

Using trait-based filtering as a predictive framework for conservation: a case study of bats on farms in southeastern Australia

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Summary

1. With world-wide changes in human land use, an important challenge for conservation biologists is to develop frameworks to predict how species will respond to landscape change. Environmental filtering, where different environments favour different species' traits, has the potential to be a useful predictive framework. Therefore, it is important to advance our understanding of how species with different traits respond to environmental variables.

2. We investigated the distribution of microbats in a 1 000 000 ha agricultural region in southeastern Australia, with specific emphasis on the effects of tree density on bat species characterized by different sizes, wing shapes and echolocation frequencies. The study area is substantially cleared, and trees are continuing to decline because grazing inhibits tree regeneration. We monitored bat activity acoustically at 80 sites spanning a wide range of tree densities. We used regression modelling to quantify the response of bats to tree density and other ecological covariates, and RLQ analysis to assess how different traits correlated with various environmental gradients.

3. Total bat activity and species richness peaked at intermediate tree densities. Species composition was explained by tree density and the traits of individual species. Sites with low tree cover were dominated by large, fast-flying species, whereas sites with dense tree cover were dominated by smaller, highly manoeuvrable species. These findings are consistent with recent findings from other locations around the world.

4. *Synthesis and applications.* Trait-based predictive frameworks enable landscape managers to assess how different management strategies and landscape modifications are likely to affect different species. Here, we propose a framework to derive general predictions of how bats respond to landscape modification, based on tree density and species traits. We apply this framework to a current conservation issue of tree decline in our study area and derive management priorities including: (i) maintaining a range of tree densities throughout the region; (ii) ensuring the persistence of locations with intermediate tree densities; and (iii) using environmentally sensitive grazing practices, for example, by incorporating long rest periods.

Key-words: grazing landscape, insectivorous bats, landscape heterogeneity, microchiroptera, mixed effects model, RLQ analysis, wing shape

Introduction

Heterogeneous landscapes used for agriculture and livestock grazing provide important opportunities for biodiversity con-

servations outside protected areas (Tschamtko *et al.* 2005; Harvey *et al.* 2006; Haslem & Bennett 2008; Ranganathan *et al.* 2008). However, human land use has also caused the decline of many species (Tschamtko *et al.* 2005). A key challenge, therefore, is to develop frameworks that can predict how different species will respond to alternative forms of human

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land use (Daily 1999, 2001). The concept of environmental filtering can be useful in this context. It suggests that the environment acts as a filter that favours species characterized by certain traits over species with different traits (Keddy 1992; Weiher & Keddy 1995; Mayfield *et al.* 2005; Lebrija-Trejos *et al.* 2010).

Environmental filtering holds great promise as a predictive framework. General patterns appear to exist, for example, for birds, plants, and freshwater organisms. For birds, body size appears to be related to species distribution patterns both in North America and Australia, with small species preferentially occupying a finely textured environment (Holling 1992; Fischer, Lindenmayer & Montague-Drake 2008). For plants, local assemblages of genotypes result from filtering via regional-scale climatic conditions, local disturbance history and interactions with other species (Diaz *et al.* 1999). One general outcome is, for example, that plants with a large specific leaf area are more likely to occupy disturbed locations than plants with a low specific leaf area (McIntyre 2008). In streams, filters also have been identified for freshwater organisms at multiple scales, including at the watershed, valley and microhabitat levels. For both macroinvertebrates and fish, conditions at each of these scales favour species with compatible life history, morphological, and flood resistance traits (Poff 1997). To develop a predictive framework for a particular set of species or environments, the same traits need to be assessed in different settings. Similar correlations between trait occurrence and environmental variables in different contexts are likely to indicate robust (and possibly causal) links. A robust predictive framework would greatly assist conservation planning: Are there specific ways to manipulate an environment to make it more or less attractive for species with particular traits?

Here, we investigated the relationship between environmental characteristics and microbat community composition in a variegated landscape used for livestock grazing in southeastern Australia. A variegated landscape is defined as one where tree density varies continuously from low to high (McIntyre & Barrett 1992). The presence of a continuous environmental gradient such as tree density provides suitable conditions to test whether this gradient is correlated with particular species traits.

Microbats are a particularly instructive group for three reasons. First, their morphological traits should make them sensitive to environmental filtering, because they affect mobility, manoeuvrability, diet and microhabitat use (Kalko & Schnitzler 1993; Arita & Fenton 1997; Fenton 1997). Second, bats provide pest control services in agricultural landscapes and therefore should receive a high priority in ecosystem management (Cleveland *et al.* 2006; Kalka, Smith & Kalko 2008; Williams-Guillen, Perfecto & Vandermeer 2008). Third, the knowledge base for bats is increasing rapidly. The nexus of species traits and environmental conditions has been examined, for example, in an urban setting in Australia (Threlfall *et al.* 2011), an urban–forest interface in Panama (Jung & Kalko 2011), and an agricultural landscape in Indiana, USA (Duchamp & Swihart 2008). This growing knowledge base

provides opportunities for general conclusions to be reached regarding trait-mediated environmental filtering in microbats.

Our study is also motivated by a pressing applied problem: the rapid decline of trees in eastern Australia's grazing landscapes. Trees are important for bats because they provide focal points for navigation and foraging (Kalko & Schnitzler 1993; Law, Chidel & Turner 2000; Lumsden & Bennett 2005) as well as roost sites (Lumsden, Bennett & Silins 2002a; Campbell *et al.* 2005; Rhodes *et al.* 2006). We used our findings to derive practical conservation recommendations for this issue. We surveyed bat communities across the full range of extant tree densities and asked: (i) How are bat species richness and activity related to tree density gradients and other environmental variables? (ii) How do individual bat species respond to various environmental variables? (iii) Do bats characterized by different traits occupy different positions along key environmental gradients, such as tree density?

Materials and methods

STUDY AREA AND EXPERIMENTAL DESIGN

We surveyed bats in a 1 000 000 ha area in the Upper Lachlan Catchment of New South Wales, Australia (Fig. 1). Prior to European settlement, the region was dominated by temperate woodland in the valleys (e.g. *Eucalyptus blakelyi*, *E. melliodora*) and dry forest on the hilltops (e.g. *E. macrorhyncha*) (Gibbons & Boak 2002). Since then, clearing for agriculture and livestock grazing has reduced tree cover to approximately 15%, with lowland areas disproportionately affected (Fischer *et al.* 2010). The resulting landscape pattern is 'variegated' (*sensu* McIntyre & Barrett 1992). That is, tree density changes continuously from high to low, and patch boundaries are difficult to delineate. Understorey is largely absent, especially in areas grazed by livestock. We worked on 33 farms (ranging in size from 236 to 3036 ha; median 900 ha) that were dominated by sheep and/or cattle grazing ($80 \pm 4\%$ of land grazed per farm [mean \pm standard error]).

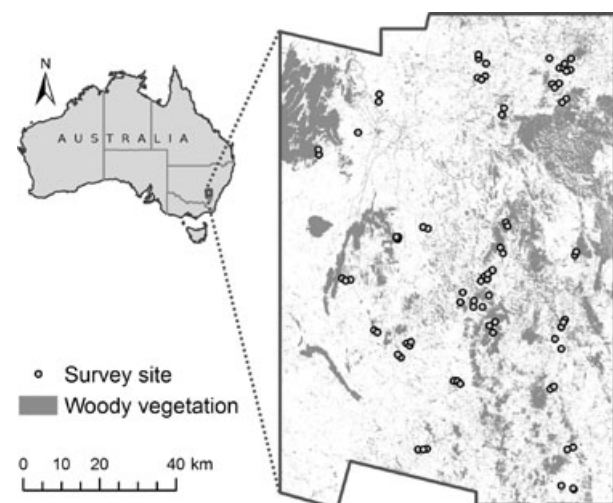


Fig. 1. Location of the study area. The map shows the 80 sites where bats were surveyed. The presence of woody vegetation cover is shown in the background (based on Fischer *et al.* 2009b).

We established 80 survey sites measuring 2 ha each (Fig. 1), which were a subset of the sites used in a parallel study on tree regeneration (Fischer *et al.* 2009b). Sites were chosen within pre-defined strata to encompass the full suite of tree densities and grazing regimes available in the study area. The choice within pre-defined strata was random, but subject to logistic constraints (primarily access). Our choice of sites resulted in 12 'open pasture sites' (approximately 10 or fewer crowns discernible on aerial photographs), 28 'scattered tree sites' (approximately 10–40 crowns), 28 'grazed woodland sites' and 12 'ungrazed woodland sites' (both with dense crown cover). Broad classes of tree density were refined by measuring the actual density of trees within a given site, with all trees > 130 cm in height counted (Fischer *et al.* 2009b). To also assess landscape context effects on bats, we calculated the proportion of tree cover within concentric circles around the centre of the site, using radii of 100, 200, 400 and 800 m (based on remotely sensed data; for a full description, see Fischer *et al.* 2009b).

The vast majority of sites were in separately fenced sections and typically were at least several hundred metres apart (range of nearest neighbour distances for sites = 278–9768 m; median = 1135 m). Because some bats can move several kilometres in a night, we cannot exclude the possibility that some individuals were recorded at two or more sites in a given night. However, because our focus was not on individuals but on activity levels by a particular species or community of species, we believe it is reasonable to consider sites as independent. Notably, we accounted for the grouped and nested design in our analyses (see below).

Information on the grazing regime of each site was obtained from landholders and related to both stocking rate (measured in DSE = dry-sheep-equivalent, based on a standard 48–50 kg wether) and extent of livestock rotation (measured in days grazed in a typical year). We measured several additional covariates, including available soil phosphorus (measured in mg kg⁻¹ using the Colwell method; a proxy for past fertilizer application; see Dorrrough & Moxham 2005), and we visually estimated percentage cover of logs and shrubs at each site. Because of logistic constraints, we were unable to measure invertebrate abundance, although we acknowledge that this would have been useful. The experimental design and measurement of covariates are described in further detail by Fischer *et al.* (2009b).

BAT SURVEYS

Within a given landscape, the two variables most likely to limit bat distribution are roost availability and access to foraging habitat (Fenton 1997). The reliable identification of roost sites requires the radiotracking of individual bats of both sexes within and outside the breeding season (Lumsden, Bennett & Silins 2002a,b; Rhodes *et al.* 2006; Watrous *et al.* 2006). Although we acknowledge the importance of roost sites, we focused on foraging habitat only – noting that roost sites may be located several kilometres away from foraging habitat and that their limited availability may provide additional constraints on bat distribution (Lumsden, Bennett & Silins 2002a). Overall bat activity was assessed via acoustic monitoring. The number of passes recorded for a given species was considered an index of its activity; high activity, in turn, was assumed to indicate highly suitable foraging habitat. Although overall activity comprises a range of activities such as searching, feeding, commuting and socializing, extensive use of a given site strongly suggests that the site represents important habitat (including for foraging).

Each site was surveyed using Anabat detectors (Titley Electronics, Australia), with two detectors per site, for a total of four nights in November/December 2008, and then again in February/March

2009, resulting in a total of 16 detector nights of data recorded from each site. November/December coincides with a warm period when bats are very active. Females lactate during this time, and resource requirements are likely to be high; activity levels therefore are also likely to be high. In January, offspring are potentially very active, which can result in artificially high activity levels (especially near maternity roosts). In February/March, nights are still often warm and thus conducive to high bat activity. Compared with January, typically local activity patterns are less inflated by the recent addition of offspring.

Detector microphones were set at a standard two-metre height in S-shaped PVC-covers to protect them against rain, angled up at 45°, and pointed into vegetation gaps. Detectors were calibrated against each other with respect to microphone sensitivity and recorded for the entire night. This survey protocol was used on the basis of a pilot study, which showed that activity levels could be accurately estimated with this amount of effort (Fischer *et al.* 2009a). We note that there are inherent limitations to acoustic monitoring data, which should be considered when interpreting the results. Most importantly, detectability is not equal across all species. Species with loud calls, for example, are more likely to be recorded than slow-flying species with soft calls. Activity levels therefore cannot be compared between bat species. However, a key objective of our study was to compare relative activity patterns between different types of sites, rather than absolute activity levels between different species. Our comparison depends on the detectability of a given species being approximately constant across all sites. We are highly confident that this was the case in our study, because even where tree density is relatively high, eucalypt woodlands are naturally very open and thus unlikely to affect microphone effectiveness; furthermore, all microphones were pointed into canopy gaps, so the immediate surroundings of the microphones were not affected by vegetation clutter.

Prior to analysis, we excluded nights with detector failure. We also excluded nights where rainfall or strong wind was recorded at nearby weather stations, and nights where the minimum nightly temperature at nearby weather stations was under 10 °C. Exclusion of nights with poor weather or detector failure yielded 566 detector nights from 75 sites.

Anabat files from suitable nights were identified using Anascheme software, as outlined by Fischer *et al.* (2009a), Law & Chidel (2006) and Adams, Law & Gibson (2010). The software used a species identification key specifically designed for the study area and tested on local reference calls (Fischer *et al.* 2009a). The key considered 10 species, all of which were subsequently recorded. We acknowledge that six additional species may occur in small portions of the study area (in the far east: *Falsistrellus tasmaniensis*, *Scotorepens orion*; in the far north-west: *Scotorepens greyii*, *Chalinolobus picatus*; one obligate cave-roosting species: *Miniopterus schreibersii oceanensis*; and one regionally rare vagrant species: *Saccolaimus flaviventris*). For each species included in the key, the number of nightly passes was considered its nightly activity level; the sum of identified passes was considered total bat activity. A pass was defined as a sequence of ultrasonic calls contained within a standard 15 s file. On average, the key identified approximately 40% of recorded calls per night.

DATA ANALYSIS

To obtain an overview of activity patterns, we first separately modelled bat species richness and total bat activity as a response of environmental variables. Species richness and total activity (log-transformed because of heavy skew) in a given night were modelled separately using linear mixed effects models conducted with the R

package lme4 (Bates, Maechler & Bolker 2011). Because species richness and log-transformed activity were positively correlated, albeit weakly (Pearson correlation coefficient = 0.54), we expected the two models to produce broadly similar results. The use of mixed effect models was necessary to account for the nested and grouped design of the study. Random effects initially were specified as detection night nested in detector, nested in site, nested in farm (farm/site/detector/night). Survey year was included as a fixed effect. Random effects were subsequently dropped from the model if a simpler model without a given random effect was not significantly different from the more complex one (likelihood ratio test, chi-squared distribution, $P < 0.05$). The following fixed effects were included as explanatory variables: tree density, squared tree density (to enable modelling of unimodal responses), percentage cover of shrubs and logs, available soil phosphorus, number of grazing days and stocking rate, as well as the interaction of the latter two. Environmental variables were not strongly collinear (Pearson correlation coefficient < 0.61) and therefore could be included together in regression models. We simplified models by deleting non-significant terms identified through model comparison (likelihood ratio test, chi-squared distribution) and using backwards selection. To improve linearity in regression analyses, environmental variables were log-transformed (except number of grazing days) and standardized by subtracting the mean and dividing by the standard deviation.

All bat species were modelled individually. For the four most widespread species, *Chalinolobus gouldii*, *C. morio*, *Mormopterus* sp. 4, and *Vespadelus vulturnus*, we modelled activity in a linear mixed effects model, after log-transforming activity. For the remaining species, activity followed a Poisson distribution with large overdispersion. For this reason, we converted activity data to presence/absence data and used generalized linear mixed effects models with a binomial error structure and a logit link function to model their probability of occurrence. Models were simplified as outlined above.

To determine the spatial scale at which tree cover was most strongly related to bats, we constructed separate models each with fully specified random structure but with only one fixed effect, namely tree cover at one of the radii listed above (see also Ricketts *et al.* 2001). The fit of each model was assessed using the Akaike Information Criterion. We found that local tree density provided a better fit

than any of the remotely sensed cover from larger radii for both richness and total activity; for individual species, goodness of fit also declined or did not change considerably with increasing radii. We concluded that local tree density was more important than the amount of tree cover surrounding a given site, and therefore, we did not use remotely sensed tree cover in subsequent analyses.

To describe the nexus of environmental conditions, species composition and species traits, we performed an RLQ analysis with the R package ade4 (Doledec *et al.* 1996). We used a matrix of environmental variables of each site (R), a matrix of species activity levels for each detector night (L) and a matrix of bat species traits (Q). Species traits were assembled from the literature (Table 1) and included wing loading (total body mass/wing area), aspect ratio (squared wing span/wing area), body mass (measured in g), forearm length (measured in cm) and echolocation frequency (low = below 38 kHz, medium = 38–48 kHz, high = above 48 kHz, linear = vertically linear calls).

RLQ analysis is an extension of correspondence analysis, which is an indirect, unconstrained ordination technique that maximizes the correlation between sites and species presence. In comparison, RLQ analysis is a direct, constrained ordination that maximizes the covariance between sites and species on the basis of site environmental variables and species' traits. This approach arranges sites according to the traits of the species they contain, and species according to the environmental variables of the sites in which they occur. Sites that contain species with similar traits are then positioned close together in the ordination space. Similarly, species that occur in sites with the same environmental variables are placed close together. The total amount of variance that the RLQ analysis can explain is limited by the variance explained in separate ordinations of the R, L and Q matrices (in this study represented by a principal components analysis, a correspondence analysis, and a Hill-Smith principal components analysis for mixed qualitative and quantitative data, respectively). Thus, to assess how well the RLQ analysis explained the nexus of environmental conditions, species composition and species traits, we compared the variance explained by the first two RLQ axes with those of the separate ordinations. We then tested the significance of the RLQ analysis using a permutation test with 1000 permutations. All statistical analyses were performed in R (R Development Core Team, 2011).

Table 1. Scientific names, common names, and species traits of the species considered in the analyses. The taxonomy of *Mormopterus* spp. follows Adams *et al.* (1988). Traits included wing loading (total body mass/wing area), aspect ratio (squared wing span divided by wing area), body mass (measured in g), forearm length (measured in cm) and echolocation frequency (low = below 38 kHz, medium = 38–48 kHz, high = above 48 kHz, linear = vertically linear calls). References for wing loading, aspect ratio, body mass and forearm length are listed. The latter two measurements were supplemented from Churchill (2008) where necessary. Echolocation frequency was assigned following Pennay, Law & Reinhold (2004)

Scientific name	Common name	Wing loading	Aspect ratio	Body mass (g)	Forearm length	Echolocation frequency	References
<i>Chalinolobus gouldii</i>	Gould's Wattle Bat	9.45	6.53	13.80	43.70	Low	(O'Neill & Taylor 1986)
<i>Chalinolobus morio</i>	Chocolate Wattle Bat	7.60	6.11	8.90	38.90	High	(Rhodes 2002)
<i>Mormopterus</i> sp.2	Eastern Freetail Bat	8.16	7.23	9.00	33.00	Low	(Rhodes 2002)
<i>Mormopterus</i> sp.4	Southern Freetail Bat	8.16	7.214	9.20	33.80	Low	(Reside & Lumsden 2011)
<i>Nyctophilus</i> spp.	Long-eared Bat species	6.78	5.77	10.25	53.20	Linear	(Brigham, Francis & Hamdorf 1997)
<i>Scotorepens balstoni</i>	Inland Broad-nosed Bat	10.43	6.26	8.700	35.60	Low	(Bullen & McKenzie 2001)
<i>Tadarida australis</i>	White-striped Freetail Bat	19.60	7.99	37.60	60.60	Low	(Rhodes 2002)
<i>Vespadelus darlingtoni</i>	Large Forest Bat	6.40	5.92	7.20	35.10	Medium	(O'Neill & Taylor 1986)
<i>Vespadelus regulus</i>	Southern Forest Bat	6.60	5.66	5.50	31.20	Medium	(O'Neill & Taylor 1986)
<i>Vespadelus vulturnus</i>	Little Forest Bat	6.38	5.19	3.90	28.40	Medium	(Rhodes 2002)

Results

We identified 208 358 bat passes from all 10 species considered (88 693 *Mormopterus* sp. 4; 51 345 *Vespadelus vulturnus*; 38 484 *Chalinolobus gouldii*; 8144 *C. morio*; 7817 *Tadarida australis*; 7370 *V. darlingtoni*; 3010 *Mormopterus* sp. 2; 1398 *Nyctophilus* sp.; 1329 *Scotorepens balstoni*; 768 *V. regulus*). Both bat species richness and activity had unimodal responses to tree density, with maximum values at approximately 50–100 trees per 2 ha plot (Table 2; Fig. 2). In addition, species richness responded negatively to the annual duration of livestock grazing and to shrub cover (Table 2). Tree density also was related to either activity or probability of occurrence of all bat species, which peaked either at intermediate tree densities or at high tree densities (see Table S1; Fig. 3). A few other explanatory variables were related to individual bat species, including

two positive responses to log cover, two negative responses to annual grazing duration, and one negative response to shrub cover (Table S1).

The RLQ analysis arranged sites along a clear gradient in species composition, with the first axis explaining 86% of the total variance (compared with 12% for the second axis) between the environmental variables and species traits (permutation test P -value = 0.004; Table 3). This represented 37% of the correlation expressed in the correspondence analysis of bat activity, and 65% and 75% of the variance expressed in the principal components analyses of the environmental variables and species traits, respectively. Highly manoeuvrable species with linear, medium and high echolocation frequencies were associated with dense tree cover and logs (Fig. 4). In comparison, larger, heavier species with long, narrow wings and low echolocation frequencies were

Table 2. Summaries of linear mixed effects models for bat species richness and total activity. Note, total activity was log-transformed prior to analysis; tree density was log-transformed and standardized prior to analysis. P -values for fixed effects were calculated based on a Markov-Chain-Monte-Carlo sample

Response	Effect	Variance	Estimate	Standard error	P -value
Species richness	Random				
	Detector	0.180	n/a	n/a	n/a
	Site	0.369	n/a	n/a	n/a
	Farm	0.766	n/a	n/a	n/a
	Fixed				
	Intercept (year 2008)	n/a	7.413	0.243	0.000
	Tree density	n/a	0.822	0.150	0.000
	Tree density squared	n/a	-0.752	0.158	0.000
	Shrubs	n/a	-0.250	0.124	0.044
Total activity	Random				
	Detector	0.189	n/a	n/a	n/a
	Site	0.249	n/a	n/a	n/a
	Farm	0.247	n/a	n/a	n/a
	Fixed				
	Intercept (year 2008)	n/a	5.513	0.167	0.000
	Tree density	n/a	0.361	0.112	0.001
	Tree density squared	n/a	-0.406	0.120	0.001
	Year 2009	n/a	-0.334	0.103	0.001

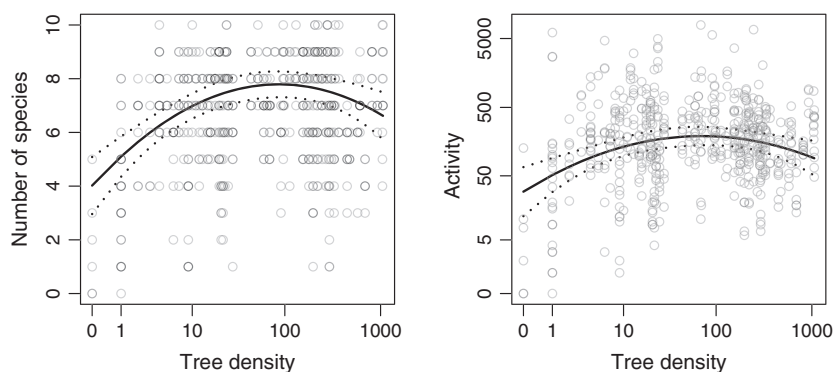


Fig. 2. Responses of bat species richness (left) and total bat activity (right) to tree density in a given 2 ha site. Fitted lines and confidence intervals (dotted lines) result from linear mixed effects models (Table 2). Over-plotting of multiple points is visualized by increasingly darker shades of grey.

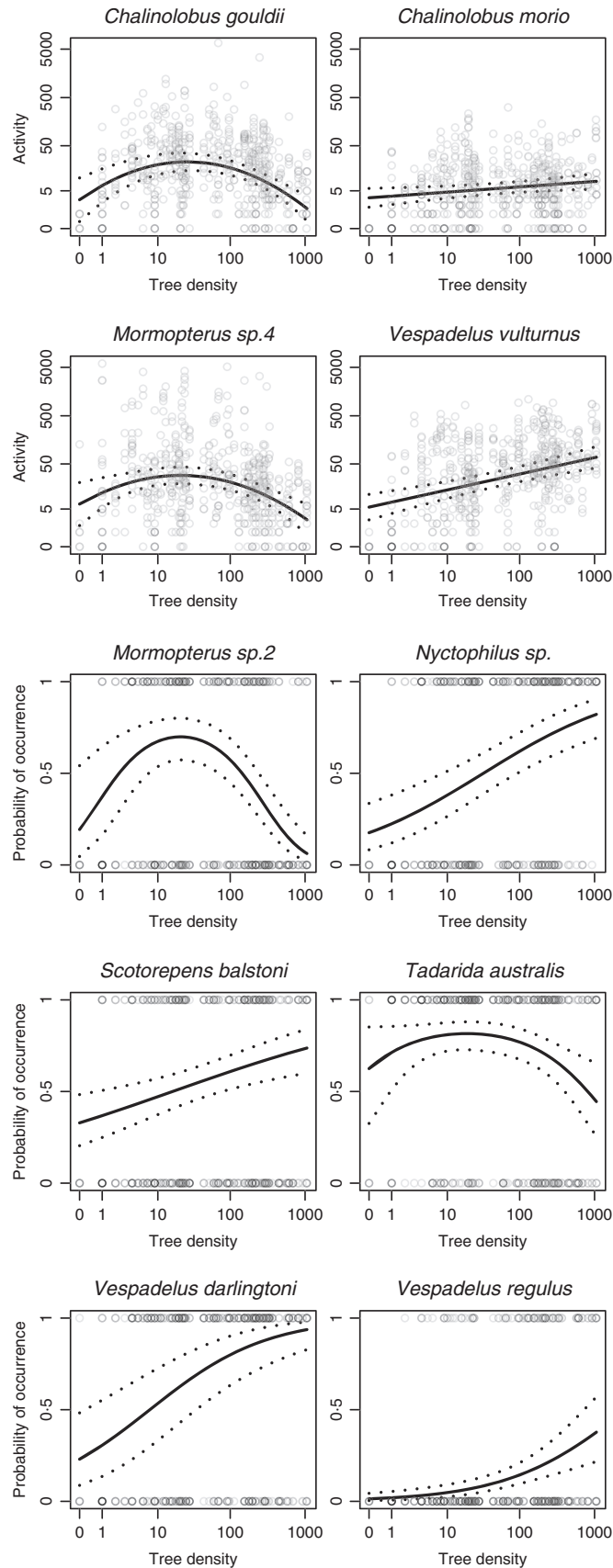


Fig. 3. Graphical summary of the mixed effects models for individual bat species, showing their response to tree density per 2 ha. Activity was modelled for the most common species only; probability of occurrence was modelled for the remainder of species. Over-plotting of multiple points is visualized by increasingly darker shades of grey.

Table 3. Results of the RLQ analysis of the environmental variables of each site (R), species activity levels recorded during individual detector nights (L) and bat species traits (Q). Separate ordinations: eigenvalues (and per cent variance explained) for the first two axes from the ordinations of the R (principal components analysis), L (correspondence analysis) and Q (Hill-Smith principal components analysis) matrices. RLQ analysis: eigenvalues (and per cent variance explained), covariance and correlation (and per cent variance) with the correspondence analysis of the L matrix, and projected variance (and per cent variance) with the R and Q matrices

	Axis 1 (%)	Axis 2 (%)
Separate ordinations		
R (PCA)	2.11 (35.17)	1.44 (23.99)
L (CA)	0.65 (25.02)	0.43 (16.30)
Q (Hill-Smith PCA)	3.80 (54.33)	1.13 (16.15)
RLQ analysis		
RLQ axis eigenvalues	0.36 (85.91)	0.05 (12.32)
Covariance	0.60	0.23
Correlation: L	0.30 (37.25)	0.16 (24.33)
Projected variance: R	1.38 (65.44)	2.50 (70.42)
Projected variance: Q	2.87 (75.48)	4.70 (95.26)

associated with higher stocking rates of grazing animals (Fig. 4).

Discussion

Developing a trait-based framework to predict how species will respond to human land use change is a fundamental challenge for applied ecologists (Daily 2001). Microbats appear to be an ideal candidate group for a globally applicable, trait-based predictive framework. Findings from around the world suggest that microbats respond predictably to structural clutter and vegetation density. Clutter has been found, for example, to be related to bat distribution in forest production landscapes in Australia (Law & Chidel 2002) and the USA (Ford *et al.* 2006; Loeb & O'Keefe 2006; Morris, Miller & Kalcounis-Rueppell 2010), as well as in semi-natural landscapes in the USA (Zimmerman & Glanz 2000). A common finding is that

structurally complex environments are favoured by highly manoeuvrable species, which are typically small and have broad wings. By contrast, fast-flying, larger species with narrow wings are associated with simplified environments (O'Neill & Taylor 1986).

The link between the traits of microbats and structural clutter is most likely to be mechanistic because it is grounded in traits that have evolved to provide adaptations to environmental conditions (Norberg & Rayner 1987; Arita & Fenton 1997). Because human-dominated landscapes tend to be simplified, fast-flying, mobile species are more likely to persist in such landscapes than smaller, less mobile species. Both existing reviews of threatened species (Jones, Purvis & Gittleman 2003; Safi & Kerth 2004) and recent empirical studies from a major city in Australia (Threlfall *et al.* 2011), a rural-urban interface in Panama (Jung & Kalko 2011), and a rural landscape in Indiana, USA (Duchamp & Swihart 2008) support the generality of this pattern.

A trait-based predictive framework such as this is very useful for conservation (Daily 1999; Fischer, Lindenmayer & Montague-Drake 2008). It enables landscape managers to assess how different management strategies are likely to affect different species of bats. For example, in our case study, small, manoeuvrable bats such as *Vespadelus* or *Nyctophilus* species preferentially used locations with relatively high densities of trees, whereas larger species such as *T. australis* had peak activity levels at lower tree densities. Depending on which species are given the highest priority in conservation planning, this understanding can guide whether trees are protected or replanted at high or low densities, respectively. Notably, high density plantings of eucalypts (approximately 800 stems ha⁻¹) in agricultural areas are used extensively by very few species, namely highly manoeuvrable *Nyctophilus* spp. (Law & Chidel 2006; Law, Chidel & Penman 2011).

Treeless areas were suboptimal for all bat species. At present, all species in this study are common and of relatively little conservation concern. However, even though a thinning out of tree cover in some locations would benefit some species, the

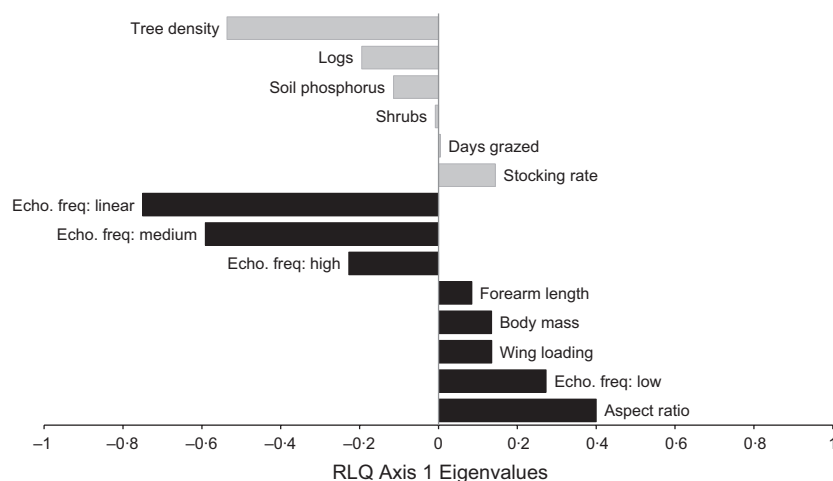


Fig. 4. Eigenvalues for axis 1 of the RLQ analysis of species activity data recorded during individual detector nights, relating environmental variables (grey bars) and species traits (black bars). Environmental variables and species traits with similar positions along the axis covary with each other.

complete loss of trees from large parts of the landscape would be detrimental to all bat species, including large, fast-flying species. Maintaining remnant vegetation therefore is critically important for all bats in Australia's sheep-wheat belt (Law, Anderson & Chidel 1999). Notably, low-density remnants of native vegetation may be just as important as denser patches. Many species of bats peaked at intermediate tree densities, and total species richness and bat activity also were highest in areas with intermediate tree densities. These findings are consistent with previous work in Victoria (Lumsden & Bennett 2005) and northern New South Wales (Law, Chidel & Turner 2000) and emphasize that scattered farm trees provide important habitat for bats. Even standing dead trees can fulfil important functions, because they provide suitable roost sites for several species (Campbell *et al.* 2005; Goldingay 2009).

The variegated nature of our study area is important because different bat species used areas characterized by different tree densities (*sensu* McIntyre & Barrett 1992). At present, most farms support a wide range of tree densities in different parts of the farm. The resulting landscape heterogeneity provides habitat for a range of different bat species, thereby contributing to landscape-scale (beta) diversity (Tscharrntke *et al.* 2005; Bennett, Radford & Haslem 2006; Harvey *et al.* 2006).

In addition to the relationships observed with tree density, a few other covariates were also significant in our regression models or the RLQ analysis. Most importantly, two bat species and species richness responded negatively to the annual duration of grazing; two responded positively to the amount of log cover at a site (Table S1); and large bat species appeared to be correlated with higher stocking rates (Fig. 4). The negative response to grazing duration underlines recent findings that rotational grazing with long rest periods may be an ecologically more benign practice in southeastern Australia than continuous livestock grazing (Fischer *et al.* 2009b). The positive effect of long rest periods is probably indirect. We speculate that both reduced grazing duration and increased log cover may be proxies for a higher invertebrate abundance and hence higher food availability. Because we did not measure invertebrate abundance directly, we were unable to test this proposition. The association of large bats with higher stocking rates was relatively weak (Fig. 4) and highlights that structurally simplified areas are tolerated primarily by large, mobile species, as opposed to smaller, manoeuvrable species.

Conclusion

When considering our findings in a global context of other recent work, it appears that general predictions of the response of bats to landscape modification are possible across the world. Applying environmental filtering theory suggests that specific environmental variables, particularly those related to vegetation structure, will selectively benefit either large, fast-flying species or smaller, more manoeuvrable species. This insight provides an applied tool for landscape management, which can be used to predict how landscapes can be manipulated to preferentially benefit different species. With respect to our study area, we recommend that to maintain bat diversity into

the future, it will be important to: (i) maintain a range of tree densities; (ii) specifically ensure that locations exist with intermediate tree densities, because this is where bat activity and richness are highest; (iii) use environmentally sensitive grazing practices, for example, by incorporating long rest periods and maintaining invertebrate habitat such as coarse woody debris.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Summaries of the mixed effects models for individual bat species.

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