretable (Schielzeth 2010). Thus, our models were structured in the following way:

$$[\text{bat activity}] \sim \text{Natura 2000} + \text{Inten. agri} + \text{Heter. agri.} + \text{Forests} + \text{Open habitat} + \text{Roads} + \text{Streams} + \text{ALAN} + \text{date of survey} + \text{wind speed} + \text{minutes after sunset} + \text{temperature} + 1|\text{year} + 1|\text{site}$$

According to the nature of the response variable (bat count) and potential over-dispersion, we chose the best error distribution among Poisson, a negative binomial distribution and zero inflation models with a negative binomial or Poisson error distribution (Zuur *et al.* 2009), and when abundance modelling did not fit well (i.e. *Myotis spp.*), we transformed the response variable (i.e. bat relative abundance) into a presence/absence variable and used a binomial error distribution, (see Supplementary Material 5, Table S5-1).

RESULTS

The survey recorded 23164 bat passes, on which analysis was conducted on the most commonly recorded species: *Pipistrellus pipistrellus* (n = 14967), *Eptesicus serotinus* (n = 2614), *Pipistrellus kuhlii* (n = 2318), (note that even after checking the identifications, we extrapolated that 8% of *P. kuhlii* calls are not entirely certain and could include *P. nathusius* calls), See Table S1 for details), *Nyctalus leisleri* (n = 1999), *Nyctalus noctula* (755) and *Myotis spp.* (261). The first species represented 65% of the dataset.

Without adjusting Natura 2000 effect to take landscape composition into account, *P. pipistrellus* and *E. serotinus* exhibited greater relative abundance within Natura 2000 than outside, and *Myotis* spp. have a greater probability to be recorded within Natura 2000, while we detected no significant effect for the three other species (Table 1). In addition, we detected a greater relative abundance, a greater richness and communities are more specialized within Natura 2000 than outside (Table 1).

When taking into account the main land uses within landscape and assessing the effect of the amount of Natura 2000 (i.e. areas of Natura 2000 in the neighbor of the sample site and not just being in a site or off site), we detected a similar relationship to the first set of analyses.

Among the six species studied, we were able to detect a positive influence of Natura 2000 in the area bordering transects for *P. pipistrellus*, *E. serotinus* and *Myotis* spp. (Table 2).

However, the detection of significant effects was scale dependent, and mainly detected at a small spatial scale (i.e. at 200 m, except for *Myotis* spp). In addition, total bat activity and community bat specialization were positively influenced by Natura 2000 areas, whereas no effect was detected for richness (Table 2). Again, we detected more significant effects at a smaller spatial scale.

The proportion of intensive agriculture had a significant negative effect on all species (except *N. noctula*). We found same results for all bat community metrics whatever the landscape scale considered. Artificial light at night, heterogeneous agriculture and open habitat, when significant, had a negative effect, whereas streams mainly had significant positive effect (except for *E. serotinus*) but again the effect was scale dependent and varied among species or bat community metrics (Table 2, Fig. 1). Forest effects depend of bat activities measured: for example *P. pipistrellus* was positively influenced by the proportion of forest while *N. lesilei* was negatively influenced, total bat relative abundance positively influenced, while richness and community specialization were negatively influenced by forest (Table 2, Fig. 1).

DISCUSSION

‘Designation effect’ of Natura 2000 areas for bats.

This paper provides evidence that bat activity is globally higher in Natura 2000 sites (+24%;). Three (*P. pipistrellus*, *E. serotinus*, *Myotis* spp) of the six species/genera studied exhibit greater relative abundance in Natura 2000 sites (this increase is noteworthy for *E. serotinus* (x 2.1) and *Myotis* spp (x 3.6)) and note that no significant negative effect was detected. The result for *Myotis* spp must be taken with caution; it did not imply that all species of this genus exhibit a similar pattern, but at least one species exhibits a greater bat activity in Natura 2000 sites. We also detected a greater richness in Natura 2000 sites (+ 14%). Finally, the bat community specialization, a mean trait community index, is greater in Natura 2000 sites (+9%).

In a second step, we evaluated if this Natura 2000 effect was consistent when, in the neighborhood of the survey, the proportion of Natura 2000 was adjusted to the land uses. For *P. pipistrellus*, *E. serotinus* and *Myotis* spp, the increase of Natura 2000 in the surrounding area positively influenced their activity but the effect was spatial scale dependent. Similarly, bat community specialization, increased when Natura 2000 areas increased in the surrounding transects. However, we did not detect any effect of the proportion of Natura 2000 areas in the surrounding of transects on species richness. Note that this latter non-detection is possibly linked to the nature of data collected (small sequence of acoustic recordings) which currently did not allow species identification within the *Myotis* group, while this group is very rich in the region considered (39% of the French species, TAXREF, Gargominy *et al.*, 2016-). With the recent arrival on the market of new generation of bat detector-recorders, we could consider recording throughout the entire night (see Newson *et al.*, 2015) and thus expect an

increase in the probability of contacting and identifying *Myotis* species. A protocol using this new technology is under development by the FBMP (Bas *et al.*, 2017), thus a more accurate assessment of Natura 2000 effect on richness could be expected in the future.

The positive Natura 2000 effect appears to be relatively small compared to the main land use pressure: intensive agriculture and to a lesser extent heterogeneous agriculture (while this category is known to include more extensive agriculture practice) and light pollution (ALAN) all of them have a deep negative impact. They impact not only the abundance of populations but also the structure of communities, leading to less rich and more generalist communities, thus contributing to a biotic homogenization process (McKinney, 2006, Karp *et al.*, 2012). These drivers are known to impact negatively bats (Wickramasinghe *et al.*, 2004; Azam *et al.* 2016) and more broadly biodiversity, both rare and endangered species (Maxwell *et al.*, 2016) as the common species and (plants: moth: Conrad *et al.* 2006; butterflies: Van Dyck *et al.* 2009; bees: Kosior *et al.*, 2007; birds: Donald. 2001) and contribute to large scale biotic homogenization (Le Viol *et al.* 2012). The negative effect of open habitat is mainly due to the requirement of the species studied to avoid large open habitat (Verboom, & Spoelstra, 1999) and select wooded edge, woodland or aquatic habitat (Walsh & Harris, 1996). The positive effect of streams is (although detected for many species or bat community measures) in accordance with many studies see the review perform by Salvarina (2016). The contrasting effect of forest areas on the species studied (dominated by aerial hawking species), positive effect on total relative abundance, while negative effect on richness and community specialization, seem to indicate that these land uses, when adjusted for the effect of Natura 2000, does not have a broad effect. Zehetmair *et al.*, (2015), in a sample of European beech forest, found that bat activity did not differ significantly between the Natura 2000 and non-Natura 2000 forest on paired comparison of stands with same structural attributes. They concluded that the current management of the Natura 2000 beech forests is almost identical to

that of non-Natura 2000 commercial forests, and thus, the Natura 2000 status has not led to an increase of bat-relevant habitat variables yet. By comparing similar beech forest habitats, Zehetmair *et al.*, (2015) may have missed the fact that the Natura 2000 network may also include a higher proportion of high quality habitats than usual non Natura 2000 forests. On the contrary, our study design (including a great number of sites and, in turn, a wide range of forest types) enables us to test for a more global Natura 2000 designation effect, which remains even after taking landscape variables into account.

When the road effect is detected, it is surprisingly positive and appears to invalidate this landscape variable as a pressure on bat foraging connectivity. Lisón & Sánchez-Fernández (2017) found that the roadless areas are not significant for the localization of bat hotspots. It should be noted however, that we could not test accurately a “road effect” because our sampling is not representative of national road network: due to security, and transects were mostly located in areas with secondary low-traffic roads. Thus, within this biased sample, we probably detected an effect of availability of hedgerows along roads, where hedgerows are positively selected for by bats (Lacoeuilhe *et al.*, 2016). The increase in relative abundance and degree of specialization may appear limited compared to the negative effect of intensive agriculture (respectively lower by a factor 6 and 2, Table 2). However, it is still notable that for common, widely distributed species, that there is still a Natura 2000 effect, after we control for land use variables like streams that are known to have a positive influence on bats (Salvarina, 2016).

It appears that the areas designated as Natura 2000 areas exhibit a ‘designation effect’ and providing evidence that such areas are most likely to be of better quality for bats with regard to their foraging activity. Similar results have been found by Lisón *et al.*, (2015) in Spain, a study involving bat distribution and not bat abundance. Indeed, the Natura 2000 areas contain less intensive agriculture areas (Supplementary material Table S1-3) and more semi-

natural areas and harbor more common biodiversity than non-Natura 2000 areas (Pellissier *et al.*, 2013). This non-random habitat composition of Natura 2000 sites is part of the raw “designation effect” of this network. Interestingly, when this habitat “bias” is partially taken into account because the effect of Natura 2000 was adjusted to the main land use types, a significant positive effect of Natura 2000 remains for most metrics. One possible interpretation is that Natura 2000 have, on average, better structural and more micro-habitats features or food webs important for bats than the same broad habitat types outside the network.

Scale and time effect

When looking at the influence of spatial scale, the positive effect of Natura 2000 tends to be more significant at a smaller scale (i.e. 200 m) while some land uses variables remain significant whatever the spatial scale considered (*i.e.* intensive agriculture, ALAN). This finding seems to indicate that Natura 2000 areas do not yet enhance adjacent areas at a large scale for common bats. However, a theoretically and empirically demonstrated reserve effect is the spillover of species richness and community complexity that highlights the important benefit for biodiversity and ecosystems of establishing reserve areas (Roberts *et al.* 2001, Russ & Alcala, 2011). However, many studies have underlined that reserves could enhance adjacent areas, but that age matters (Claudet *et al.*, 2008, Russ & Alcala, 2011). It should be emphasized that the purpose of this paper is not to assess the efficiency of the management measures actually occurring in the Natura 2000 areas; here we only assess a designation effect. Indeed, management is probably too recent to be able to produce measurable effects, because during the period studied (2006-2013) only 53% of Natura 2000 sites had endorsed their management plan, and moreover 69% of recordings were collected between 2006 and 2009 (see Supplementary Material 1, Fig S1-1). We hypothesize that effect of Natura 2000 at

large landscape scale should become more significant in the future with the effects of Natura 2000 sites management and the implementation and green infrastructure policies, which aim to connect patches of protected areas. Future research should now focus on comparing biodiversity state before and after the designation of N2000 sites (see Lisón & Sánchez-Fernández, 2017), especially since conservation policy may moderate land-cover transformation (Kallimanis *et al.*, 2015).

Car-based bat survey and policy implications

The French bat monitoring program has proven to be a useful tool for evaluating the Natura 2000 network owing to its large spatial coverage and its standardized monitoring based on volunteers. This finding emphasizes that public participation in scientific research is a promising approach that can significantly help scientists to address questions relating to biodiversity, as suggested by Bell *et al.*, (2008) and Couvet *et al.*, (2008). Volunteer-based monitoring is likely to have high resilience (Couvet *et al.*, 2008), which is key to maintaining the monitoring program over time and, thus, providing extended time-series (Battersby, 2010). However, questions can be raised about more efficient ways to monitor biodiversity of a protected network, between surveying rarer species and habitats or to survey more common and widespread elements not targeted during the designation process. Indeed, rare species (due to lower abundance, lower detection, or their specialization to particular habitats) need focused sampling (Barlow *et al.*, 2015). From a financial point of view, it should be noted that the monitoring of common species does not involve funds dedicated to Natura 2000 surveys.

Conclusion and conservation implications

Our study showed a sampling effect induced by the designation process of Natura 2000. The species studied are only listed in the Annex IV of the habitat directive (not Annex

II), despite the fact that they benefit from a strict protection regime, they are not target species for the designation of Natura 2000 areas. In addition, in the meta analysis performed in Spain, Lisón *et al.*, (2017) found that bats were not "emblematic" species for the managers, especially the bat species of Annex IV. However, they remain policy relevant because they are species of European concern and it is a highly valuable feature the Natura 2000 network benefits common biodiversity. This result is congruent with many studies that assert that the establishment and management of statutory protected areas are widely regarded as key strategies and efficient tool for safeguarding key biodiversity areas (Jackson *et al.*, 2009; Watson *et al.*, 2014). Although gap analysis have clearly demonstrated that the global protected area network is still far from complete for encompassing broader biodiversity (Rodrigues *et al.*, 2004), our results suggest that Natura 2000 is able to encompass non-targeted species, at higher level of relative abundance than outside the same landscapes. As this network is the most important conservation effort in Europe (Evans, 2012), it is important to recognize that its biodiversity coverage extends beyond the rare or threatened targeted species and habitats and potentially promote management measures towards this more common part of biodiversity and its functional role.

Additionally, most of the Natura 2000 areas designated for the protection of bat species are limited to roosting sites and immediate surroundings. Indeed, for species with a complex life cycle, reproduction is most often considered the most important part of the cycle, and, thus, the protection of reproduction sites is emphasized (Stebbing, 1988). However, whilst sites for bat reproduction are restricted in space, they have a large foraging territory, even during reproduction (Stebbing, 1988). Therefore, protecting hunting territories, which can be quite large and far from roosting sites, is of prime importance from a conservation point of view (Vaughan *et al.*, 1997). In this study, we assessed the influence of Natura 2000 areas on measures of foraging activity for six common Chiroptera species and three measures

of community. Given the trophic level occupied by all the Chiroptera species in Europe (top predators), the implications of our results may extend beyond the taxa considered and have important implications for the conservation of biodiversity as a whole.

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REFERENCES

- Azam, C., Le Viol, I., Julien, J.-F., Bas, Y., Kerbiriou, C. 2016. Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. *Landscape Ecol.* 31, 2471–2483. <http://dx.doi.org/10.1007/s10980-016-0417-3>
- Barataud, M. 2015. Acoustic Ecology of European Bats, Species identification, study of their habitat and foraging behavior. Biotope, Mèze; Muséum national d’histoire naturelle, Paris (Inventaires et biodiversité Series), 352 p.
- Barlow, K.E., Briggs, P.A., Haysom, K.A., Hutson, A.M., Lechiara, N.L., Racey, P.A., Walsh, A.L., Langton, S.D., 2015. Citizen science reveals trends in bat populations: The National Bat Monitoring Program in Great Britain. *Biol. Conserv.* 182, 14-26.
- Bas, Y., Bas, D., Julien, J.F. 2017. Tadarida: A Toolbox for Animal Detection on Acoustic Recordings. *Journal of Open Research Software* 5, 6. <http://dx.doi.org/10.5334/jors.154>
- Battersby, J. 2010. Guidelines for surveillance and monitoring of European bats. EUROBATS Publication Series, 51–95.
- Bell, S., M. Marzano, J. Cent, H. Kobierska, D. Podjed, D. Vandzinskaite, H. Reinert, A. Armaitiene, M. Grodzińska-Jurczak, and R. Muršič. 2008. What counts? Volunteers and their organisations in the recording and monitoring of biodiversity. *Biodivers. Conserv.* 17, 3443–3454.

518 Couvet, D., Jiguet, F., Julliard, R., Levrel, H., Teyssedre, A. 2008. Enhancing citizen
 519 contributions to biodiversity science and public policy. *Interdiscipl. Sci. Rev.* 33, 95–103.
 520 Boughey, K.L., Lake, I.R., Haysom, K.A., Dolman, P.M. 2011. Effects of landscape-scale
 521 broadleaved woodland configuration and extent on roost location for six bat species
 522 across the UK. *Biol. Conserv.* 144(9), 2300-2310
 523 Ciechanowski, M., Zajac, T., Bilas, A., Dunajski, R., 2007. Spatiotemporal variation in
 524 activity of bat species differing in hunting tactics: effects of weather moonlight, food
 525 abundance, and structural clutter. *Revue Canadienne de Zoologie* 85, 1249–1263.
 526 Claudet, J., Osenberg, C. W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.-A.,
 527 Pérez-Ruzafa, Á., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., Culioli, J.-
 528 M., Dimech, M., Falcón, J. M., Guala, I., Milazzo, M., Sánchez-Meca, J., Somerfield, P.
 529 J., Stobart, B., Vandeperre, F., Valle, C., Planes, S. 2008. Marine reserves: size and age
 530 do matter. *Ecol. Lett.* 11, 481–489. <http://dx.doi.org/10.1111/j.1461-0248.2008.01166.x>
 531 Conrad, K.F., Warren, M.S., Fox R., Parsons, M.S., Woiwod, I.P., 2006. Rapid declines of
 532 common, widespread British moths provide evidence of an insect biodiversity crisis,
 533 *Biol. Conserv.* 132(3), 279-291, doi.org/10.1016/j.biocon.2006.04.020.
 534 Crawley, M.J., 2009. *The R book*. John Wiley & Sonc, Chicago, USA.
 535 Devictor, V., Godet, L., Julliard, R., Couvet, D., Jiguet, F. 2007. Can common species benefit
 536 from protected areas? *Biol. Conserv.* 139, 29-36.
 537 Denzinger A, Schnitzler H-U. Bat guilds, a concept to classify the highly diverse foraging and
 538 echolocation behaviors of microchiropteran bats. *Frontiers in Physiology.* 4,164.
 539 [doi:10.3389/fphys.2013.00164](https://doi.org/10.3389/fphys.2013.00164).
 540 Donald, P.F., Green, R. E., Heath, M. F. 2001. Agricultural intensification and the collapse of
 541 Europe's farmland bird populations. *P. Roy. Soc. Lond. B. Bio.* 268 25-29.
 542 <http://dx.doi.org/10.1098/rspb.2000.1325>.

543 Donald, P.F., Sanderson, F.J., Burfield, I.J., Bierman, S.M., Gregory, R.D., Waliczky, Z.
 544 2007. International conservation policy delivers benefits for birds in Europe. *Science*
 545 317, 810-813.

546 Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies,
 547 R.D., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I., Ohlemüller, R., Peres-Neto,
 548 P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R. 2007. Methods to account
 549 for spatial autocorrelation in the analysis of species distributional data: a review.
 550 *Ecography* 30, 609-628.

551 Donald, P.F., Sanderson, F.J., Burfield, I.J., Bierman, S.M., Gregory, R.D., Waliczky, Z.
 552 2007. International Conservation Policy Delivers Benefits for Birds in Europe. *Science*.
 553 317(5839), 810–813.

554 European Commission, Environment, Nature & Biodiversity
 555 http://ec.europa.eu/environment/nature/index_en.htm

556 European Commission 2000. Managing Natura 2000 sites. The provisions of Article 6 of the
 557 ‘Habitats’ Directive 92/43/EEC. European Communities, Luxembourg.

558 Evans, D. 2012. Building the European Union’s Natura 2000 network. *Nature Conservation* 1,
 559 11. <http://dx.doi.org/10.3897/natureconservation.1.1808>

560 Fox, J., Monette, G. 1992. Generalized collinearity diagnostics. *Journal of the American*
 561 *Statistics Association* 87, 178–183.

562 Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R., Obrist, M.K. 2013. Landscape connectivity,
 563 habitat structure and activity of bat guilds in farmland-dominated matrices. *J. Appl. Ecol.*
 564 50: 252–261.

565 Gargominy, O., Tercerie, S., Régnier, C., Ramage, T., Schoelinck, C., Dupont, P., Vandel, E.,
 566 Daszkiewicz, P., Poncet, L. 2016. TAXREF v10.0, référentiel taxonomique pour la
 567 France : méthodologie, mise en oeuvre et diffusion. Muséum national d’Histoire
 568 naturelle, Paris. Rapport SPN 2016 – 101. 144 pp.

569 Gaston, K.J. 2011. Common Ecology. *BioScience* 61, 354–362.
 570 <http://dx.doi.org/10.1525/bio.2011.61.5.4>

571 Gaston, K.J. 2011. Common Ecology. *BioScience* 61, 354–362. doi:10.1525/bio.2011.61.5.4

572 Gaston, K.J., Jackson, S.E., Nagy, A., Cantu-Salazar, L., Johnson, M. 2008. Protected areas in
573 Europe - Principle and practice. *Ann. NY Acad. Sci.* 1134, 97-119.

574 Genet, K.S., Sargent, L.G. 2003. Evaluation of Methods and Data Quality from a Volunteer-
575 Based Amphibian Call Survey. *Wildlife Soc. B.* 31, 703-714.

576 Grindal, S.D., Brigham, R.M., 1999. Impact of forest harvesting on habitat use by foraging
577 insectivorous bats at different spatial scales. *Ecoscience* 6, 24e34.

578 Jackson, S.F., Evans, K.L., Gaston, K.J. 2009. Statutory protected areas and avian species
579 richness in Britain. *Biodiv. Conserv.* 18, 2143-2151.

580 Jiguet, F., Devictor, V., Julliard, R., Couvet, D. 2011. French citizens monitoring ordinary
581 birds provide tools for conservation and ecological sciences. *Acta Oecologica in press*

582 Julliard, R., Jiguet, F., Couvet, D., 2004. Common birds facing global changes: what makes a
583 species at risk? *Global Change Biol.* 10, 148-154.

584 Kallimanis, A.S., Touloumis, K., Tzanopoulos, J., Mazaris A.D., Apostolopoulou, E.,
585 Stefanidou, S., Scott, A.V., Potts, S.G., Pantis, J.D. 2015. Vegetation coverage change in
586 the EU: patterns inside and outside Natura 2000 protected areas. *Biodiv. Conserv.* 24,
587 579-591.

588 Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R. and Daily, G.C. 2012.
589 Intensive agriculture erodes β -diversity at large scales. *Ecol. Lett.* 15, 963–970.
590 doi:10.1111/j.1461-0248.2012.01815.x

591 Kerbiriou, C., Bas, Y. Dufrêne, L. Robert, A. & Julien J.F. 2010. Long term trends
592 monitoring of bats, from biodiversity indicator production to species specialization
593 assessment. Society for Conservation Biology - 24th Annual Meeting, 3 - 7 July, 2010,
594 Edmonton, Alberta, Canada.

595 Kosior, A., Celary, W., Olejniczak, P., Fijal, J., Król, W., Solarz, W., Plonka, P. 2007. The
 596 decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of
 597 Western and Central Europe. *Oryx* 41, 79-88.
 598 <http://dx.doi.org/10.1017/S0030605307001597>.

599 Kukkala, A.S., Santangeli, A., Butchart, S.H.M., Maiorano, L., Ramirez, I., Burfield, I.J.,
 600 Moilanen, A. 2016. Coverage of vertebrate species distributions by Important Bird and
 601 Biodiversity Areas and Special Protection Areas in the European Union. *Biol. Conserv.*
 602 202, 1–9. <http://dx.doi.org/10.1016/j.biocon.2016.08.010>

603 Kukkala, A.S., Arponen, A., Maiorano, L., Moilanen, A., Thuiller, W., Toivonen, T., Zupan,
 604 L., Brotons, L., Cabeza, M. 2016. Matches and mismatches between national and EU
 605 wide priorities: examining the Natura 2000 network in vertebrate species
 606 conservation. *Biol. Conserv.* 198, 193–201.

607 Kurta, A., Teramino, J.A. 1992. Bat Community Structure in an Urban Park. *Ecography*, 15,
 608 259-261.

609 Lacoëuilhe, A., Machon, N., Julien, J.F., Kerbiriou, C. 2016. Effects of hedgerows on bats
 610 and bush crickets at different spatial scales. *Acta Oecol.* 71, 61-72.

611 Le Viol, I., Jiguet, F., Brotons, L., Herrando, S., Lindström, A., Pearce-Higgins, J.W., Reif, J.,
 612 Van Turnhout, C., Devictor, V. 2012. More and more generalists: two decades of changes
 613 in the European avifauna. *Biol. Lett.* 8, 780–782. <http://dx.doi.org/10.1098/rsbl.2012.0496>

614 Lisón, F., Palazón, J.A. Calvo, J.F. 2013. Effectiveness of the Natura 2000 Network for the
 615 conservation of cave-dwelling bats in a Mediterranean region. *Animal Conservation*
 616 16:528–537. <http://dx.doi.org/10.1111/acv.12025>

617 Lisón, F., Sánchez-Fernández, D., Calvo, J.F. 2015. Are species listed in the Annex II of the
 618 Habitats Directive better represented in Natura 2000 network than the remaining
 619 species? A test using Spanish bats. *Biodiv. Conserv.* 24(10), 2459–2473.
 620 <http://dx.doi.org/10.1007/s10531-015-0937-1>

621 Lisón, F., Sánchez-Fernández, D. 2017. Low effectiveness of the Natura 2000 network in
622 preventing land-use change in bat hotspots. *Biodiv. Conserv.* 26, 1989-2006.

623 Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U.,
624 Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle D.A. 2001. Biodiversity
625 and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science* 294,
626 (5543), 804-808.

627 Maresca, B., Poquet, G., Ranvier, M., Temple, P., Benevise, F., Dubois, G., Raoul-Duval, J.,
628 Ughetto, A.-L. 2006. Evolution économique et institutionnelle du programme Natura
629 2000 en France, CREDOC. 193 p

630 Martínez, I., Carreño, F., Escudero, A., Rubio, A. 2006. Are threatened lichen species well-
631 protected in Spain? Effectiveness of a protected areas network. *Biol. Conserv.* 133, 500–
632 511.

633 Maxwell, S.L., Fuller, R.A., Brooks, T.M., Watson, J.E.M. 2016. Biodiversity: The ravages of
634 guns, nets and bulldozers. *Nature* 536, 143–145. <http://dx.doi.org/10.1038/536143a>

635 McKinney, M.L. 2006. Urbanization as a major cause of biotic homogenization, *Biol.*
636 *Conserv.* 127(3), 247-260.

637 Newson, S.E., Evans, H.E., Gillings, S. 2015. A novel citizen science approach for large-scale
638 standardised monitoring of bat activity and distribution, evaluated in eastern England,
639 *Biol. Conserv.* 191: 38-49.

640 O'Donnell, C.F.J. 2000. Conservation status and causes of decline of the threatened New
641 Zealand long-tailed bat *Chalinolobus tuberculatus* (Chiroptera: Vespertilionidae).
642 *Mammal Rev.* 30, 89–106.

643 Orlikowska, E.H., Roberge, J.M., Blicharska, M., Mikusiński, G. 2016. Gaps in ecological research
644 on the world's largest internationally coordinated network of protected areas: a review
645 of Natura 2000. *Biol. Conserv.* 200, 216–227.

646 Pellissier, V., Touroult, J., Julliard, R., Sibley, J.P., Jiguet, F. 2013. Assessing the Natura 2000
 647 network with a common breeding birds survey. *Ani. Conserv.* 16, 566–574.
 648 <http://dx.doi.org/10.1111/acv.12030>

649 Rainho, A., Palmeirim, JM 2011 The Importance of Distance to Resources in the Spatial
 650 Modelling of Bat Foraging Habitat. *PLoS ONE* 6(4): e19227

651 Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., Goodridge, R. 2001. Effects of Marine
 652 Reserves on Adjacent Fisheries. *Science* 294(5548), 1920-1923
 653 <http://dx.doi.org/10.1126/science.294.5548.1920>

654 Rodrigues, A.S.L., Andelman, S.J., Bakarr M.I., Boitani L., Brooks T.M., Cowling R.M.,
 655 Fishpool L.D.C., Fonseca G.A.B., Gaston K.J., Hoffmann M., Long J.S., Marquet
 656 P.A., Pilgrim J.D., Pressey R.L., Schipper J., Sechrest W., Stuart S.N., Underhill L.G.,
 657 Waller R.W., Watts M.E.J., Yan X. 2004. Effectiveness of the global protected area
 658 network in representing species diversity. *Nature* 428, 640-643.

659 Roche, N., Langton, S., Aughney, T., Russ, J. M., Marnell, F., Lynn, D., Catto, C. 2011. A
 660 car-based monitoring method reveals new information on bat populations and
 661 distributions in Ireland. *Ani. Conserv.* 14, 642–651.

662 Rosati, L., Marignani, M., Blasi, C. 2008. A gap analysis comparing Natura 2000 versus
 663 National protected area network with potential natural vegetation. *Community*
 664 *Ecology* 9, 147–154

665 Russ, J.M., Montgomery, W.I. 2002. Habitats associations of bats in Northern Ireland:
 666 implications for conservation. *Biol. Conserv.* 108, 49-58.

667 Russ, G.R., Alcala, A.C. 2011. Enhanced biodiversity beyond marine reserve boundaries: The
 668 cup spillth over. *Ecol. Applications*, 21, 241–250. doi:10.1890/09-1197.1

669 Russo, D., Jones, G. 2003. Use of foraging habitats by bats in a Mediterranean area
 670 determined by acoustic surveys: conservation implications. *Ecography* 26: 197-209

671 Salvarina, I. 2016. Bats and aquatic habitats: a review of habitat use and anthropogenic
672 impacts. *Mammal Review* 46, 131–143.

673 Sánchez-Fernández, D., Abellán, P., Picazo, F., Millán, A., Ribera, I., Lobo, J.M. 2013. Do
674 protected areas represent species' optimal climatic conditions. A test using Iberian
675 water beetles. *Diversity and Distribution* 19, 1407–1417.

676 Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients.
677 *Methods in Ecology and Evolution* 1:103–113

678 Schmeller, D.S., Henry, P.-Y., Julliard, R., Gruber, B., Clobert, J., Dziock, F., Lengyel, S.,
679 Nowicki, P., Déri, E., Budrys, E., Kull, T., Tali, K., Bauch, B., Settele, J., Van Swaay, C.,
680 Kobler, A., Babij, V., Papastergiadou, E., Henle, K. 2009. Advantages of Volunteer-
681 Based Biodiversity Monitoring in Europe. *Conserv.Biol.* 23, 307–316.

682 Smith, M.D., Knapp, A.K. 2003. Dominant species maintain ecosystem function with non-
683 random species loss. *Ecol Lett* 6, 509–517.

684 Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L., Srivastava,
685 D.S. 2004. Extinction and Ecosystem Function in the Marine Benthos. *Science* 12, 1177-
686 1180.

687 Stebbings, R.E, 1988 *Conservation of European bats*, Christopher Helm, London

688 Trochet, A., Schmeller, D.S. 2013. Effectiveness of the Natura 2000 network to cover
689 threatened species. *Nature Conservation* 4: 35–53.
690 <http://dx.doi.org/10.3897/natureconservation.4.3626>

691 Van Dyck, H., Van Strien, A.J., Maes, D., Van Swaay, C.A.M. 2009. Declines in Common,
692 Widespread Butterflies in a Landscape under Intense Human Use. *Conserv. Biol.* 23:
693 957–965. <http://dx.doi.org/10.1111/j.1523-1739.2009.01175.x>

694 Vaughan, N., Jones, G., Harris, S. 1997 Habitat Use by Bats (Chiroptera) Assessed by Means
695 of a Broad-Band Acoustic Method. *J. Appl. Ecol.* 34, 716-730.

- Verboom, B., Huitema, H., 1997. The importance of linear landscape elements for the
pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. Landscape.
Ecol. 12, 117-125.
- Verboom, B. Spoelstra, K. 1999. Effects of food abundance and wind on the use of tree lines
by an insectivorous bat, *Pipistrellus pipistrellus*. Revue Canadienne de Zoologie 77(9):
1393-1401, <https://doi.org/10.1139/z99-116>
- Vigie Nature : <http://vigienature.mnhn.fr/> (accessed 17.06.13).
- Voigt, C.C., Kingston, T. 2016. Bats in the Anthropocene: conservation of bats in a changing
world. SpringerOpen, New York.
- Walsh, A.L., Harris, S. 1996. Foraging Habitat
Preferences of Vespertilionid Bats in Britain J. Appl. Ecol. 33(3), 508-518
- Watson, J.E. M., Dudley, N., Segan, D.B. Hockings, M. 2014. The performance and potential
of protected areas. Nature 515, 67–73. <http://dx.doi.org/10.1038/nature13947>
- Wickramasinghe, L.P., Harris, S., Jones, G., Vaughan Jennings, N. 2004. Abundance and
Species Richness of Nocturnal Insects on Organic and Conventional Farms: Effects of
Agricultural Intensification on Bat Foraging. Conserv. Biol. 18, 1283–1292.
- Zehetmair, T., Müllerb, J., Runkel, V., Stahlschmidt, P., Winter, S., Zharov, A., Grupp, A.,
2015. Poor effectiveness of Natura 2000 beech forests in protecting forest-dwelling bats.
Journal for Nature Conservation 23, 53–60.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models
and Extensions in Ecology with R. Statistics for Biology and Health, Springer, New
York, USA. 574p.

Table 1. Partial regression coefficient of the raw Natura 2000 effect for the 3 community metrics and 6 taxa.

Bat activity metric	Natura 2000 effect Estimate	P-value	Factor of variation
<i>Relative abundance</i>	$\beta = 0.2195 \pm 0.035$	$P < 0.001$	x 1.24 number of bat passes/2km transect
<i>Richness</i>	$\beta = 0.130 \pm 0.052$	$P = 0.010$	x 1.14 number of species/2km transect
<i>CSI</i>	$\beta = 0.061 \pm 0.020$	$P = 0.002$	x 1.09 the degree of community specialization
<i>P. pipistrellus</i>	$\beta = 0.186 \pm 0.041$	$P < 0.001$	x 1.14 number of passes/2km transect
<i>P. kuhlii</i>	$\beta = 0.113 \pm 0.128$	$P = 0.378$	
<i>E. serotinus</i>	$\beta = 0.721 \pm 0.090$	$P < 0.001$	x 2.05 number of passes/2km transect
<i>N. noctula</i>	$\beta = -0.346 \pm 0.387$	$P = 0.371$	
<i>N. leisleri</i>	$\beta = 0.272 \pm 0.254$	$P = 0.280$	
<i>Myotis spp.</i>	$\beta = 1.372 \pm 0.209$	$P < 0.001$	x 3.68 occurrence of contact/2km transect

Table 2. Standardized partial regression coefficients from GLMMs model for the 8 landscape effects included in the analysis (i.e. the proportion of the Natura 2000 (Natura 2000), intensive agriculture (*Inten. Agri.*), heterogeneous agriculture (*Heter. agri.*), forests (*Forests*), open habitat (*Open habitat*) the total length of primary roads (*Roads*) and streams (*Streams*) and the average luminance (ALAN)), for the 3 community metrics and 6 taxa and at 4 landscape scales considered. P-value level of significance associated are ‘***’ P < 0.001; ‘**’ P < 0.01; ‘*’ P < 0.05; ‘.’ P < 0.1

	Scale	<i>Natura 2000</i>	<i>Inten. agri.</i>	<i>ALAN</i>	<i>Heter. agri.</i>	<i>Forests</i>	<i>Open Habitat</i>	<i>Roads</i>	<i>Streams</i>
<i>Community metrics</i>									
<i>Relative abundance</i>	200	0.057***	-0.257***	-0.079***	-0.081***	-0.008	-0.110***	0.0317***	0.016*
	500	0.022*	-0.200***	-0.013	-0.029*	0.051*	-0.047**	0.029***	0.028***
	700	0.028*	-0.165***	0.015	-0.009	0.075***	-0.028.	0.024**	0.030***
	1000	0.030.	-0.149***	0.023	-0.010	0.081***	-0.033	0.031***	0.044***
<i>Richness</i>	200	0.002	-0.206***	-0.083***	-0.039.	-0.045*	-0.071**	0.010	0.020
	500	-0.006	-0.157***	-0.055*	-0.001	-0.001	-0.026	0.010	0.032*
	700	-0.009	-0.204***	-0.080***	-0.039.	-0.048*	-0.064**	0.005	0.034*
	1000	-0.013	-0.217***	-0.089***	-0.047*	-0.061*	0.076**	0.015	0.031.
<i>CSI</i>	200	0.016***	0.040***	-0.028***	-0.042***	-0.009	-0.030***	0.017*	0.012*
	500	0.013*	-0.025*	-0.019*	-0.029**	0.007	0.019.	0.011*	0.010*
	700	0.013*	-0.049***	-0.031***	-0.0503***	-0.016.	-0.039***	0.015***	0.009.

	1000	0.011.	-0.059***	-0.036***	-0.053***	-0.022*	-0.047***	0.017***	0.008
<i>Taxa</i>									
<i>P. pipistrellus</i>	200	0.038**	-0.219***	-0.087***	-0.073***	0.028.	-0.109***	-0.007	0.027*
	500	0.014	-0.175***	-0.046**	-0.021	0.068***	-0.043*	-0.042***	0.034**
	700	0.026 .	-0.152***	-0.027.	-0.004	0.078***	-0.028	0.004	0.031**
	1000	0.043**	-0.174***	-0.027.	-0.021	0.050*	-0.072**	0.009	0.048***
<i>P. kuhlii</i>	200	0.069 .	-0.328***	-0.169***	-0.029	-0.150***	-0.037	0.078***	-0.036
	500	0.009	-0.255***	-0.120 .	0.062	-0.014	0.078	0.072***	-0.016
	700	-0.027	-0.300***	-0.148*	0.019	-0.022	0.048	0.052***	0.007
	1000	-0.061	-0.370***	-0.204**	-0.006	-0.030	0.021	0.045*	0.037
<i>E. serotinus</i>	200	0.081**	-0.706***	-0.353***	-0.346***	-0.062***	-0.346***	0.089***	-0.121***
	500	0.036	-0.436***	-0.140*	-0.190***	0.207***	-0.182***	0.116 *	-0.061*
	700	0.026	-0.703***	-0.411***	-0.357***	0.007	-0.345***	0.077***	-0.059*
	1000	0.029	-0.722***	-0.297***	-0.397***	0.013	-0.441***	0.099***	-0.023
<i>N. noctula</i>	200	-0.001	0.220	0.121	-0.486***	-0.235 .	-0.676***	0.025	0.153
	500	-0.001	-0.242	0.043	-0.556***	-0.319 .	-0.807***	0.022	0.204*
	700	-0.038	-0.197	0.0001	-0.678***	-0.204	-0.812***	0.175 .	0.212*
	1000	-0.028	-0.312	-0.060	-0.830***	-0.297	-0.996***	0.203*	0.167
<i>N. leisleri</i>	200	0.121	-0.600***	-0.161	-0.463***	-0.286**	-0.408***	0.065	0.198**
	500	0.133	-0.417**	-0.027	-0.390***	0.098	-0.329*	0.004	0.188**
	700	0.117	-0.571***	-0.137	-0.585***	-0.277*	-0.475***	0.067***	0.190**

	1000	0.093	-0.598***	-0.153	-0.638***	-0.320**	-0.551***	0.106 .	0.207**
<i>Myotis ssp.</i>	200	0.234***	-0.505***	-0.208*	-0.112	-0.070	-0.150 .	0.084 .	0.092 .
	500	0.214**	-0.526***	-0.109	-0.074	-0.068	-0.078	-0.097	0.130*
	700	0.225**	-0.527***	-0.081	-0.076	-0.067	-0.077	0.093 .	0.114**
	1000	0.213**	-0.553***	-0.062	-0.064	-0.056	-0.049	0.106 .	0.056

Fig.1 Standardized partial regression coefficients and associated standard errors from GLMMs model for the proportion of the Natura 2000 (*Natura 2000*), intensive agriculture (*Inten. Agri.*), forests (*Forests*), streams (*Streams*) and average luminance (*ALAN*) for the total relative abundance (a) and Community Specialization Index (b). The gray gradients correspond to the different buffer sizes. P-value level of significance associated are ‘***’ $P < 0.001$; ‘**’ $P < 0.01$; ‘*’ $P < 0.05$; ‘.’ $P < 0.1$.

Supplementary Material 1: Detailed information on the French Bat Monitoring Program (FBMP)

Table S1-1: Characteristics of the protocol and sampling design the two bat surveys

Aim of the program	Monitoring the temporal trends of bat populations at a national scale	
Car transect survey sampling protocol		
<i>Scope</i>	10 km around surveyors' home.	
<i>Circuit length</i>	30 km	
<i>Number of transect per circuit</i>	10	
<i>Transect length</i>	2 km separated of at least 1 km	
<i>Period of sampling</i>	from the 15 th of June to the 31 th of July and 15 August to 31 September	
<i>Weather conditions</i>	no rain, low wind speed (< 7 m/s), temperature > 12°C	
<i>Survey start</i>	as possible 30 minutes after sunset	
Count point survey sampling protocol		
<i>Scope</i>	square of 2km-side randomly chosen (by the Museum) in a radius of 10km from the observer's home, (i.e. on average one square randomly chosen between 80 possible squares).	
<i>Circuit length</i>	square of 2km-side	
<i>Number of point per circuit</i>	10	
<i>Recording duration</i>	6 minutes	
<i>Period of sampling</i>	from the 15 June to 31 July and 15 August to 31 September	
<i>Weather conditions</i>	no rain, low wind speed (< 7 m/s), temperature > 12°C	
<i>Survey start</i>	as possible 30 minutes after sunset	
Bat recording characteristics		
<i>Acoustic detectors</i>	Tranquility Transect Bat detector&D240x	
<i>Intercalibration of detectors</i>	At the MNHN	
Acoustic settings	Tranquility Transect	D240x
<i>Suppliers</i>	Courtpan Design Ltd, UK	Pettersson Elektronik
<i>High pass filter</i>	5 kHz	18 kHz
<i>Frequency</i>	96 000 sample/sec	96 000 sample/sec
<i>Recording device</i>	Zoom H2 digital recorder (Samson technologies, USA)	
<i>File storage format</i>	WAV	
Bat identification		
<i>Software</i>	Syrinx 2.6	
<i>Procedure</i>	<ul style="list-style-type: none">- Training: 2-day training course+ online self-training courses- Bat first identification: by volunteers- Bat identification validation: by MNHN	
<i>Taxon identification level</i>	Species level except for <i>Myotis sp.</i> Extensive data expertise evaluated that <i>Pipistrellus kuhlii</i> may potentially include 8 % <i>Pipistrellus nathusius</i> , as these two species overlap in their acoustic signatures.	
Meteorological data		
	<ul style="list-style-type: none">- Temperature (°C) and cloud cover (% in four classes: 0-25%, 25-50%, 50-75%, 75-100%) were recorded by volunteers during the survey.- Wind speed was also recorded by volunteers using Beaufort scale but this empirical categorical measure was not used in the analyses. However we used this field this measure to confirm the appropriateness of the use of the wind speed measure provide by the closest meteorological station.- Wind speed (km/h) and humidity (%) was provided by the closest meteorological station using the public archives the web site Infoclimat [http://www.infoclimat.fr/]	
Habitat data		
	Volunteers were involved in collecting habitat variable on a detailed and adapted hierarchical system (see hereafter).	

Figure S1-1: Example of one road circuit composed of 10 transects

Figure S1-2: Distribution of car transect surveys of the French national bat monitoring program

1. Assessment of potential biases in habitat sampling

We estimated biases occurring in our monitoring scheme at local and national scales. First, we compared the proportion of different habitats in the 10 km radius around observers houses in relation to the proportion within 200 meters buffer around each 2 km transect. Second, we compared to the proportion of different habitats at the French scale to the proportion in 200 meters buffer around each 2 km transect. We used Corine Land Cover data base. With one such sampling design, habitats surveyed are representative of the habitat at the local scale ($R^2=0.96$; Fig 2-S1) and the national scale ($R^2=0.95$; Fig 3-S1). The correlation is quite good especially for the commonest habitat and as expected the major difference occurred with rare habitats. The main bias is towards urban areas and particularly discontinuous artificial surfaces which in a 10 km radius around volunteer's house, represented 5% of habitat while in the sampled transect the proportion of this habitat reached 10%. The difference is similar when comparing the national habitat proportion to sampled habitat (3% vs 10%)

Fig. S1-3: Correlation between habitat proportion at local scale (10 km radius) and proportion sampled in the bat survey. Proportion of Corine Land Cover classes are log transformed.

Fig. S1-4: Correlation between habitat proportion at national scale and proportion sampled in the bat survey. Proportion of Corine Land Cover classes are log transformed.

The coverage of our 160 road circuits representing 1608 different transects was largely representative of French landcover (Table S1-2).

Table S1-2: The land-cover variables surrounding each transect at a range of spatial scales (200–1000 m), as well as their representativeness in mainland France Landscape. The variables are the proportions of Natura 2000 (*Natura 2000*), intensive agriculture (*Inten. agri.*), heterogeneous agriculture (*Heter. agri.*), deciduous forests (*Forests*), *Open Habitat* and mean length per hectare of roads (*Roads*) and streams (*Streams*) and the Artificial Light At Night (ALAN). The range represents the minimum and the maximum values encountered for each variable around transects at 1000m landscape-scale (similar range were observed for the 3 other landscape scales tested). Proportion of Natura 2000 were similar among landscape-scale, however a slight significant positive trend were detected ($P=0.03$).

Landscape Variables	Continental France	Transects (200 m)	Transects (500 m)	Transects (700 m)	Transects (1000 m)	Range (min-max)
	12.5	12.1	12.7	13.1	13.3	0-100
<i>Inten. agri. (%)</i>	28.1	32.5	34.0	34.3	34.9	0-100
<i>Heter. agri. (%)</i>	11.0	12.9	11.5	11.8	11.4	0-92
<i>Forests (%)</i>	19.9	18.6	24.7	20.7	21.2	0-100
<i>Open habitat (%)</i>	18.5	15.9	15.7	15.7	16.3	0-99
<i>Imper. surf. (%)</i>	5.2	11.3	8.74	7.3	6.5	0-92
<i>Roads (m)</i>	1.92	12.8	6.8	5.4	4.3	0-9391
<i>Streams (m)</i>	6.67	12.9	10.5	9.8	9.1	0-22262
<i>ALAN</i>	3.2	2.2	2.2	2.1	2.1	0.1-35

No obvious correlation ($\rho \geq 0.5$; Freckleton, 2002) was detected between landuse variables and Natura2000 (Table S1-3)

2. Assessment of potential bias of habitat characteristics between sampling within and outside Natura 2000 areas.

Because foraging activity of bats is not only influenced by the type of natural habitat type but also by small scale habitat characteristics in the agricultural landscape, such as the presence of linear elements like hedges (Limpens *et al.*, 1989; Krusic *et al.*, 1996; Verboom & Huitema, 1997; Downs & Racey, 2006), we have attempt to evaluate possible bias between sampling areas surveyed within and outside Natura 2000 areas. In forest habitat, we evaluated potential bias linked with the recording position: recording along forest paths or at forest edge.

2.1. Methods

2.1.1. Data

In the French national bat monitoring volunteers were involved in collecting habitat variable on a detailed and adapted basis. Habitat information is recorded on the first reconnaissance visit to the circuit. The appropriate habitat codes are chosen from an established hierarchical system which is very similar to widely use habitat code in bird monitoring schemes (see Crick 1992 for the UK and Barnagaud *et al.*, 2012 for the French monitoring), but adapted to take account of bat foraging specifics and particularly linear element (for more details about the French Bat monitoring see the website [<http://vigienature.mnhn.fr/page/relevés-d-habitats>]).

Volunteers are invited to record habitat characteristic every 400m along 2km transects. Currently more than 55% of circuits have been described by volunteers.

2.2.2. Statistical analysis

We assess the presence of potential sampling bias among areas within Natura 2000 designation or without using Generalized Linear Model (GLM) with a quasi-binomial error distribution.

In agricultural habitat, we test the possible difference of linear element within or without Natura 2000 areas according to agricultural habitat classes (Heterogeneous agricultural areas, Arable land, Pastures, Vineyards & orchard). We detect a slight trend of lower proportion of hedgerow within an Natura 2000 area (Table S1-3), not however that except for the Arable land the differences are quite weak.

Table S1-3: Probability to encounter a hedgerow, in the collected samples, according the fact being within or without a Natura 2000 area.

	Effect	P-value	Probability
<i>Arable land (n=454)</i>	$\beta=-1.460$	$P<0.0001$	Within Natura 2000 area: 0.09 Without Natura 2000 area: 0.28
<i>Heterogeneous agricultural areas (n=811)</i>	$\beta=-0.850$	$P<0.0001$	Within Natura 2000 area: 0.79 Without Natura 2000 area: 0.90
<i>Pastures (n=643)</i>	$\beta=-0.377$	$P=0.11$	Within Natura 2000 area: 0.85 Without Natura 2000 area: 0.89
<i>Vineyards & orchard (n=63)</i>	$\beta=-0.000$	$P=1$	Within Natura 2000 area: 0.50 Without Natura 2000 area: 0.50

In forest habitat, we evaluate the existence of potential bias of recording position (in forest path or in forest edge) among areas within Natura 2000 designation or without. This effect was adjusted to forest habitat classes (Broad-leaved forest, Coniferous forest, Mixed forest dominant broad-leaved, Mixed forest dominant coniferous). Except for the Coniferous forest (note the small sample) the differences are quite weak, even if statistically significant (table S1-4).

Table S1-4: Probability to being located in a forest path instead a forest edge, in the collected samples, according the fact being within or without a Natura 2000 area.

	Effect	P-value	Probability
<i>Broad-leaved forest (n=989)</i>	$\beta=0.465$	$P=0.009$	Within Natura 2000 area: 0.82 Without Natura 2000 area: 0.75
<i>Mixed forest dominant broad-leaved (n=572)</i>	$\beta=-0.603$	$P=0.04$	Within Natura 2000 area: 0.87 Without Natura 2000 area: 0.92
<i>Coniferous forest (n=55)</i>	$\beta=-16.99$	$P=0.9$	Within Natura 2000 area: 0.14 Without Natura 2000 area: 0.66
<i>Mixed forest dominant coniferous (n=263)</i>	$\beta=-1.331$	$P=0.02$	Within Natura 2000 area: 0.86 Without Natura 2000 area: 0.96

3. Device fastener

Fig S1-1: arrangement of the detector. The detector was fixed to the passenger-side window at a 45° angle so that the distance to road edges was similar all along the circuits

Recording characteristic

Bats calls were detected using a Tranquility Transect Bat detector (Courtpan Design Ltd, UK) and D240x (Pettersson Elektronik) and recorded on a Zoom H2 digital recorder (Samson technologies, USA). Before used all detector are calibrated at the French National Museum History in order to obtain the same level of sensibility. Signal from the condenser microphone of the bat detector was internally amplified and high pass filtered with a 5 kHz corner frequency and fed to the Zoom H2 which recorded it at 96 000 sample/s as PCM files. Sound was stored on Secured Card in Waveform Audio File Format more commonly known as WAV format, a format without compression. Tranquility Transect set to record 0.32 s of sound at x10 time expansion. Each recorded 0.32 s is followed by 3.2 s of playback, during which time the detector does not record. For the D240x the most similar storage time is 0.1 seconds of sound instead of 0.32, thus we performed a posteriori elimination of time expansion sequences that were spaces of less than 3.2 seconds. All ultrasound detectors were previously calibrated by the French National Museum of Natural History in order to have the trigger level.

Bat identification

Species acoustic identification was done by volunteer surveyors using Syrinx software version 2.6 (Burt 2006), followed by an identification validation by Museum experts. This approach allows identification difficulties to be highlighted, also volunteers become expert through training sessions (each year the museum offers free training for volunteers) and through some kind of self-training thanks to the corrected identification forms we send back.

Table S1-6: Identification error rate of volunteers after one training session

<i>Pipistrellus pipistrellus</i>	1.6 % (± 0.5)
<i>Pipistrellus kuhlii</i>	7.8 % (± 1.9)
<i>Nyctalus leisleri</i>	6.4 % (± 1.5)
<i>Eptesicus serotinus</i>	9.7 % (± 2.7)

Identifications were analyzed call by call and in the case of ambiguous call patterns, we encourage volunteers to use Scan'R (Binary Acoustic Technology, 2010) to isolate each bat vocalization and automate the measurement of relevant parameters (Russ 1999; Barataud

2012; Gannon *et al.*, 2004; Obrist *et al.*, 2004). The main relevant parameters used were: call duration (msec), time elapsed since between calls (msec), maximum frequency detected (Fmax, KHz), minimum frequency detected (Fmin, KHz), total bandwidth [Fmax - Fmin] (KHz), frequency at strongest sound pressure level (KHz), location of dominant Frequencies (% of total duration), high end of characteristic (KHz) [Similar to Fk], low end of characteristic (KHz) [Similar to Fc], global slope of the call (KHz per msec), time of the heel or High Fc (percent of duration), upper slope [start to High Fc] (KHz per msec), lower slope [High Fc to Low Fc] (KHz per msec), fundamental frequency (KHz), 2nd harmonic frequency (KHz), curvature measurement as a way to characterize the shape of bat calls, curve fit error parameter; a measurement of how much error exists between the curvature model and the actual shape of the call.

Each contact was assigned to the species level, however due to the lack of general consensus for some species about the acoustic criteria and some overlap between acoustic repertoires, it was not possible to assign the exact species with certainty for all calls; thus

- (i) we constructed a group for species from the *Myotis* genus. Note that some species included in the same group may have different ecology, however, from a foraging behavior perspective, these groups have some convergences. The *Myotis* group primarily included species considered to be gleaners, which capture the majority of their prey from substrates in cluttered environments (Arlettaz *et al.*, 2001). These species eat mainly diurnal brachyceran Diptera and non-volant arthropod such as weevils, lepidopteran larvae, harvestmen and spiders (Dietz *et al.*, 2007). In addition note that the group *Myotis* exhibit avoidance behavior to artificial light points such street lamp (Lacoeuilhe *et al.* 2014; Azam *et al.*, 2015). Among this *Myotis* ssp. group, the majority of *Myotis* identified at the species level were *Myotis daubentoni*.
-
- (ii) we estimate that among *P. kuhlii* may potentially include some *P. nathusii*, indeed these two species have some overlap between acoustic repertoires. Extensive validations with experts on more than 58% of the whole data indicate that probably less than 8% of the *P. kuhlii* identifications are not entirely certain and that it resides a small probability that it can be alternatively be *P. nathusius*. Note that these two species forage mostly on flying prey in open spaces (Dietz *et al.*, 2007) and are “attracted” by artificial light points such street lamp (Lacoeuilhe *et al.* 2014, Azam *et al.* 2015).

Table S1-7: composition of the *Myotis* spp category

Species	%
<i>Myotis alcathoe</i>	0.1
<i>Myotis bechsteinii</i>	0.2
<i>Myotis brandtii</i>	0.6
<i>Myotis capaccini</i>	0.0
<i>Myotis daubentoni</i>	34.7
<i>Myotis emarginatus</i>	0.5
<i>Myotis myotis</i>	1.8
<i>Myotis mystacinus</i>	1.9
<i>Myotis nattereri</i>	1.8
<i>Myotis puniclus</i>	0.0
<i>Myotis sp</i>	58.3

Bat activity measure

We stored the same bat signal with the two possible outputs of the detector: time expansion (t_{exp}) and high frequency (t_{hf}). Time expansion is the format widely used from the beginning of the FBMP and **bat activity index (name in this study relative abundance) is built with this format**. It is often possible to discern echolocation pulses from more than one individual bat in one sound interval, based for example on differing frequencies of maximum energy (F_{max}) and inter-pulse intervals between echolocation calls. Time expansion is used from the Bat Ireland monitoring (Roche et al. 2011) and in numerous countries through the *ibats* programs. With time expansion and with our setting each recorded 0.32 s is followed by 3.2 s of playback, during which time the detector does not record. High frequency outputs, is a continuous sound recording that allow considers the duration of bat call passes. Thus this measure is certainly a best descriptor of bat activity, however identification on this format it is very time consuming and require greater expert knowledge. Volunteers are not requested to identify high frequency format and thus very few identification of the FBMP come from this format. **This format was used to assess bat pass duration (Fig S1-2).**

Fig S1-2: Distribution of bat passes duration from the car transect survey (vertical axis are the number of bat pass)

With the bat detector setting, (each recorded 0.32 s is followed by 3.2 s), a detector is able to detect the following contact only 3.52s after the previous contact. This following contact could be either the same individual or another individual. However, according that (i) the car rolls at 25Km/h at the time of the recordings, 3.52 s mean that car is 25meters away (ii) the bat pass duration distribution (see Fig S1-2) and (iii) the distance of detection of bat (see Barataud 2015), **we hypothesize that multiple counts of the same individual may be rare and concern mainly *Nyctalus spp* and *E. serotinus*.**

Variation of the sampling between years

Fig S1-3 .Number of available transects surveyed per years

LITTERATURE CITED

- Azam C., Kerbiriou C., Vernet A., Julien J.F., Bas Y., Plichard L., Maratrat J., Le Viol I., 2015. Part-night lighting: an efficient measure to limit the impacts of light pollution on bats? *Global Changes Biol.* 21, 4333–4341.
- Barataud, M., 2012. *Ecologie acoustique des chiroptères d'Europe. Identification des espèces, études de leurs habitats et comportements de chasse.* Biotope, Mèze ; Muséum national d'histoire naturelle, Paris (collection Inventaires et biodiversité), 344 p.
- Barnagaud J.-Y., Devictor V., Jiguet F., Barbet-Massin M., Le Viol I., *et al.* 2012. Relating Habitat and Climatic Niches in Birds. *PLoS ONE* 7(3), e32819.
- Crick, H.Q.P. (1992): A bird-habitat coding system for use in Britain and Ireland incorporating aspects of land-management and human activity. *Bird Study* 39, 1-12.
- Dietz, C., Nill, D., Von Helvesen, O., Lina, P.H.C., Hutson, A.M., 2007. *Bats of Britain, Europe and Northwest Africa.* Franck-Kosmos Verlags, London, UK, pp. 400pp.
- Downs, N.C., Racey, P.A. 2006. The use by bats of habitat features in mixed farmland in Scotland. *Acta Chiropterologica* 8, 169-185
- Freckleton, R.P. 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *J. Anim. Ecol.* 71, 542–545.
- Gannon, W.L., O'Farell M.J., Corben, C., Bedrick, E., 2004. Call character Lexicon and analysis of field recorded bat echolocation calls. *Echolocation in bats and dolphins-* Edited by J.A. Thomas, CF Moss, and Vater. 2004. University of Chicago Press, Chicago, IL, USA, 604 pp.
- Krusic, R.A., Yamasaki, M., Neefus, C.D. and Pekins, P.J. 1996. Bat Habitat Use in White Mountain National Forest. *The Journal of Wildlife Management* 60, 625-631
- Lacoeuilhe A., Machon N., Julien J.F., Le BocqA., Kerbiriou C. 2014. The influence of low intensities of light pollution on bat communities in a semi-natural context. *PLOS ONE.* published 31 Oct 2014
- Limpens A.H., Helmer W., Van Winden A., and Mostert, K. 1989. Bats (Chiroptera) and linear landscape elements: a review of our present knowledge of the importance of linear landscape elements to bats. *Lutra* 32, 1-20

- Obrist, M.K., Boesch, R., Flückiger, P.F. 2004. Variability in echolocation call design of 26 Swiss bat species: consequences, limits and options for automated field identification with a synergetic pattern recognition approach. *Mammalia* 68 (4), 307-322.
- Russ J 1999. The Bats of Britain and Ireland: Echolocation Calls, Sound Analysis and Species Identification. Alana Books, Bishop's Castle. 103 p.
- Verboom, B., Huitema H. 1997. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecol.* 12, 117-125

Supplementary material 2: Detailed information on the calculation of specialization indices

In the French national bat monitoring volunteers were involved in recording habitat. Habitat information is recorded on the first reconnaissance visit to the circuit. The appropriate habitat codes are chosen from an established hierarchical system allowing describe more than 950 habitat type, which is very similar to widely use habitat code in birds monitoring schemes (see Crick 1992 for the UK and Barnagaud *et al.*, 2012 for the French monitoring), but adapted to take into account bat foraging specificities and particularly linear element (for more details about the French Bat monitoring see the website [<http://vigienature.mnhn.fr/page/relevés-d-habitats>]). Habitat classes are collected in a radius of 100m around the sampled point and grouped into 18 classes in order to obtain sufficient number of sample per class (for more methodological information see Julliard *et al.*, 2006; DeVicor *et al.*, 2008; Kerbiriou *et al.* 2010).

Specialization species index (SSI)

We quantified the species specialization index (SSI), which is the degree of habitat specialization for a species, as the coefficient of variation (SD/mean) of its densities across habitats following Julliard *et al.*'s approach (2006). SSI is thus independent to species habitat preferences. However, it is also possible to assess the species specializations to forest habitats by calculating the average density of a species inventoried in forest habitats divided by the average density in non-forest habitats.

Table S2-1: Habitat Specialization Index, NA indicates that data are insufficient for this species to allow a robust estimate of SSI.

Bat species	Habitat Specialization Index
<i>Barbastella barbastellus</i>	3.64
<i>Eptesicus serotinus</i>	1.50
<i>Myotis myotis</i>	NA
<i>Myotis daubentonii</i>	3.48
<i>Myotis mystacinus</i>	3.86
<i>Myotis nattereri</i>	2.40
<i>Nyctalus leisleri</i>	0.95
<i>Nyctalus noctula</i>	1.58
<i>Pipistrellus kuhlii</i>	0.75
<i>Pipistrellus nathusii</i>	3.06
<i>Pipistrellus pipistrellus</i>	0.54
<i>Pipistrellus pygmaeus</i>	1.79
<i>Plecotus sp (mainly austriacus)</i>	1.36
<i>Rhinolophus hipposideros</i>	NA

Assessment of bat community specializations indices

The Community Specialization Index (CSI) is calculated as the arithmetic mean of the species specialization index (SSI) of the species detected, weighted by the abundances (Julliard *et al.*, 2006).

$$CSI_j = \frac{\sum_{i=1}^n a_{ij} (SSI_i)}{\sum_{i=1}^n a_{ij}}$$

where n is the total number of species recorded, a_{ij} is the abundance of individuals of species i (with a SSI specialization index) in segment j (Devictor et al., 2008).

The CSI reflects the relative abundance of more or less specialized species in local assemblages and is therefore expected to decrease following the relative declines of specialists (species with a high SSI). For the analyses, we kept only site with a non-null abundance because a null CSI does not describe a generalist community.

LITTERATURE CITED

- Barnagaud J.-Y., Devictor V., Jiguet F., Barbet-Massin M., Le Viol I., et al. 2012. Relating Habitat and Climatic Niches in Birds. PLoS ONE 7(3), e32819. doi:10.1371/journal.pone.0032819
- Crick, H.Q.P. 1992. A bird-habitat coding system for use in Britain and Ireland incorporating aspects of land-management and human activity. *Bird Study* 39: 1-12
- Devictor, V., Julliard, R., Jiguet, F., 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* 117: 507–514.
- Julliard, R., Clavel, J., Devictor, V., Jiguet, F., Couvet, D., 2006. Spatial segregation of specialists and generalists in bird communities. *Ecol. Lett.* 9: 1237-1244.
- Kerbiriou, C., Bas, Y., Dufrêne, L., Robert, A., Julien, J.F., 2010. Long term trends monitoring of bats, from biodiversity indicator production to species specialization assessment. Society for Conserv. Biol. - 24th Annual Meeting, 3 - 7 July, 2010, Edmonton, Alberta, Canada.

Supplementary material 3: Description of the Natura 2000 network in France

The Natura 2000 network is regulated by two directives: following the Bird Directive of the European Union (79/409/EC), 384 Special Protection Areas (thereafter SPA, Fig.S1) were designated in France to protect endangered bird species, from 1986 onwards. The other Natura 2000 areas are Special Areas of Conservation (thereafter SAC, Fig.S2) which are defined following the Habitat Directive of the European Union (92/43/EEC) to protect non-bird animals and plant species and habitats listed in the Annexes I and II of this directive. These areas are identified as Sites of Community Importance (thereafter SCI, Fig.S2) and after approval of the European Union designated as SAC. To date, in France, *circa* the half of the 1369 SCI were further designated as SAC and thus effectively protected, since 2005. As a whole (SCI/SAC and SPA combined), the Natura 2000 networks represents 12.5% of the continental territory of France. After the designation phase occurring in 2000/2005, the Natura 2000 network is now engaged in a growing management process, based on management plans, voluntary measures and impact assessment prior to new human activities.

Figure S3-1. Location of the 384 Special Protection Areas (SPA) in France

Figure S3-2. Location of the 1369 Sites of Community Interest (SCI) to be designated as Special Areas for Conservation (SACs) by the European Union

Supplementary material 4: Detailed information on the variable Artificial Light at Night (ALAN)

We used radiance as a measure of ALAN as it is defined as the radiant flux (i.e., radiant power) reflected or emitted by a given surface. We used the VIIRS nighttime lights (2012) which is a 2-months composite raster of radiance data (in $\text{nW/ cm}^2 \text{ sr}$) collected by the Suomi NPP-VIIRS Day/ Night Band during 2 time-periods in 2012 (20 nights in total) on cloud-free nights with zero moonlight (Baugh et al. 2013). We then computed the average radiance within each buffer with the tool “Zonal statistics as Table” from the package “Spatial Analyst” (Fig. S1, see also Azam et al. 2016).

Fig. S1 Demonstration of the procedure done to calculate average radiance within the buffers of (a) 200 m, (b) 500 m, (c) 700 m and (d) 1000 m width from the VIIRS Nighttime Light raster used to. The average radiance was computed by the tool “zonal statistics as Table” from the package “Spatial Analyst” of ArcGIS 10.2 which proceed by creating a raster (yellow) from the polygon shapefile input (red) before applying an internal resampling so that input raster resolution match with the value raster resolution.

LITERATURE CITED

- Azam C., Le Viol I., Julien J.-F., Bas Y., Kerbiriou C. 2016. Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. *Landscape Ecol.* 31(10), 2471–248.
- Baugh K., Hsu F.-C., Elvidge C.D., Zhizhin M 2013. Nighttime lights compositing using the VIIRS day-night band: preliminary results. *Proc Asia-Pac Adv Netw* 35, 70–86

Supplementary material 5: Detailed information on statistical analysis

Table S5-1 Correlation coefficients of the 8 landscape variables included in the analysis (i.e. The variables are the proportions of Natura 2000 (*Natura 2000*), intensive agriculture (*Inten. agri.*), heterogeneous agriculture (*Heter. agri.*), deciduous forests (*Forests*), *Open Habitat* and mean length per hectare of roads (*Roads*) and streams (*Streams*) and the Artificial Light At Night (ALAN), at the 1000 m landscape-scale which showed the strongest the correlation coefficients between landscape variables.

	ALAN	Inten. agri	Heter. agri..	Forests	Open Habitat	Roads	Streams
<i>Natura 2000</i>	-0.25	-0.36	0.004	0.14	0.32	0.09	0.19
<i>ALAN</i>	.	-0.10	-0.14	-0.07	-0.39	0.13	0.02
<i>Inten. agri.</i>	/	.	-0.32	-0.46	-0.58	0.04	-0.30
<i>Heter. agri.</i>	/	.	/	-0.25	0.23	-0.007	0.09
<i>Forest</i>	/	.	/	/	-0.15	-0.02	-0.007
<i>Open Habitat</i>	-	.	-	-	-	0.06	0.33
<i>Roads</i>	/	.	/	/	-	/	-0.009

Table S5-2: Selected modelling and error distribution

Bat activity	Model	Error distribution	Non-linear effect included
Abundance	GLMM	Poisson	$date\ of\ survey^2 + minutes\ after\ sunset^2 + temperature^2$
Richness	GLMM	Poisson	$date\ of\ survey^2 + minutes\ after\ sunset^2 + temperature^2$
CSI	GLMM	Gaussian	$date\ of\ survey^2 + minutes\ after\ sunset^2 + temperature^2$
<i>P. pipistrellus</i>	GLMM	Poisson	$date\ of\ survey^2 + minutes\ after\ sunset^2 + temperature^2$
<i>P. kuhlii</i>	GLMM	Poisson	$date\ of\ survey^2 + minutes\ after\ sunset^2 + temperature^2$
<i>E. serotinus</i>	GLMM	Poisson	$date\ of\ survey^2 + minutes\ after\ sunset^2 + temperature^2$
<i>N. leislerii</i>	GLMM	zero-inflation, negative binomial	
<i>N. noctula</i>	GLMM	zero-inflation, negative binomial	
<i>Myotis ssp</i>	GLMM	Quasibinomial	$date\ of\ survey^2 + minutes\ after\ sunset^2 + temperature^2$

GLMM were performed using R package *lme4* (function *glmer*, *glmer.nb*); (2) indicated that we use a quadratic effect to fit nonlinear relationships. We found similar result when non-linear effects were performed with Generalized Additive Mixed Models (GAMM; Wood, 2006, R package *mgcv*) to handle nonlinear relationships between the response and some predictive variables; Zero-inflated model were performed using R package *glmmADMB* (function *glmmadmb*); quasibinomial were performed using R package *MASS* (function *glmmPQL*). Choice and validation of model were based on a multi-criteria approach (residual pattern, AIC, pseudo R^2) following Zuur et al. (2009).

Specific analyses according to the European Union Directives

Natura 2000 sites include two network: special protection area (SPA, i.e. sites designated under the European Union Directive on the Conservation of Wild Birds) and Sites of Community Importance, (SCI), i.e. sites designated under the European Union's Habitats Directive, also known as the Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora), we performed modelling at three level SPA, SIC and Natura 2000 sites (both together). SPA, SIC modelling were similar than performed in Table 1 and Table 2

Table S5-3: Partial regression coefficient of the raw Natura 2000 effect for the 3 community metrics and 6 taxa. P-value level of significance associated are ‘***’ P < 0.001; ‘**’ P < 0.01; ‘*’ P < 0.05; ‘.’ P < 0.1

<i>Bat activity metric</i>	<i>Natura 2000</i>	<i>SICs</i>	<i>SPA</i>
<i>Abundance</i>	$\beta = 0.220 \pm 0.035$ ***	$\beta = 0.196 \pm 0.02$ ***	$\beta = 0.142 \pm 0.040$ ***
<i>Richness</i>	$\beta = 0.130 \pm 0.052$ **	$\beta = 0.154 \pm 0.036$ ***	$\beta = 0.070 \pm 0.058$
<i>CSI</i>	$\beta = 0.061 \pm 0.020$ **	$\beta = 0.060 \pm 0.013$ ***	$\beta = 0.066 \pm 0.020$ **
<i>P. pipistrellus</i>	$\beta = 0.186 \pm 0.041$ ***	$\beta = 0.097 \pm 0.026$ ***	$\beta = 0.137 \pm 0.046$ **
<i>P. kuhlii</i>	$\beta = 0.113 \pm 0.128$	$\beta = 0.181 \pm 0.062$ **	$\beta = -0.278 \pm 0.153$.
<i>E. serotinus</i>	$\beta = 0.721 \pm 0.090$ ***	$\beta = 0.346 \pm 0.056$ ***	$\beta = 0.703 \pm 0.101$ ***
<i>N. noctula</i>	$\beta = -0.346 \pm 0.387$	$\beta = -0.105 \pm 0.235$	$\beta = -0.357 \pm 0.002$
<i>N. leisleri</i>	$\beta = 0.272 \pm 0.254$	$\beta = 0.488 \pm 0.159$ **	$\beta = 0.187 \pm 0.269$
<i>Myotis spp.</i>	$\beta = 1.372 \pm 0.209$ ***	$\beta = 0.694 \pm 0.141$ ***	$\beta = 1.368 \pm 0.233$ ***

Table S5-4: Standardized partial regression coefficients from GLMMs model for the proportion of SPA, SACs and Natura 2000 sites for the three community metrics and 6 taxa and at 4 landscape scales considered. P-value level of significance associated are ‘***’ P < 0.001; ‘**’ P < 0.01; ‘*’ P < 0.05; ‘.’ P < 0.1

	Scale	<i>Natura 2000</i>	<i>SICs</i>	<i>SPA</i>
<i>Abundance</i>	200	0.057***	0.045 ***	0.045 ***
	500	0.022*	0.024 .	0.025 *
	700	0.028*	0.023	0.036 **
	1000	0.030.	-0.009	0.033 **
<i>Richness</i>	200	0.002	0.022	-0.009
	500	-0.006	0.014	-0.013
	700	-0.009	0.010	-0.016
	1000	-0.013	-0.001	-0.019
<i>CSI</i>	200	0.016***	0.026 ***	0.016 *
	500	0.013*	0.024 ***	0.014 *
	700	0.013*	0.023 ***	0.015 *
	1000	0.011.	0.022 ***	0.013 *
<i>P. pipistrellus</i>	200	0.038**	-0.002	0.032 *
	500	0.014	-0.025	0.001
	700	0.026 .	-0.017	0.021
	1000	0.043**	-0.006	0.038 *
<i>P. kuhlii</i>	200	0.069 .	0.080 *	0.038
	500	0.009	0.066 .	-0.017
	700	-0.027	0.051	0.005
	1000	-0.061	-0.098 *	-0.031
<i>E. serotinus</i>	200	0.081	0.030	0.114 ***
	500	0.036	0.026	0.076 *
	700	0.026	0.021	0.057 .
	1000	0.029	0.034	0.051
<i>N. noctula</i>	200	-0.001	0.090	-0.011
	500	-0.001	0.123	0.006
	700	-0.038	0.114	-0.023
	1000	-0.028	0.142	-0.111
<i>N. leisleri</i>	200	0.121	0.056	0.116
	500	0.133	0.096	0.124
	700	0.117	0.121	0.077
	1000	0.093	0.094	0.050
<i>Myotis spp.</i>	200	0.234***	0.237 ***	0.191 ***
	500	0.214**	0.230 ***	0.220 **
	700	0.225**	0.280 ***	0.231 **
	1000	0.213**	0.229 **	0.255 ***

LITTERATURE CITED

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M. 2009. Mixed Effects Models and Extensions in Ecology with R. Statistics for Biology and Health, Springer, New York, USA. 574p.