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Disentangling effects of local and landscape variables on attractiveness of restored gravel-sand pits for bat foraging activities

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Abstract

Despite the impacts of extraction activities, quarries have great potential for conservation of biodiversity, and their restoration can be considered a major task in restoration ecology. A particularly important issue is to quantify the roles of the following various factors that may influence biodiversity and restoration success: (a) local variables, (b) landscape variables and (c) ecological management. Following a multi-model inference, we identify which variables were the most useful predictors of bat activity in gravel-sand pits. We used data from 21 French gravel-sand pits provided by the biodiversity-monitoring scheme, ROSELIERE. Our results suggest that within these restored gravel-sand pits, landscape variables appear to be better predictors of the attractiveness of restored gravel-sand pits for the foraging activity of bats than local variables. Species or community indexes appeared to be more sensitive to landscape variables measured at a large scale (i.e., 1,000 m). Among local variables, the time elapsed after operation was a better predictor of bat foraging activity than the description of the habitat itself. The effect was more obvious within a site with an elapsed time since operation greater than 10 years. Our findings suggest that to increase the attractiveness of gravel-sand pits for bat foraging activities, planning policies should consider not only the intrinsic characteristics of a project (i.e., local variables) but also the surrounding environment (i.e., landscape variables).

KEYWORDS
bat community, gravel-sand pit, quarry rehabilitation, scale effect, time of restoration

1 | INTRODUCTION

The large number of abandoned quarries represents a challenge for the restoration of these impacted habitats (Yuan et al., 2006). Quarrying operations have profoundly altered preexisting ecosystems: the original topography has changed, the organic soil has been removed and hydrological regimes could have been perturbed (Khawlie, Shaban, Awad, Faour, & Haddad, 1999; Shaban, El-Baz, & Khawlie, 2007). In many sites, the previous ecological functions have been irreversibly disrupted (Milgrom, 2008), and trying to restore the past state may sometimes be impossible (McDonald & Dixon, 2018). By offering substitution habitats, postmining sites may provide a haven for various taxa (Benes, Kepka, & Konvicka, 2003; Bizoux, Brevers, Meerts, Graitson, & Mahy, 2004; Brändle, Durka, & Altmoos, 2000; Dekoninck, Hendrick, Dethier, & Maelfait, 2010; Dolezalova, Vojar, Smolova, Solsky, & Kopecky, 2012; Harabis, 2016; Kerbiriou et al. 2018b; Krauss, Alfert, & Steffan-Dewenter, 2009; Šálek, 2012; Tropek et al. 2010; Vojar et al., 2016), particularly in intensively human-dominated landscapes (Tropek et al. 2010). According to the potential conservation value of these postindustrial sites, restoration

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management of quarries is now an important task in global restoration ecology (Tischew & Kirmer, 2007).

Restoration intervention can vary along a gradient from passive approaches based on unassisted regeneration to active approaches, including seeding, planting native species or restoring topography or hydrological regimes (Holl & Aide, 2011). In terms of management, several studies have underlined that ecological gains were greater in the case of passive restoration based on natural evolution than when restoration was essentially based on human intervention through reclamation works (Brändle et al., 2000; Hodacova & Prach, 2003; Prach, Řehounková, Řehounek, & Konvalinková, 2011; Šálek, 2012; Tropek et al., 2012; Tropek & Konvicka, 2008). Some authors highlight expensive costs associated with active restoration (Catteral and Harrison Catterall & Harrison, 2006), while others suggest that passive restoration is laden with unrecognised costs and only slowly reaches its objectives (Zahawi, Holl, & Reid, 2014). The debate is still ongoing, but Prach and del Moral (2015) suggest that criteria to choose between passive, intermediate (Uebel, Wilson, & Shoo, 2017) and active restoration may depend on the landscape. Yet, relatively few studies have simultaneously considered within site (i.e., local variables such as habitat, age, etc.) and landscape variables (surrounding habitats, distance to habitat source, landscape connectivity…etc.) (see Tropek et al., 2010). A better understanding of the relative importance of local and landscape variables could help to mediate the choice between passive and active restoration and to define targets while taking into account the surrounding landscape.

In addition to the restoration strategy, success also depends on target species and their specific traits: rareness, habitat or food specialisation (Bezombes, Kerbiriou, & Spiegelberger, 2019; Krauss et al., 2009; Tropek et al., 2010). Some studies highlight the importance of the time since the end of the exploitation as a criteria of recovery success on species richness, such as birds (Šálek, 2012), terrestrial plants (Prach et al., 2011, 2013) or butterflies (Benes et al., 2003), while some others did not detect any age-related effect; see Brändle et al. (2000) on dwelling beetle richness or Krauss et al. (2009) on wild bee richness, which identified a habitat variable as the best predictor of recovery success.

Disentangling the relative effects of local and landscape variables could allow a better account of the cumulative impacts on species and habitats resulting from the additive effects of several projects operating in the same region (Bezombes, Gaucherand, Kerbiriou, Reinert, & Spiegelberger, 2017). Such information could improve the sizing of offset measures according to the choice of the restoration processes, their efficiency and the surrounding landscape (Bezombes et al., 2019).

We determined which variables, local- (i.e., age, habitat type) or landscape-scale (i.e., surrounding habitat areas or distance to a major resource), were the most useful predictors of bats activity (species relative abundance, richness, community specialisation indexes) in 21 French gravel-sand pits. We chose to focus on bats, this group being increasingly threatened worldwide (Mickleburgh, Hutson, & Racey, 2002). In the European Union, all bat species are strictly protected by the Habitats Directive (Council of the European Union 1992), throughout the life cycle of a development project, including quarries, developers must demonstrate that they will establish mitigation measures to prevent, reduce and compensate for impacts that result in any loss of bat foraging habitats (Bezombes et al., 2017). The purpose of this study is therefore to highlight the most important variables to consider during the rehabilitation of quarry sites to optimise the biodiversity potential.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in France between 2009 and 2013 and involved the survey of 21 gravel-sand pits (Figure 1). Data were provided by ROSELIERE, a biodiversity-monitoring scheme implemented in quarries (for more detail see: Data S1 and Kerbiriou et al. 2018).

The exploitation of these gravel-sand pits often results in the formation of a water body due to the underlying presence of the water table. The aquatic surface represents an average of 42% of the total pit area.

The dataset included quarries at different stages of their life cycle, allowing for the testing of the influence of local characteristics: 17% were quarries under operation, while the others were quarries under rehabilitation, with an ecological purpose (Table 1). Rehabilitation was based on passive restoration, and a spontaneous succession process occurred, leading to the presence of various semi-natural habitats, such as grasslands, wetlands, bushes and woods.

In order to maintain an equal sampling effort between sites, we adjusted the number of sampled points per site (from 1 to 5 points, mean 3.6 ± 0.3) according to the sites size (mean 74.8 ha ± 2.1). Therefore, the density of points sampled by sites is of the same order of magnitude as that recommended by the French Bat Monitoring Program (FBMP, 2012, for more detail on the FBMP count point survey see Kerbiriou et al. 2019a). Points were spaced out by 200 m to avoid, as much as possible, contacting the same bat at different points. Sampled points were relatively close to aquatic habitats (mean average distance to water 202 m ± 68 (SE). Between 2009 and 2013, a total of 547 samples were performed.

2.2 | Local and landscape variables

We tested the effect of environmental variables on bat activity using variables describing local characteristics and variables describing the surrounding landscape.

Local characteristics, which relate to the different stages of the quarries' life cycle and vegetation dynamics, were noted in the field in a homogeneous patch of habitat (within a radius of 50 m around the recording point, in accordance with the maximum distance of detection for the most commonly contacted species in this region, Kerbiriou et al. 2019b). They were defined in two ways: (a) as a categorical variable with five categories of seminatural habitats (bare soil, seminatural grassland, bush (shrubs smaller than 7 m), woodlands (trees taller than 7 m), and water bodies (with water present predominantly over the year)) and (b) as a categorical variable with four categories describing

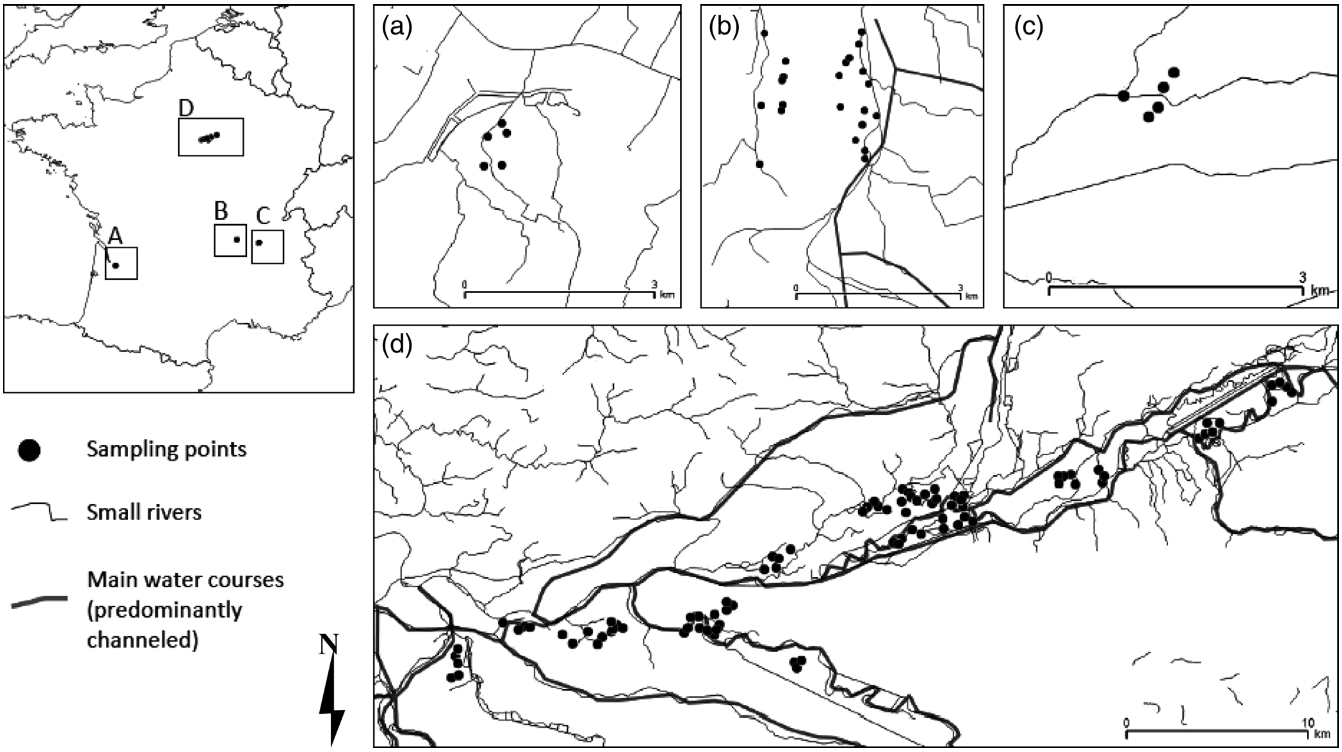

FIGURE 1 Map of the gravel-sand pits sites of ROSELIERE program and sampled points

TABLE 1 Local characteristics of sites sampled

Seminatural habitat	
Bare soil	80
Seminatural grassland	211
Bush	19
Woodland	35
Waterbody	202
Gravel-sand pit state	
During quarrying	95
Restoration states <5 years	77
Restoration states 5 << 10 years	164
Restoration states >10 years	211

the gravel-sand pit state (during quarrying and three categories of rehabilitation according to the time elapsed after operation [<5 years; 5 << 10 years; >10 years]).

At the landscape scale, we selected land-use variables that are known to influence bat activity. We computed the proportion of the following 9 land-use variables in a 1,000-m buffer around the recording points using CORINE Land Cover (http://www.eea.europa.eu/data-and-maps): (a) discontinuous artificial surfaces; (b) mineral extraction sites are expected to negatively influence bat activity due to the loss of semi-natural habitat (Kerbiriou et al. 2018a; Russo & Ancillotto, 2015); (c) arable land is related to agriculture intensification and is identified as one of the major pressures on bats (Walsh & Harris, 1996; Jaberg & Guisan, 2001; Azam, Le Viol, Julien, Bas, & Kerbiriou, 2016); (d) pastures; (e) heterogeneous agricultural areas; (f) land principally occupied by agriculture with significant areas of natural vegetation; (g) broad-leaved forest were included because they include different proportions of semi-natural habitat that could potentially benefit bats (Walsh & Harris, 1996; Boughley et al. Boughey, Lake, Haysom, & Dolman, 2011, Azam et al., 2016); and two variables describing aquatic habitats; (h) water courses (in the study area, the main water course was channeled) and (i) bodies of water—because they are identified as key habitat for many bat species (Rainho, 2007; Salvarina, 2016; Walsh & Harris, 1996). These continuous variables represent the most important habitats of the studied area, covering an average of 96% of the total 1,000 m buffer area (min, 71%: max:100%). According to the fact that distance to water is among the variables regularly identify for improves drastically the accuracy of bat abundance modelling (Rainho & Palmeirim, 2011; Santos et al. 2013; Sirami et al. 2013), we included in our analysis the distance to nearby water bodies or rivers using BD Cartage (IGN, http://professionnels.ign.fr/bdcarthage).

2.3 | Design sampling

2.3.1 | Bat sampling

Bats were surveyed using standardised echolocation recordings, a robust method for assessing the relationship between bat activities and the corresponding habitat (Stahlschmidt & Brühl, 2012). We followed a similar protocol to the one designed for the French Bat Monitoring Program (see Kerbiriou et al. 2018a). Echolocation calls were automatically detected using a Tranquility Transect Bat detector (Courtpan Design Ltd, UK) and recorded over 6 min on a Zoom H2 digital recorder (Samson technologies) at a sampling rate of 96 ks/s from the two possible outputs of the detector: time expansion (1.28 s of sound at ×10 time expansion) and high frequency. Bat activity was assessed using the high-frequency output, and the time expansion output was used only for species emitting echolocation calls >48 kHz. All ultrasound detectors were previously calibrated by the French National Museum of Natural History in order to have the same sensitivity levels and enable the detection of echolocation calls while minimising background noise due to wind or insects (for more detail see Kerbiriou et al. 2018a). In each plot, echolocation recordings were carried out in two visits corresponding to peaks of bat activity: once during the 15th June to 31st July period, during which females are expected to feed their offspring; and second, during the 15th August to 30th September period, during which individuals are expected to be less dependent on their reproductive roost. All points of a site were sampled during the same night. Within each site, the sampling of each 6 min points occurred early in the night (not earlier than 30 min after dusk and no later than 3 hrs after dusk, thus corresponding to peak bat activity, with such design, time effect on bat abundance is drastically reduce, see Pauwels et al., 2019, Mimet, Kerbiriou, Simon, Julien, & Raymond, 2020). Observers sampled bats only when weather conditions were favourable (no rain, temperature higher than 12°C and wind speed lower than 5 m/sec).

2.3.2 | Bat identification

We used Adobe Audition and Syrinx software version 2.6 (Burt, 2006) for spectrogram and spectral analysis. We manually identified bat echolocation after isolating each bat vocalisation and extracting relevant parameters (for more details see Kerbiriou et al. 2018b) using Scan'R (Binary Acoustic Technology, 2010). Species were identify at the species level except for two genera: *Plecotus* sp., for which there is a lack of consensus about the acoustic criteria for identification at the species level (Barataud, 2015; Obrist, Boesch, & Flückiger, 2004) and *Myotis* sp. because of the very low occurrence of each single *Myotis* species and some uncertainties in acoustic identification at the species level (Barataud, 2015; Obrist et al., 2004).

2.3.3 | Bat activity measurements

Distinguish individuals from echolocation calls is currently impossible, so we measured an index of relative bat activity defined as the mean number of bat passes per species over 6 min (following Kerbiriou et al. 2019a for the definition of a bat pass). This definition of bat activity is a commonly used measure of relative bat abundance. Although a bat could be detected more than once, bat activity measured over a short time (6 min) is highly correlated with the number of recorded individuals flying is a site (Mimet et al., 2020). The response variables were (a) relative abundance of bat passes of the most abundant species recorded (*Pipistrellus pipistrellus* (Schreber, 1774), *Pipistrellus kuhlii* (Kuhl, 1817), *Pipistrellus nathusii* (Keyserling & Blasius, 1839), *Nyctalus noctula* (Schreber, 1774), *Nyctalus leisleri* (Kuhl, 1818), and *Myotis* ssp.), (b) total relative abundance of bat passes, (c) species richness, (d) Community Habitat Specialization Index (CSI) and (e) Community Specialization to Forest (CSF).

The CSI is a mean trait community index based on the average habitat specialisation of each species present in the community. Each species was characterised for habitat specialisation through the calculation of a Species Specialization Index (SSI). The SSI varied between 0.54 and 3.86 (Table S2 in Data S2). The Community Habitat Specialization Index (CSI) is calculated as the arithmetic mean of the SSI of the detected species weighted by their relative abundances (Data S2).

We calculated the Community Specialization to Forest (CSF) index as the arithmetic mean of the species specialisation to forest habitat (SSF) weighted by their relative abundances. The SSF was the average density of a species in forest habitats divided by its average density in non-forest habitats. It was calculated using the French Monitoring of Bat Populations data, (see Regnery, Couvet, Kubarek, Julien, & Kerbiriou, 2013, Data S2).

2.4 | Data analysis

We tested the effect of local and landscape variables on bat activities using a generalised linear mixed model (GLMM, R package lme4). The response variable was either species relative abundance (n = 7 taxa) or bat community metrics (total relative abundance, richness, CSI, CSF). The explanatory variables were the two local variables (seminatural habitat and gravel-sand pit state) and the ten landscape variables (nine land-use variables and the distance to closest water). We added as covariables the temperature, the season and the year (as a factorial variable) because we assumed that bat activity might be influenced by weather conditions (Ciechanowski, Zajac, Bilas, & Dunajski, 2007) and because we can expect changes in bat relative abundance among periods of the bat life cycle and between years. We also hypothesised that close points, even if their habitats are different, may likely have a similar bat population density due to similar climatic conditions or large-scale landscape compositions. Thus, we included a site effect, and we added an autocovariate (i.e., a distance-weighted function of neighboring response values; Dormann et al. 2007, function autocov_dist package spdep, Bivand R. et al.) with the aim to account for spatial autocorrelation. According to the hierarchical structure of our sampling design (same sites were sampled year to year), we treated the variable 'site' as a random effect, while considering the other explanatory variables as fixed effects (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). For the total relative abundance, rather than summing in a unique metric the raw data of abundance of each species, we included species identity as random intercepts to account for non-independence of observations corresponding to the same species (see Donald et al., 2007; Gamero et al., 2017; Pierret & Jiguet, 2018). The explanatory variables were centered and standardised so that the regression coefficients were comparable in magnitude (Schielzeth, 2010). According to the nature of the response variable (i.e., count data), we used a negative binomial error distribution (Zuur et al., 2009) to model relative abundance, total relative abundance, and richness. Because the *N. noctula* model did not fit well, we transformed the response variable (i.e., relative abundance) to presence/absence and then used a binomial error distribution. For CSI and CSF, we used a Gaussian error.

Thus, our global models were structured as follows:

[Bat activity] ~ local variables + landscape variables + season + temperature + year + autocovariate + 1|Site,where bat activity could be the relative abundance of a bat species (n = 7) or total relative abundance, or richness or CSI or CSF.

Following a multi-model inference (Burnham, Anderson, & Huyvaert, 2011; Grueber, Nakagawa, Laws, & Jamieson, 2011), we generated a set of candidate models containing all possible variable combinations. We ranked them using the Akaike information criterion corrected for a small sample using the *dredge* function (R package MuMIn). We only built models complying with the following conditions: (a) models do not include more than five variables to avoid overparameterisation, (b) models do not include simultaneously correlated covariates (R^2 > 0.5 or non-independent variables such as habitat or

TABLE 2 Species detected and number of contacts

Species	Number of contact(s)
Myotis alcathoe	1
Myotis brandtii/mystacinus	1
Myotis emarginatus	2
Myotis daubentonii	40
Myotis sp.	83
Myotis spp. total	127
Nyctalus leisleri	106
Nyctalus noctula	82
Eptesicus serotinus	21
Pipistrellus kulhii	50
Pipistrellus nathusii	86
Pipistrellus pipistrellus	829
Plecotus spp.	4

TABLE 3 Relative importance of each variable (i.e., relative values of each variable calculated as a sum of the AICc weights over the set of top models in which the term appears)

	P. pipistrellus	*P. kuhlii*	*P. nathusii*	*E. serotinus*	*N. leisleri*	*N. noctula*	*Myotis spp.*	Richness	Total relative abundance	CSI	CSF
Local landscape variables											
Seminatural habitat	—	—	—	—	—	—	—	—	—	—	—
Gravel-sand pit state	28	—	—	—	—	—	88	92	100	100	—
Landscape scale variables											
Disc. Artificial	—	—	—	17	24		82	10	5	—	—
Min. Extraction	—	31	—	—	14	100	22	—	78	—	—
Arable	—	—	—	70	—	—	—	15	—	—	—
Past.	—	—	64	22	—	67	19	8	20	—	—
Hetero. Agri.	24	17	—	46	—	33	88	100	49	—	—
Agri. Natural.	—	100	44	100	48	—	—	—	—	—	—
Wood.	—	—	—	35	—	—	—	—	—	—	—
Channel	100	18	17	—	—	—	24	100	100	100	33
Water bodies	—	—	—	70	11	100	—	—	17	—	—
Dist. Water	72	100	100	—	89	100	—	—	—	—	—
Covariables											
Autocovariate	—	100	40	—	100	—	19	9	15	100	100
Year	100	—	100	—	—	—	—	100	—	—	—
Season	100	56	100	66	100	100	72	12	36	—	—
Temperature	76	54	6	49	90	—	—	10	13	—	—

Abbreviations: Agri. natural., land principally occupied by agriculture, with significant areas of natural vegetation; Arable, arable land; Channel, water courses, in the study area, the main water course is channeled; Disc. artificial, discontinuous artificial surfaces; Dist. Water, distance to closest water bodies or river; Hetero. Agri., heterogeneous agricultural areas; Min. extraction, mineral extraction sites; Past., pastures; Water, bodies of water; Wood, broadleaved forest.

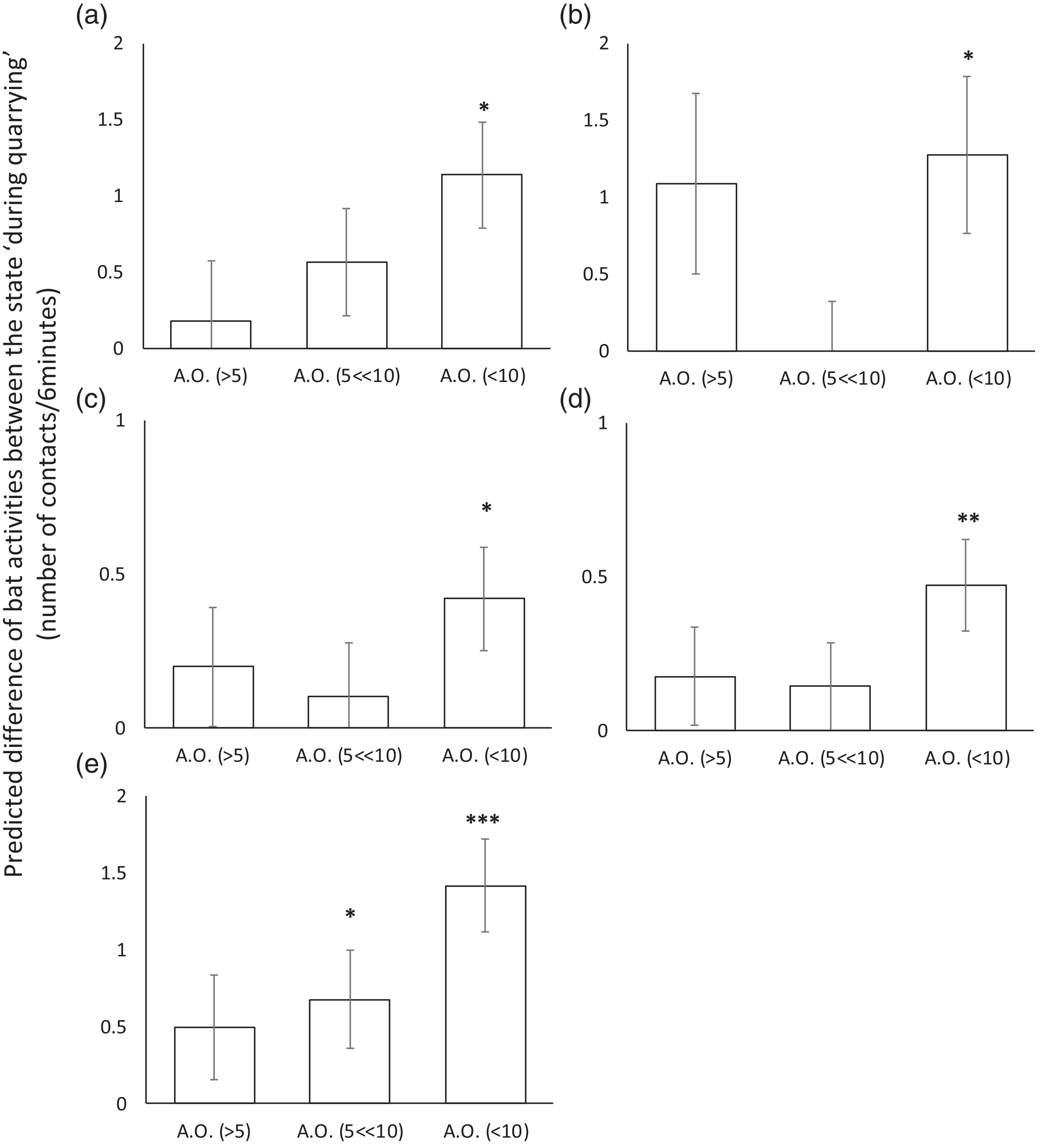

FIGURE 2 Predicted difference of bat activities between the state 'during quarrying' (i.e., the intercept) and the three gravel-sand pit restoration states (<5 years; 5 <<10 years; and > 10 years). *P. pipistrellus* relative abundance (a), *Myotis* spp. relative abundance (b), richness (c), community habitat specialization index (d) and the total relative abundance of foraging calls (e). (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $p < 0.1$)

gravel-sand pit state, that is, there is rarely water bodies and woodland at the state 'during carrying', while when rehabilitated >10 years the more common local habitats are water bodies and woodland see Data S1). For each set of candidate models, we did multi-model inference averaging on a delta AICc <2 using the *model.avg* function (Table S3 in Data S3) to obtain an averaged regression coefficient for each fixed effect (R package MuMIn). Finally, we performed variance-inflation factors (VIF, vif function, package car) on each top model (Fox & Monette, 1992). Because all variables showed a VIF value <3, and the mean of VIF values was <2, there was no striking evidence of multicollinearity (Chatterjee, Hadi, & Price, 2000). All analyses were performed using R statistical software v 3.1.5.

3 | RESULTS

A total of 1,542 bat passes belonging to 11 species were recorded on the 21 gravel-sand pit sites (Table 2). According to the recording

TABLE 4 Conditional average estimate and adjusted SE of the effect of landscape variables on bat activity

	P. pipistrellus	P. kuhlii	P. nathusii	E. serotinus	N. leisleri	N. noctula	Myotis	Richness	Total relative abundance	CSI	CSF
	β_{cond}	β_{cond}	β_{cond}	β_{cond}	β_{cond}	β_{cond}	β_{cond}	β_{cond}	β_{cond}	β_{cond}	β_{cond}
Disc. Artificial				.441 ± .433	−.557 ± .284*		−.527 ± .204**	−.056 ± .070	.008 ± .130		
Min. Extraction		−.486 ± .278			−.427 ± .288	−.446 ± .213*	.333 ± .132*	.019 ± .060	−.198 ± .105		
Arable				−1.016 ± .467*				−.067 ± .052			
Past.			−1.394 ± 0.716	.621 ± .414		−1.109 ± .890	.859 ± .430*	.053 ± .086	.225 ± .178		
Hetero. Agri.	.079 ± .157*	.384 ± .284				−.376 ± .238	.949 ± .211***	.150 ± .066*	.217 ± .136		
Agri. Natural.		.733 ± .186***	.400 ± .156*	.738 ± .319*	−.515 ± .262				−.020 ± .088		
Wood.				.964 ± .449*							
channel	−.566 ± .168***	.497 ± .409	−.614 ± .308*				−.436 ± .274	−.239 ± .081**	−.562 ± .139***	−.207 ± .072**	−.036 ± .013**
Water bodies				−.878 ± .469	.430 ± .318	−.452 ± .197*			.103 ± .124		

Notes: For abbreviations, see Table 3 legend. (***$p < .001$, **$p < .01$, *$p < .05$, $p < .1$).

sampling (547 records of 6 minutes each), the mean bat activity was 28 bats passes/hr (min:0 to max: 850 bat passes/hr). The majority of echolocation calls from the 11 bat species came from three *Pipistrellus* bat species (Table 1).

3.1 | Effects of local variables

Among the two local variables, only the gravel-sand pit state appeared in the set of the top models (Table 3, see also Data S3). When this variable was selected, the relative importance was only of concern for community metrics (richness, CSI and total relative abundance) and not for taxa except for the *Myotis* spp. group (Table 3). The difference between the 'during quarrying' state and the three other states was only significant for the older state (>10 years elapsed after operation), which exhibited greater relative abundance (Figure 2).

3.2 | Effects of landscape variables

Among the 11 bat activity metrics tested, the proportion of mineral extraction sites within a radius of 1,000 m had a strong negative effect on *N. noctula*, a slight negative but non-significant effect on the total relative abundance and a positive effect on *Myotis* spp. (Table 3, see also Data S3); however, it is noteworthy that the relative importance of this variable for *Myotis* spp. was very weak (Table 3). For the other highly anthropised habitats present in the sites' surroundings (proportion of discontinuous artificial surfaces), we identified a strong negative effect on *N. leisleri* and *Myotis* spp. While the distance to water had a strong negative effect on *P. pipistrellus*, *P. nathusii*, *P. kuhlii*, *Myotis ssp.*, *N. leisleri* and *N. noctula* (Table 4). Therefore, the farther away the surrounding water was from the site, the lower the relative abundance of those species. However, we did not detect any effect of the distance to water on bat community metrics (Table 4). Surprisingly, the proportion of watercourses exhibited a strong negative effect on *P. pipistrellus*, *P. kuhlii* and all the community metrics (Table 4). Moreover, bodies of water never exhibited any strong effect, except on *N. noctula*. Arable land negatively influences *E. serotinus* relative abundance, whereas land principally occupied by agriculture with significant areas of natural vegetation positively influences *P. kuhlii*, *P. nathusii* and *E. serotinus*, and heterogeneous agricultural areas positively influenced *P. pipistrellus*, *Myotis* ssp. and richness. Pastures had a weak positive effect on *Myotis* ssp. Finally, broadleaved forest exhibited a positive influence on *E. serotinus* only.

4 | DISCUSSION

4.1 | Local variable effect

The local variable based on habitat type was not a good predictor of bat activity, whereas the gravel-sand pit state appeared to be a better predictor but mainly for community metrics. This result suggests that within these gravel-sand pit sites in the process of rehabilitation, the time elapsed after operation is a better predictor of bat activity and gives more information than the description of the habitat itself. Whatever the bat activity considered – relative abundance of *P. pipistrellus* or *Myotis* spp., richness, Community Habitat specialisation index, the total relative abundance of foraging calls—the effect is more obvious within a site with an elapsed time since operation of greater than 10 years.

This result found in previous analysis (Kerbiriou, Parisot-Laprun, & Julien, 2018) is still robust when this effect is adjusted to landscape variables. This result is consistent with other studies that also highlighted the positive influence of aged quarries on the richness of species such as birds (Šálek, 2012) or terrestrial plants (Prach et al., 2011, 2013), but it contrasts with studies that found a negative effect, such as Benes et al. (2003) on butterflies, or studies that did not detect any age-related effects (Brändle et al. (2000) on dwelling beetle richness, Krauss et al. (2009) on wild bee richness. In the latter, although the authors tested an age gradient of over 120 years, effective habitats were the best predictors. These contrasting findings among taxa are probably linked to their habitat requirements, and bee and butterfly communities are most likely favoured by open habitats such as grasslands present in the early stages of succession; while birds and bats need more wooded habitats that require more time to develop. In our study, the bat guild did not include open specialised species: habitat-specialist species were linked to wetlands (*M. daubentonii*, *P. nathusii*) or woodlands (*N. noctula*). In addition, as trees grow and age, they may have cavities that birds or bats could use to nest and harbor insects that are prey for these insectivores (Regnery et al., 2013). The time lag (<10 years) to detect a significant effect on bat activity highlights the need for offset policies to consider the dimension of time between project impacts and gains provided by offset measures (McKenney & Kiesecker, 2010). Such results highlight the need of proactive approaches that assess ecological possibilities very far upstream of development projects are needed to better adapt development projects to ecological equivalence principles (i.e., equivalence between impact sites and offsets sites, Bezombes et al., 2017).

4.2 | Landscape variable effect

At the landscape scale, distance to the closest waterbody or river (*Dist. water*) and the proportion of watercourses channeled in a 1,000-m buffer (*Channel*) are among those we identified with the greatest number of strong effects and relative importance (Tables 3 and 4). Numerous studies based on acoustic methods and carried out on the species studied here, identified aquatic habitat as favourable and where species relative abundance is greater (Rainho & Palmeirim, 2011; Russ & Montgomery, 2002). However, in our study, the three variables linked to the aquatic habitat showed contrasting effects: (a) the proportion of bodies of water in a 1,000-m buffer (*Water bodies*) did not exhibit any strong effects on bat activity, (b) the proportion of water courses channeled in a 1,000-m buffer (*Channel*) exhibited a strong negative effect and no positive effect and (c) the distance to the closest water body or river (*Dist. water*) exhibited a strong negative effect, that is, the greater the distance to water, the lower the bat total relative abundance. These results seem somewhat contradictory. The effect of distance to the closest water body or river is congruent with many studies (Barré et al., 2019; Rainho & Palmeirim, 2011). The apparent contradiction between distance to water (*Dist. water*) and the proportion of water courses channeled in a 1,000-m (*Channel*) could be explained by the fact that, in our study, the proportion of water courses was extracted from the CORINE Land Cover shape were the water courses digitalised are mainly wide, channeled rivers (i.e., with artificialised banks) and consequently probably of lesser ecological interest (see Corbacho & Sánchez, 2001). Second, the accuracy of the two types of variables used was not similar: *Channel* is assessed using CORINE Land Cover, whose precision is very limited (minimum unit of 25 ha), whereas the distance to water was calculated using BD Cartage with a metric spatial resolution. Thus, differences in response patterns could be linked to spatial data quality or to the lack of precision concerning the ecological characteristics of the water courses or bodies analysed (small ponds with natural banks are considered by the distance of the water variable vs. the proportion of water habitats variable, which includes only large bodies of water or channeled rivers).

4.3 | Disentangling the relative importance of local and landscape variables

Among the 11 bat activity measures, local variables performed equally than landscape variables for *Myotis* spp. and total relative abundance and never performed better than landscape variables (Table 3). Thus, in our study, landscape variables appear to be better predictors of the attractiveness of gravel-sand pits for the foraging activity of bats than local variables. This importance of landscape variables is consistent with the requirements of the species studied. Indeed, their home range matches with a radius ranging from 400 to 1,000 m (see Davidson-Watts & Jones, 2005 for *P. pipistrellus* and Flaquer et al., 2009 for *P. nathusii)*. Lacoeuilhe, Machon, Julien, and Kerbiriou (2016) studied the effect of landscapes on bat activity and showed a positive scale effect: the set of species we studied here appeared to be more sensitive to large-scale variables (i.e., 1,000 m) rather than ones at a smaller scale. Our findings suggest that, with the aim of increasing the attractiveness of rehabilitated gravel-sand pits for bat foraging activities, planning policies should consider not only the intrinsic characteristics (i.e., local variables) of a new quarrying project but also the surrounding landscape (i.e., landscape variable), particularly when defining the conditions for the restoration process. One way of doing that could consist of adopting a proactive approach for the implementation of offsets. In such frameworks, biodiversity offsets of different projects could be used jointly with the aim to restore connectivity between those postexploitation sites and seminatural or natural habitats at the landscape scale and, in turn, reach a functional level of this restored habitat (i.e., a size in accordance with home-range requirements, see Quétier, Regnery, & Levrel, 2014). Bearing in mind that different companies finance these individual quarry projects, so the provision of connectivity by aggregation and layout of biodiversity offsets of different projects requires the existence of an efficient coordination at the landscape/regional scale. Such coordination could potentially be effective through the implementation of a 'market'-type nature mitigation banking system (Vaissière & Levrel, 2015); however, several studies provide empirical evidence of the risks of this system (BenDor, Riggsbee, & Doyle, 2011; Hannis & Sullivan, 2012; Robertson, 2009; Robertson & Hayden, 2008). Another way could be to mobilise tools dedicated to land-use planning by national/regional governments, such as regulations regarding ecological corridors at national scale (e.g., Polish legislation in an amended Nature Conservation Act of October 16, 1991, Kozieł, Jędrzejewski, & Górny, 2010; and French regional ecological coherence scheme Act of July 12, 2010, Billon et al., 2017) or at the EU scale.

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CONFLICT OF INTEREST

The authors have declared that no competing interests exist.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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