

Deciduous trees increase bat diversity at stand and landscape scales in mosaic pine plantations

Yohan Charbonnier · Pierre Gaüzère ·
Inge van Halder · Julien Nezan · Jean-Yves Barnagaud ·
Hervé Jactel · Luc Barbaro

Received: 30 September 2014 / Accepted: 14 July 2015 / Published online: 28 July 2015
© Springer Science+Business Media Dordrecht 2015

Abstract

Context In heterogeneous landscapes, habitat complementation is a key process underlying the distribution of mobile species able to exploit non-substitutable resources over large home ranges. For instance, insectivorous bats need to forage in a diversity of habitat patches offering varied compositions and structures within forest landscape mosaics to fulfill their life cycle requirements.

Objectives We aimed at analyzing the effects of forest structure and composition measured at the stand and landscape scales on bat species richness, abundance and community composition in pine plantation forests of south-western France.

Methods We sampled bat communities at different periods of the summer season using automatic

ultrasound recorders along a tree composition gradient from pine monocultures to pure oak stands. We analyzed bat species activity (as a proxy for bat abundance) and species richness with linear mixed models. Distance-based constrained ordinations were used to partition the spatio-temporal variation in bat communities.

Results Deciduous tree cover increased bat activity and modified community composition at both stand and landscape scales. Changes in bat communities were mostly driven by landscape-scale variables while bat activity responded more to stand-scale predictors.

Conclusions The maintenance of deciduous trees at both stand and landscape scales is likely critical for bat communities living in fast-growing conifer plantations, by increasing the availability and diversity of prey and roosting sites. Our study suggests that bats respond to forest composition at both stand and landscape scales in mosaic plantation landscapes, mainly through a resource complementation process.

Electronic supplementary material The online version of this article (doi:[10.1007/s10980-015-0242-0](https://doi.org/10.1007/s10980-015-0242-0)) contains supplementary material, which is available to authorized users.

Y. Charbonnier · I. van Halder · J. Nezan ·
H. Jactel · L. Barbaro (✉)
INRA, UMR 1202 BIOGECO, 33610 Cestas, France
e-mail: luc.barbaro@pierroton.inra.fr

Y. Charbonnier · I. van Halder · J. Nezan ·
H. Jactel · L. Barbaro
UMR 1202, BIOGECO, Univ. Bordeaux, 33600 Pessac,
France

P. Gaüzère
Institut des Sciences de l'Evolution, UMR CNRS-UM2
5554, 34095 Montpellier, France

J.-Y. Barnagaud
Ecoinformatics and Biodiversity, Department of
Biosciences, Aarhus University, 8000 Aarhus, Denmark

J.-Y. Barnagaud
CEFE UMR 5175, CNRS - Université de Montpellier,
EPHE, 34293 Montpellier, France

Keywords Bat communities · Chiroptera · Complementation · Mixed forests · Mosaic landscapes · South-western France

Introduction

Forest landscape mosaics are currently submitted to a widespread loss of habitat heterogeneity triggered by the intensification of forest management, notably where native tree mixtures are replaced by fast growing conifer plantations (Brockerhoff et al. 2008; Pawson et al. 2013). In such landscapes devoted to production forests, insectivorous vertebrates of high trophic levels such as birds and bats face a large-scale homogenization of their habitats (Nájera and Simonetti 2010; Le Viol et al. 2012; Cisneros et al. 2015). The residual presence of deciduous fragments within landscapes dominated by a heavily managed conifer matrix can however contribute to the maintenance of diverse insectivore communities that include species of conservation concern (Estades and Temple 1999; Barbaro et al. 2008; Jung et al. 2012; Meynard et al. 2014). Although temperate forest bat communities include several taxa of high conservation value (Boughey et al. 2011; Stone et al. 2013), only few studies to date have investigated how they respond to deciduous tree cover in conifer-dominated plantations (Rodríguez-San Pedro and Simonetti 2013; Meynard et al. 2014).

How habitat structure and composition influence the diversity and composition of forest bat communities remains largely unexplored. However, bats are increasingly acknowledged as natural enemies that contribute significantly to the regulation of insect pests (Kunz et al. 2011; Charbonnier et al. 2014). Within plantation stands, tree species identity as well as tree diversity per se are likely to enhance bat diversity through increased habitat heterogeneity and cascading effects on prey abundance and diversity (Tews et al. 2004). Deciduous trees host a richer arthropod fauna and more microhabitats providing more suitable roost sites for bats than conifers (Regnery et al. 2013; Müller et al. 2014). Moreover, the accessibility of prey and roost sites varies with tree density, height and understorey cover, with different effects expected among bat species and functional guilds (Jung et al. 2012; Müller et al. 2013). As food availability and roost density are two key resources for temperate bats,

embedding deciduous trees within conifer stands is expected to enhance the diversity and persistence of bat communities (Russo et al. 2010; Boughey et al. 2011).

In mosaic landscapes, bats can modify their foraging behaviour and adjust their home range size across seasons in order to match resource location and phenology (Akasaka et al. 2009; Klingbeil and Willig 2010). However, studies that quantify the effects of stand and landscape structure and composition on bat communities are generally restricted to the breeding period (Boughey et al. 2011; Ethier and Fahrig 2011; Meynard et al. 2014). Assessing changes in bat habitat use across the entire summer season may highlight temporal variations in their resource requirements (Frey-Ehrenbold et al. 2013; Cisneros et al. 2015). Bats are known to use different habitats within mosaic landscapes to find non-substitutable resources across seasonal life cycles, mainly through a process of landscape complementation (Dunning et al. 1992). Despite evidence that resource complementation is a key process of habitat selection at the landscape scale in birds (Brotans et al. 2004; Barbaro et al. 2008; Mueller et al. 2009), there is still a lack of knowledge regarding the importance of this landscape-level process for insectivorous bats in mosaic landscapes (Ethier and Fahrig 2011).

We investigated how the occurrence of oaks (*Quercus* spp) at both stand and landscape scales in a matrix of planted maritime pines (*Pinus pinaster*) modifies the composition and diversity of bat communities across the summer season. We asked the following questions: (i) does deciduous tree cover and forest structure measured at stand or landscape scales affect bat species richness, abundance and community composition? (ii) what are the relative effects of the two spatial scales considered? and (iii) does the effect of deciduous tree cover change during bat life cycle in accordance with seasonal requirements?

Methods

Study area

We set our study in an intensively managed plantation forest spanning ca 10,000 km² in the Landes de Gascogne, south-western France. It is a low-elevation region (50 m a.s.l.) with a thermo-atlantic climate

where landscapes are dominated by plantations of native maritime pine *P. pinaster*. These plantations are managed with a rotation cycle of 40–50 years, creating mosaics dominated by even-aged, pure pine stands interspersed with herbaceous clearcuts, heathlands, firebreaks and sandy tracks. In addition to remnant riparian forests, small and isolated fragments of deciduous woodlands dominated by *Quercus robur*, *Q. pyrenaica* and *Betula pendula* represent the only patches of deciduous forest habitats within the pine plantation matrix (Barbaro et al. 2008).

Stand-scale habitat variables

We sampled 21 forest stands, located at least 0.8 km apart from each other and selected along a gradient of pine-oak mixtures ranging from pine monocultures to pure oak stands (Appendix S1). In each stand, we defined a circular plot with a radius of 50 m matching the theoretical maximum range of bat ultrasound recorders, and located at least 100 m from stand margins to avoid edge effects on bat activity (Bellamy et al. 2013). We inferred the level of pine-oak mixture as the percentage cover of deciduous trees within a given stand, as measured by tree basal areas. We visually assessed percentage vegetation cover in four vertical strata (<0.5, 0.5–2, 2–16 and 16–32 m). We quantified stand structure using four variables supposed to be relevant for bats: mean basal area of deciduous trees, tree height recorded as the mean height of the 10 highest trees, Shannon's diversity index of stratification based on the percentage cover of the four strata and number of standing dead trees (Russ and Montgomery 2002; Müller et al. 2013; Regnery et al. 2013).

Landscape-scale habitat variables

We GIS-mapped land cover with high resolution aerial orthophotographs of the study area from summer 2012 and calculated the area covered by four land use types: pine plantations, deciduous woodlands, open habitats (e.g., firebreaks, pastures, crops) and urban areas within buffers of 250 and 500 m centred on each stand. We also computed a Shannon index of landscape diversity using the proportions of the four habitat types as descriptors of landscape composition. The spatial extents of landscape buffers encompass mean bat home range sizes and can be considered relevant to explain bat species distribution (Bellamy et al. 2013).

Preliminary analyses revealed that the two buffer sizes display similar results; hence, we only present further those obtained with the 500 m radius.

Bat sampling

We sampled bat communities with automatic ultrasound bat detector systems (Sound Meter SM2Bat, Wildlife acoustics) fitted with multidirectional microphones. Timers were set up to record all night long, from 1 h before sunset to 1 h after sunrise. We sampled bats in each of the 21 stands in 2012 during two consecutive nights, avoiding rain, wind speeds >30 km h⁻¹ and temperatures lower than 10 °C. We repeated this sampling scheme three times, in May during the gestation period, in June during the suckling period and in late August when individuals disperse before the swarming and overwintering periods. A trained operator (YC) identified bat calls using dedicated softwares (Sonochiro v3.2.3 and Batsound 4.1) based on identification keys (Barataud and Tupinier 2012) and a regional atlas of bat distribution (Ruys and Bernard 2014). We achieved species level identification for most calls, but we had to pool four pairs of closely-related species to avoid misidentification: *Myotis* spp (Myosp), *Pipistrellus kuhlii* and *P. nathusii* (KuhlNat), *Plecotus austriacus* and *P. auritus* (Plesp) and *Eptesicus serotinus* and *Nyctalus leisleri* (Nyctaloid). We approximated bat species abundance as the total number of bat passes per species, i.e., bat species activity (Jung et al. 2012). A bat pass was defined as a sequence of two or more pulse calls, separated from other calls by at least one second (Jung et al. 2012). Prior to data analyses, we applied species-specific coefficients to account for the variation in species detection rates according to call frequency (Barataud and Tupinier 2012).

Data analyses

We tested the effects of forest structure and composition at the stand scale on bat activity and species richness using linear mixed models. We accounted for the hierarchical structure of data (repeated sampling periods for each stand) by adding stand identity as a random effect on the intercept of all models. As our response variables exhibited large variability between two consecutive nights, we averaged bat activity per species, stand and sampling period, and log-

transformed the mean bat activity to approach normality. In addition to standard data quality checks, we assessed the homoscedasticity of residual errors. The models were based on the following structure:

$$Ba = \alpha + (\beta DecidCov + \gamma Stratif + \delta Dt + \varepsilon Th) \times \varphi Sp + (1|stand)$$

where the response variable (Ba) was the bat activity or the species richness per stand and the stand-level explanatory variables were proportion of deciduous forest cover ($DecidCov$), stratification diversity index ($Stratif$), number of dead trees (Dt) and tree height (Th). All explanatory variables were tested in interaction with the sampling period (Sp). We ranked all possible sub-models nested within this maximum model structure using AICc (Burnham and Anderson 2002), and considered that the best model had to be separated from others by at least two AICc units. If several model structures were retained, we accounted for uncertainty in model selection by computing model-averaged parameter estimates, considering a variable as significant if its 95 % confidence interval did not bracket zero (Burnham and Anderson 2002; Grueber et al. 2011). We further computed the Relative Variable Importance (RVI) of each predictor as the sum of AICc weights over all the selected models (Barton 2015).

We tested the effects of landscape composition on bat activity and species richness using a similar model structure and model selection procedure:

$$Ba = \alpha + (\beta DecidCov + \gamma OpHab + \delta UrbHab + \varepsilon LandDiv) \times \varphi Sp + (1|stand)$$

where the response variable (Ba) was the bat activity per stand or the species richness per stand, the landscape explanatory variables were deciduous forest cover ($DecidCov$), open habitat cover ($OpHab$), urban area cover ($UrbHab$) and landscape diversity ($LandDiv$) within 500 m-buffers.

We compared the effects of stand and landscape variables on bat community composition based on a multivariate analysis of the species-stand data table. We used distance-based Redundancy Analysis (dbRDA) (Legendre and Anderson 1999; Anderson and Willis 2003) to partition the effects of habitat variables at stand and landscape scales. We first performed dbRDA to estimate the separate effects of stand- and landscape-scale variables. Then, we tested the joint effects of the two spatial scales in a global dbRDA. In all analyses, we introduced sampling

period as a covariate. Finally, we performed several partial dbRDA with variation partitioning to decompose the variance explained by independent and joint effects of stand variables, landscape variables and sampling period (Anderson and Cribble 1998; Legendre et al. 2005). The total amount of explained variance was then partitioned into seven fractions: independent effect of stand variables (a); independent effect of landscape variables (b); independent effect of sampling period (c); joint effect of stand and landscape (d); joint effect of stand and sampling period (e); joint effect of landscape and sampling period (f); joint effect of the three sets of variables (g) (Legendre et al. 2005). We also performed these analyses for each sampling period separately, considering only three fractions: independent effect of stand variables, independent effect of landscape variables and joint effect of stand and landscape variables. We performed significance tests for each term assessed sequentially and marginal tests (marginal term in a model with all other terms as covariables) to analyze separately the effect of each predictor (Walsh and Mac Nally 2015). The significance of each effect was assessed with Monte Carlo permutation tests (9999 permutations). We performed all analyses with lme4, MuMin, hier.part and vegan R-packages (Grueber et al. 2011; Barton 2015; Walsh and Mac Nally 2015).

Results

Effect of deciduous tree cover on bat activity and richness

We recorded 107,999 passes identifiable to species or species pair level. Among them, 56,224 (52 % of the identifiable passes) were attributed to *Pipistrellus pipistrellus*, 42,692 (39.5 %) to *P. kuhlii/nathusii*, and 4378 (4 %) to nyctaloids. The remaining 4.5 % corresponded to *Myotis* spp (2976 passes), *Barbastella barbastellus* (752), *Plecotus* spp (720), *Rhinolophus hipposideros* (180), *Rhinolophus ferrumequinum* (50) and *Nyctalus noctula* (27). At the stand scale, a higher proportion of oaks increased bat activity while other variables were non significant (Figs. 1, 2; see also Appendix S1, S3). Bat species richness did not respond to any stand-level variable (Fig. 2; Appendix S3), but was significantly lower in May and June than in August (Fig. 2; Appendix S3). At the landscape scale, bat

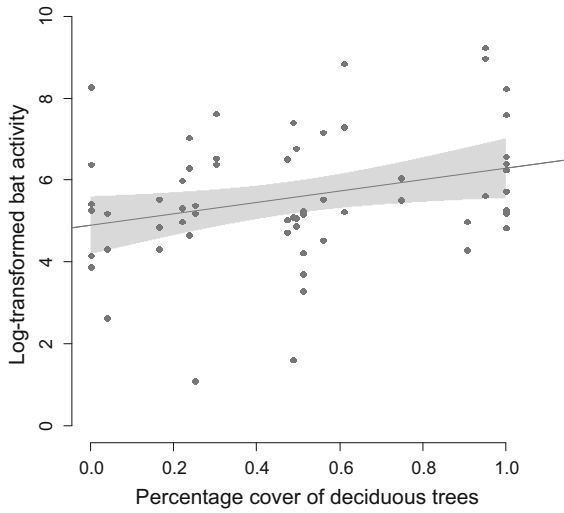


Fig. 1 Log-transformed bat activity as a linear function of deciduous tree cover measured by tree basal area at the stand scale. Grey area refers to the 95 % confidence interval

activity and richness were not significantly affected by any single variable (Fig. 3). However, bat activity was significantly lower in June than in the other sampling periods (Fig. 3; Appendix S2, S3) and there was a significant interaction between deciduous tree cover and sampling period with a positive effect of deciduous trees on bat activity in May (Fig. 3).

Effect of deciduous tree cover on bat communities

Deciduous tree cover and sampling period were the main variables driving the ordination of bat communities (Fig. 4; Appendix S4). Bat species such as *P. austriacus/auritus* and *P. kuhlii/nathusii* were associated with low deciduous tree cover at both stand and landscape scales on the ordination axes, while other species (nyctaloids, *R. ferrumequinum*, *R. hipposideros*, *N. noctula*, *Myotis* ssp, *B. barbastellus* and *P. pipistrellus*) were associated with mixed to oak-

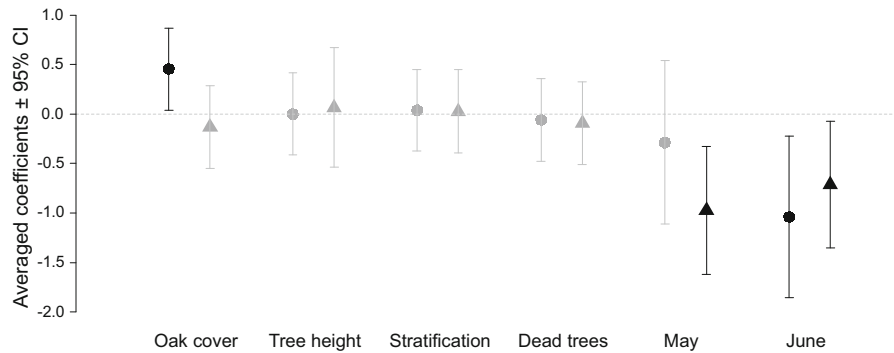


Fig. 2 Estimates (\pm confidence intervals) of coefficients for the stand-level variables selected by model averaging for bat activity (circles) and bat species richness (triangles). Significant effects are indicated in black

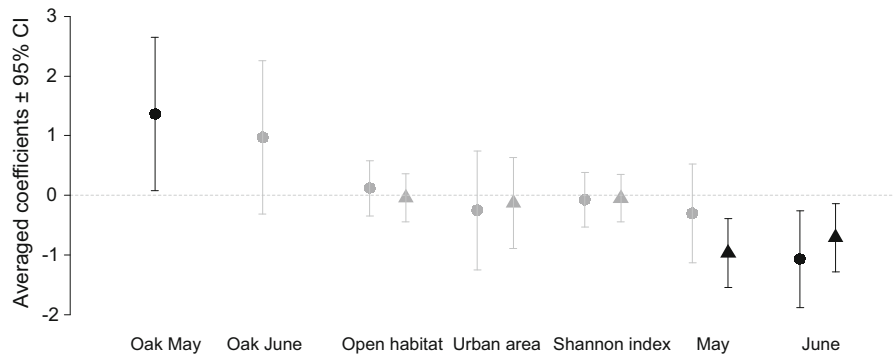


Fig. 3 Estimates (\pm confidence intervals) of coefficients for the landscape-level variables selected by model averaging for bat activity (circles) and bat species richness (triangles). Significant effects are indicated in black

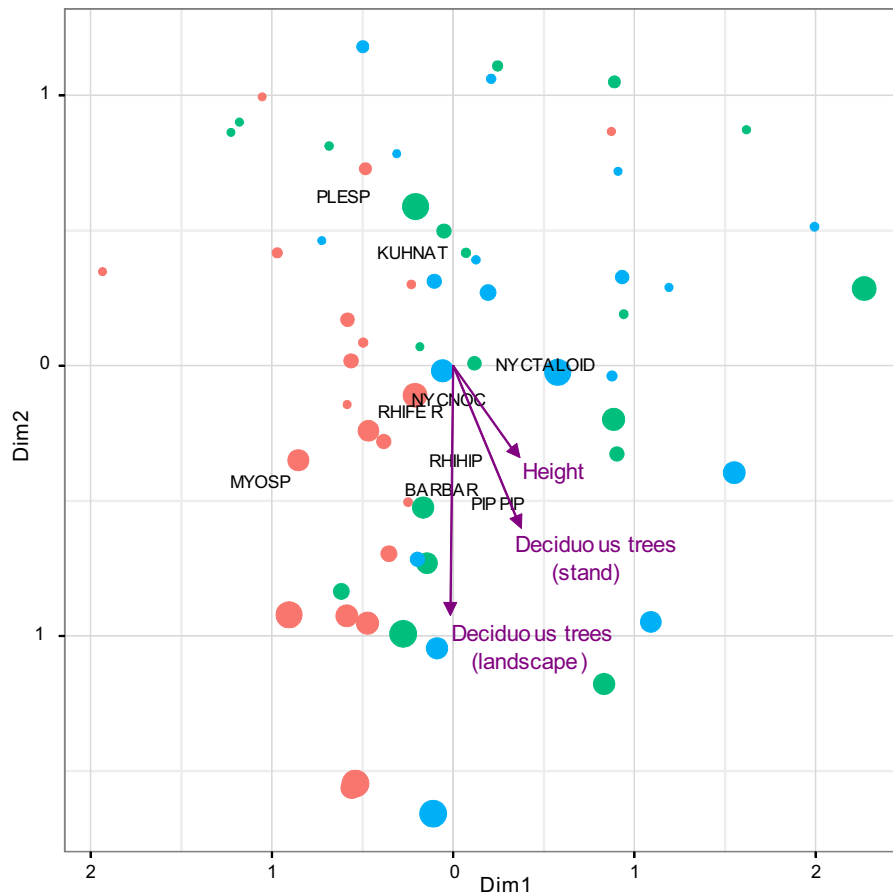


Fig. 4 dbRDA ordination biplot of bat communities according to stand and landscape variables. Significant environmental predictors (see Appendix S4) are indicated by purple arrows. Stand-scale percentage cover of deciduous trees is proportional to dot size and dot colour indicates sampling period (blue May; green June; red August). Abbreviations of species or species

pairs are as follows: PLESP *Plecotus* spp; KUHNAT *Pipistrellus kuhlii*/*P. nathusii*; NYCTALOID *Eptesicus serotinus*/*Nyctalus leislerii*; RHIFER *Rhinolophus ferrumequinum*; MYCNOC *Nyctalus noctula*; RHIHIP *R. hipposideros*; MYOSP *Myotis* spp; BARBAR *Barbastella barbastellus*; PIPPIP *P. pipistrellus*. (Color figure online)

dominated stands and landscapes. At the stand scale, mean tree height influenced significantly bat community composition together with the oak-pine mixture gradient: *Myotis* spp, *Plecotus austriacus/auritus* and *P. kuhlii/nathusii* were less abundant in stands with taller trees contrary to nyctaloids. Bat community composition was similar in May and June but changed in August with increasing occurrence of *Myotis* spp while nyctaloids decreased (Fig. 4).

Variance partitioning

Taken together, the set of variables explained 12.7 % of the total variation in bat communities (Fig. 5).

Variance partitioning indicated that the separate effects of stand variables, landscape variables and sampling period were all significant at $P < 0.05$ (Monte Carlo tests with 9999 permutations). Sampling period accounted for the highest part of variation (5.5 %, $P < 0.01$), followed by landscape-scale variables (5.1 %, $P < 0.05$) and stand-scale variables (3.8 %, $P < 0.05$). The independent effect (after removing the joint effects of the two other sets of variables) of sampling period explained more variance (6.2 %, $P < 0.01$) than landscape (3.1 %, $P < 0.05$) and stand variables (1.7 %, $P < 0.05$). The joint effect of stand and landscape variables explained 2.4 % of the total variance, and the parts of variance explained

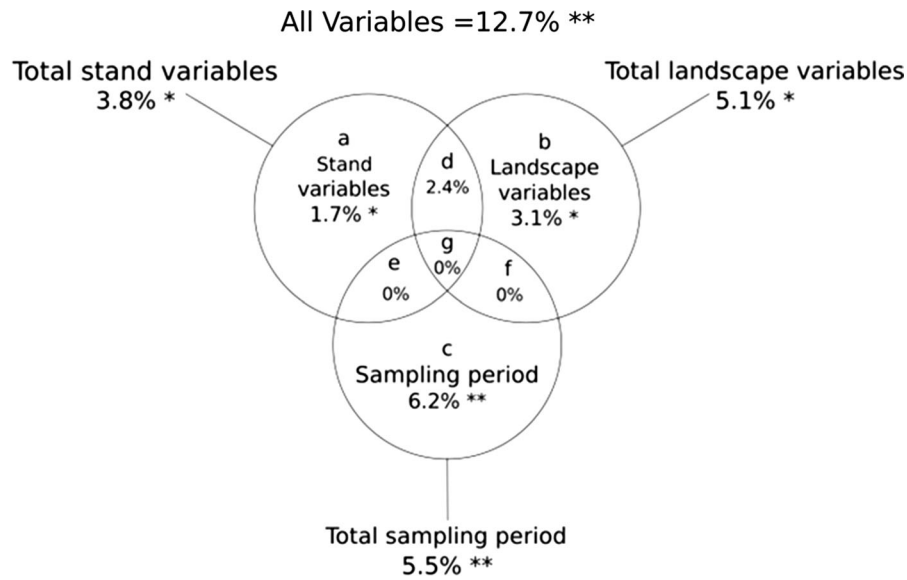


Fig. 5 Variance partitioning in percentage of variation in the bat species-stand data matrix explained by a set of partial dbRDAs (adjusted R squared) for three set of explanatory variables: stand variables, landscape variables and sampling period. *a*, *b* and *c* are separate effects of stand variables,

landscape variables and sampling period, respectively; *d*, *e*, *f* and *g* are fractions indicating their joint effects. Significance was assessed with Monte Carlo permutation tests (9999 permutations): *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, *ns* non-significant

by other combinations of variables (*e*, *g* and *f*) were null (Fig. 5).

Discussion and conclusion

Most European bat species use woodlands to some extent for foraging or roosting, but their responses to forest structure and composition measured at several scales is still poorly documented (Ethier and Fahrig 2011; Boughey et al. 2011). Here, we showed that bat diversity was influenced by deciduous tree cover at both stand and landscape scales in pine plantation mosaics. Bat species activity increased with deciduous tree cover at the stand scale to reach a maximum in pure oak stands, while bat communities mainly depended on landscape composition. Deciduous forests are known to hold higher insect prey diversity and availability (Russ and Montgomery 2002; Boughey et al. 2011) and more microhabitats for roosting than conifer forests in Europe (Ciechanowski 2005; Müller et al. 2014). Even anthropophilous bat species like serotine bat *Eptesicus serotinus* or common pipistrelle *P. pipistrellus* are known to forage more actively in the presence of deciduous trees than

conifers (Boughey et al. 2011; Fuentes-Montemayor et al. 2013). Foraging requirements, more than roosting needs, are thus likely to explain the positive effect of stand-level oak cover on bat activity. The percentage of deciduous trees at landscape and stand scales also modified bat community composition towards more diverse assemblages including rarer species such as the lesser horseshoe bat *R. hipposideros* or the common noctule bat *N. noctula*, which are virtually absent from pine monocultures. However, higher oak cover at either stand or landscape scales did not significantly increase bat species richness. These results are consistent with previous studies showing that bat species richness is similar in plantations and unmanaged forests in spite of high species turnover (Harvey and Gonzalez Villalobos 2007; Meynard et al. 2014). However, deciduous stands have comparatively higher conservation value because they favour the occurrence of endangered species, including *B. barbastellus*, *R. hipposideros*, *R. ferrumequinum*, *Myotis emarginatus* and *M. myotis* (Russo et al. 2004; Ruys and Bernard 2014).

In the study area, bat activity increased with deciduous tree cover at the landscape scale only in the early summer season (May). Bat local occurrence

is mainly determined by prey availability, while the amount of habitat and the distance to roosting sites have more influence on their occurrence at the landscape scale (Bellamy et al. 2013). Bats rely on spatially scarce or clustered resources such as prey aggregates (Müller et al. 2012; Charbonnier et al. 2014) and roosting cavities (Rainho and Palmeirim 2011). Consistently with other studies (Meynard et al. 2014), our results indicated that the composition of bat communities was more affected by surrounding landscape composition than stand-scale attributes. Deciduous forest patches within a pine-dominated landscape matrix likely provide a larger range of prey and microhabitats to bats through a complementation process acting at the landscape scale (Dunning et al. 1992; Brotons et al. 2004; Barbaro et al. 2008). Bats actually have to deal with marked seasonal changes in their foraging and roosting sites which are highly clustered in favourable microhabitats. As a consequence, they tend to use larger and more heterogeneous home ranges in space and time than other forest predatory vertebrates such as passerine birds, sometimes more limited in their movements by conifer plantations (Villard and Haché 2012). Individual bats need to adjust their foraging strategies all year long in accordance with seasonal variability in abiotic conditions and prey abundance (Cisneros et al. 2015). For instance, in summer, females face higher energetic demands to feed their offspring, matching the peak in insect prey abundance (Crichton and Krutzsch 2000). Home range size is therefore reduced to a short range around the roost site during that critical period (Klingbeil and Willig 2010). By contrast, bats forage across larger areas in early spring or late summer once the reproductive constraint is released and less prey is available. They thus increase their activity in forest stands with high percentage of oak trees where prey abundance is higher during these periods (Klingbeil and Willig 2010).

Our study showed that higher proportions of deciduous trees within conifer-dominated stands and landscape mosaics increase bat activity and modify community composition. Deciduous trees also increase the conservation value of plantation forests for bats by providing suitable feeding and roosting resources to locally endangered species such as the western barbastelle bat or the lesser horseshoe bat. Interestingly, the magnitude of these beneficial effects seems to be more important at the landscape scale than

at the stand scale. As managing stand mixtures is complex in planted forests, efforts to maintain deciduous tree patches within conifer matrices may be efficient enough to ensure bat persistence, especially if they harbour large and tall trees with higher availability of prey, as well as more nesting and roosting microhabitats (Regnery et al. 2013). The maintenance and restoration of semi-natural forest remnants within large conifer plantations would not only improve the conservation of bat communities but also enhance the ecosystem service of pest regulation that bats can provide to forests (Brockerhoff et al. 2008; Kunz et al. 2011; Charbonnier et al. 2014). Further studies combining multiple spatial and temporal scales are however needed to better quantify the key ecological functions of bat communities in forests and enhance their associated services through appropriate conservation measures.

Acknowledgments We are grateful to Groupama and Office National des Forêts for the permission to access their sites. We also thanks C Kerbirou, C Vacher, F Archaux, M Deconchat, A Theillout, F Vetillard, B Castagnyrol, Groupe Chiroptères d'Aquitaine and Elyomis for their help and EG Brockerhoff for improving the English. JYB received partial funding from the Aarhus University Research Foundation and the Aquitaine Regional Council, and YC, IVH, HJ and LB benefited from partial fundings for the FunDivEurope project, European Union Seventh Framework Programme (FP7/2007-2013) under Grant agreement No 265171.

References

- Akasaka T, Nakano D, Nakamura F (2009) Influence of prey variables, food supply, and river restoration on the foraging activity of Daubenton's bat (*Myotis daubentonii*) in the Shibetsu River, a large lowland river in Japan. *Biol Conserv* 142:1302–1310. doi:10.1016/j.biocon.2009.01.028
- Anderson MJ, Cribble NA (1998) Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. *Aust J Ecol* 23:158–167. doi:10.1111/j.1442-9993.1998.tb00713.x
- Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* 84:511–525. doi:10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2
- Barataud M, Tupinier Y (2012) Écologie acoustique des chiroptères d'Europe identification des espèces, étude de leurs habitats et comportements de chasse. Biotope and Muséum National d'Histoire Naturelle, Paris
- Barbaro L, Couzi L, Bretagnolle V, Nezan J, Vetillard F (2008) Multi-scale habitat selection and foraging ecology of the eurasian hoopoe (*Upupa epops*) in pine plantations.

- Biodivers Conserv 17:1073–1087. doi:[10.1007/s10531-007-9241-z](https://doi.org/10.1007/s10531-007-9241-z)
- Barton K (2015) Package “MuMIn”. Model selection and model averaging based on information criteria (AICc and alike). R package version 1121. <http://www.CRANR-project.org/package=MuMIn>
- Bellamy C, Scott C, Altringham J (2013) Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. *J Appl Ecol* 50:892–901. doi:[10.1111/1365-2664.12117](https://doi.org/10.1111/1365-2664.12117)
- Boughey KL, Lake IR, Haysom KA, Dolman PM (2011) Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. *Biol Conserv* 144:2300–2310. doi:[10.1016/j.biocon.2011.06.008](https://doi.org/10.1016/j.biocon.2011.06.008)
- Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J (2008) Plantation forests and biodiversity: oxymoron or opportunity? *Biodivers Conserv* 17:925–951. doi:[10.1007/s10531-008-9380-x](https://doi.org/10.1007/s10531-008-9380-x)
- Brotons L, Herrando S, Martin JL (2004) Bird assemblages in forest fragments within Mediterranean mosaics created by wild fires. *Land Ecol* 19:663–675
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Charbonnier Y, Barbaro L, Theillout A, Jactel H (2014) Numerical and functional responses of forest bats to a major insect pest in pine plantations. *PLoS ONE* 9:e109488. doi:[10.1371/journal.pone.0109488](https://doi.org/10.1371/journal.pone.0109488)
- Ciechanowski M (2005) Utilization of artificial shelters by bats (Chiroptera) in three different types of forest. *Folia Zool* 54:31–37
- Cisneros LM, Fagan ME, Willig MR (2015) Effects of human-modified landscapes on taxonomic, functional, and phylogenetic dimensions of bat biodiversity. *Divers Distrib* 21:523–533
- Crichton EG, Krutzsch PH (2000) Reproductive biology of bats. Academic Press, London
- Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175. doi:[10.2307/3544901](https://doi.org/10.2307/3544901)
- Estades CF, Temple SA (1999) Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine plantations. *Ecol Appl* 9:573–585. doi:[10.1890/1051-0761\(1999\)009\[0573:DFBCIA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[0573:DFBCIA]2.0.CO;2)
- Ethier K, Fahrig L (2011) Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. *Land Ecol* 26:865–876. doi:[10.1007/s10980-011-9614-2](https://doi.org/10.1007/s10980-011-9614-2)
- Frey-Ehrenbold A, Bontadina F, Arlettaz R, Obrist MK (2013) Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *J Appl Ecol* 50:252–261. doi:[10.1111/1365-2664.12034](https://doi.org/10.1111/1365-2664.12034)
- Fuentes-Montemayor E, Goulson D, Cavin L, Wallace JM, Park KJ (2013) Fragmented woodlands in agricultural landscapes: the influence of woodland character and landscape context on bats and their insect prey. *Agric Ecosyst Environ* 172:6–15. doi:[10.1016/j.agee.2013.03.019](https://doi.org/10.1016/j.agee.2013.03.019)
- Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. *J Evol Biol* 24:699–711. doi:[10.1111/j.1420-9101.2010.02210.x](https://doi.org/10.1111/j.1420-9101.2010.02210.x)
- Harvey CA, Gonzalez Villalobos JA (2007) Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. *Biodivers Conserv* 16:2257–2292. doi:[10.1007/s10531-007-9194-2](https://doi.org/10.1007/s10531-007-9194-2)
- Jung K, Kaiser S, Böhm S, Nieschulze J, Kalko EKV (2012) Moving in three dimensions: effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. *J Appl Ecol* 49:523–531. doi:[10.1111/j.1365-2664.2012.02116.x](https://doi.org/10.1111/j.1365-2664.2012.02116.x)
- Klingbeil BT, Willig MR (2010) Seasonal differences in population-, ensemble- and community-level responses of bats to landscape structure in Amazonia. *Oikos* 119:1654–1664. doi:[10.1111/j.1600-0706.2010.18328.x](https://doi.org/10.1111/j.1600-0706.2010.18328.x)
- Kunz TH, Braun de Torrez E, Bauer D, Lobova T, Fleming TH (2011) Ecosystem services provided by bats. *Ann N Y Acad Sci* 1223:1–38. doi:[10.1111/j.1749-6632.2011.06004.x](https://doi.org/10.1111/j.1749-6632.2011.06004.x)
- Le Viol I, Jiguet F, Brotons L, Herrando S, Lindström Å, Pearce-Higgins JW, Reif J, Van Turnhout C, Devictor V (2012) More and more generalists: two decades of changes in the European avifauna. *Biol Letters* 8:780–792
- Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol Monogr* 69:1–24. doi:[10.1890/0012-9615\(1999\)069\[0001:DBRATM\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2)
- Legendre P, Borcard D, Peres-Neto PR (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol Monogr* 75:435–450. doi:[10.1890/05-0549](https://doi.org/10.1890/05-0549)
- Meynard CN, Soto-Gamboa M, Iii PAH, Frick WF (2014) Bats of the Chilean temperate rainforest: patterns of landscape use in a mosaic of native forests, eucalyptus plantations and grasslands within a South American biodiversity hotspot. *Biodivers Conserv*. doi:[10.1007/s10531-014-0697-3](https://doi.org/10.1007/s10531-014-0697-3)
- Mueller T, Selva N, Pugaciewicz E, Prins E (2009) Scale-sensitive landscape complementation determines habitat suitability for a territorial generalist. *Ecography* 32:345–353
- Müller J, Mehr M, Bäessler C, Fenton MB, Hothorn T, Pretzsch H, Klemmt HJ, Brandl R (2012) Aggregative response in bats: prey abundance versus habitat. *Oecologia* 169:673–684. doi:[10.1007/s00442-011-2247-y](https://doi.org/10.1007/s00442-011-2247-y)
- Müller J, Brandl R, Buchner J, Pretzsch H, Seifert S, Stratz C, Veith M, Fenton B (2013) From ground to above canopy—bat activity in mature forests is driven by vegetation density and height. *For Ecol Manag* 306:179–184. doi:[10.1016/j.foreco.2013.06.043](https://doi.org/10.1016/j.foreco.2013.06.043)
- Müller J, Jarzabek-Müller A, Bussler H, Gossner MM (2014) Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. *Anim Conserv* 17:154–162. doi:[10.1111/acv.12075](https://doi.org/10.1111/acv.12075)
- Nájera A, Simonetti JA (2010) Enhancing avifauna in commercial plantations. *Conserv Biol* 24:319–324. doi:[10.1111/j.1523-1739.2009.01350.x](https://doi.org/10.1111/j.1523-1739.2009.01350.x)
- Pawson SM, Brin A, Brockerhoff E, Lamb D, Payn TW, Paquette A, Parrotta J (2013) Plantation forests, climate change and biodiversity. *Biodivers Conserv* 22:1203–1227. doi:[10.1007/s10531-10013-10458-10538](https://doi.org/10.1007/s10531-10013-10458-10538)

- Rainho A, Palmeirim JM (2011) The importance of distance to resources in the spatial modelling of bat foraging habitat. PLoS ONE 6:e19227. doi:[10.1371/journal.pone.0019227](https://doi.org/10.1371/journal.pone.0019227)
- Regnery B, Couvet D, Kubarek L, Julien JF, Kerbiriou C (2013) Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. Ecol Indic 34:221–230. doi:[10.1016/j.ecolind.2013.05.003](https://doi.org/10.1016/j.ecolind.2013.05.003)
- Rodríguez-San Pedro A, Simonetti JA (2013) Foraging activity by bats in a fragmented landscape dominated by exotic pine plantations in central Chile. Acta Chiropterologica 15:393–398. doi:[10.3161/150811013X679017](https://doi.org/10.3161/150811013X679017)
- Russ J, Montgomery W (2002) Habitat associations of bats in Northern Ireland: implications for conservation. Biol Conserv 108:49–58. doi:[10.1016/S0006-3207\(02\)00089-7](https://doi.org/10.1016/S0006-3207(02)00089-7)
- Russo D, Cistrone L, Jones G, Mazzoleni S (2004) Roost selection by barbastelle bats (*Barbastella barbastellus*, Chiroptera: Vespertilionidae) in beech woodlands of central Italy: consequences for conservation. Biol Conserv 117:73–81. doi:[10.1016/S0006-3207\(03\)00266-0](https://doi.org/10.1016/S0006-3207(03)00266-0)
- Russo D, Cistrone L, Garonna AP, Jones G (2010) Reconsidering the importance of harvested forests for the conservation of tree-dwelling bats. Biodivers Conserv 19:2501–2515. doi:[10.1007/s10531-010-9856-3](https://doi.org/10.1007/s10531-010-9856-3)
- Ruys T, Bernard Y (2014) Atlas des mammifères sauvages d'Aquitaine. Tome 4: les chiroptères. Cistude Nature, Le Haillan
- Stone EL, Jones G, Harris S (2013) Mitigating the effect of development on bats in England with derogation licensing. Conserv Biol 27:1324–1334. doi:[10.1111/cobi.12154](https://doi.org/10.1111/cobi.12154)
- Tews J, Brose U, Grimm V, Tielborger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92. doi:[10.1046/j.0305-0270.2003.00994.x](https://doi.org/10.1046/j.0305-0270.2003.00994.x)
- Villard MA, Haché S (2012) Conifer plantations consistently act as barriers to movement in a deciduous forest songbird: a translocation experiment. Biol Conserv 155:33–37
- Walsh C, Mac Nally R (2015) Hierarchical partitioning: Package hier.part. R package version 1.0-4, <http://www.CRANR-project.org/package=hier.part>