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Terrestrial laser scanning reveals below-canopy bat trait relationships with forest structure

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ABSTRACT

Three-dimensional structure of vegetation plays a key role in animal ecology and the arrival of LiDAR technologies has given ecologists the ability to understand species-habitat relationships in increasing detail. However, few studies have investigated the trait-environment relationships that underpin diverse animal relationships with vegetation structure. We used terrestrial laser scanning (TLS) and acoustic bat surveys to investigate relationships between forest structure and bat communities across a vegetation structural gradient at community, species and trait levels. We developed 20 measures of site scale vegetation structure and also quantified landscape scale vegetation cover and water availability. We predicted that overall bat activity would increase in open and decrease in cluttered vegetation, but this would vary with species, underpinned by ecomorphological traits. Overall bat activity was negatively associated with stem density, with total activity halving (from 380 to 190 calls night^{-1}) as stem densities increased from 60 to 1350 stems ha^{-1}, while foraging activity declined from 8 to <1 feeding buzzes night^{-1} over the same range. Bat activity varied among species and structures and foraging strategy explained more of this variability than call, body size or wing traits. As predicted, above-canopy and edge-space foraging bats were negatively associated with local-scale clutter, while closed-space species were positively associated with cluttered stands. Stem density was the strongest predictor of bat-environment relationships, although there was evidence for differences in bat habitat use across different structural elements. Our study is the first to link detailed LiDAR-derived 3D forest structural metrics to multiple animal traits.

1. Introduction

Three-dimensional structure of vegetation drives patterns in species richness (Tews et al., 2004) and determines how animals interact with their environment (Vierling et al., 2008). Dense, or cluttered vegetation can conceal prey from predators (Olsoy et al., 2015), but also hamper navigation (Cheng et al., 2009), maneuverability and prey capture (Schnitzler et al., 2003). Vegetation structure is a major driver of habitat use and community composition for a diverse array of taxa including arthropods (Müller and Brandl, 2009), amphibians (Petranka et al., 1994), reptiles (Abom and Schwarzkopf, 2016), birds (Bradbury et al., 2005) and mammals (Carey and Wilson, 2001). Ground-based and airborne light detection and ranging techniques (LiDAR or laser scanning) have revolutionized characterization of vegetation structure (Lefsky et al., 2002; Vierling et al., 2008). These methods have allowed detection of increasingly subtle differences in habitat use, including: distribution of breeding habitat and nesting success of birds (Boelman et al., 2016; Bradbury et al., 2005; Garcia-Feced et al., 2011), dynamics of habitat use across life-stages and seasons in moose *Alces alces* (Melin et al., 2016), prediction of richness and community composition in hyperdiverse taxa (beetles) (Müller and Brandl, 2009) and location of key habitat resources such as dead trees (snags) (Martinuzzi et al., 2009) and tree hollows (Owers et al., 2015).

Moving from understanding species relationships with vegetation structure to identifying the traits that underpin these relationships is a critical step in community ecology (McGill et al., 2006). While LiDAR technologies are allowing increasingly sophisticated methods to quantify structure of animal habitats (Eitel et al., 2016; Vierling et al., 2008), few studies have applied these technologies to trait-environment

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relationships (Davies and Asner, 2014). The studies that have examined trait-environment relationships using LiDAR have focused on singular traits such as body size or mass (Bradbury et al., 2005; Müller and Brandl, 2009; Vierling et al., 2011) or foraging strategy (Froidevaux et al., 2016; Jung et al., 2012). Animals that use echolocation experience vegetation clutter acoustically, as a series of echoes that complicate their ability to orient themselves or capture prey (Schnitzler et al., 2003). Bats are the most sophisticated echolocators in the animal kingdom (Jones and Teeling, 2006) and the second most diverse order of mammals (Ceballos and Brown, 1995) exhibiting a wide range of adaptations to structures of vegetation (Denzinger and Schnitzler, 2013). For these reasons, bats are an interesting group in which to examine the trait-environment relationships that underpin animal responses to vegetation structure.

Ecomorphological theory predicts that traits of bats, including echolocation calls and morphology, equip bats for differently structured habitats (Norberg and Rayner, 1987; Schnitzler et al., 2003). High frequency calls with linear structures (large bandwidths and short pulse durations) (Grinnell, 1995) allow some bat species to retrieve high resolution acoustic information in complex environments, typical of high clutter (Schnitzler et al., 2003). Other bat species use long duration, low frequency calls, with a small bandwidth which travel long distances, detecting insect wing beats, and so are suited to scanning open habitats (Schnitzler et al., 2003). Small bat species with low wing loading and short, broad wings (low wing aspect ratio), are more maneuverable in clutter than large bat species with high wing loading and long narrow wings, which are adaptations to flying in open spaces (Norberg and Rayner, 1987). Bat species with intermediate traits often use vegetation edges. These trait-habitat relationships have been observed in bat communities in North America (Humes et al., 1999; Loeb and Waldrop, 2008; Morris et al., 2010; O'Keefe et al., 2014; Patriquin and Barclay, 2003), Europe (Jung et al., 2012; Müller et al., 2013, 2012) and Australia (Blakey et al., 2016; Hanspach et al., 2012; Law and Chidel, 2002; Threlfall et al., 2011). However, ecomorphological traits are usually inferred using guilds that group bats with similar adaptations and foraging strategies (Denzinger and Schnitzler, 2013). Very few studies have directly tested relationships between ecomorphological traits of bats to forest structure, none of which have used LiDAR technology to quantify vegetation structure (Farneda et al., 2015; Hanspach et al., 2012; Threlfall et al., 2011).

While there is a large body of literature concerning relationships between bat communities and vegetation structure, LiDAR has only recently been used to support these studies (Fabianek et al., 2015; Froidevaux et al., 2016; Jung et al., 2012; Müller et al., 2013, 2012). Airborne LiDAR has been used to quantitatively estimate vegetation structure across relatively large spatial scales (Froidevaux et al., 2016; Jung et al., 2012). However Terrestrial Laser Scanning (TLS) has so far only been used to record single metrics of below-canopy vegetation density (Müller et al., 2012) and percentage of vegetation-free space (Müller et al., 2013), though these metrics showed promise in identifying understorey structure suitable for foraging bats (Müller et al., 2013, 2012). The structure of understorey is likely important for bats that fly below the canopy such as clutter-tolerant and edge-adapted bats, influencing their ability to navigate and capture prey (Brigham et al., 1997a; Rainho et al., 2010). As TLS describes below-canopy vegetation structure more accurately than airborne LiDAR (Dassot et al., 2011; Hilker et al., 2012) further exploration of this method is needed to characterise habitats of the many bats that fly below the canopy (Denzinger and Schnitzler, 2013).

For this study, we bring together TLS-derived structural variables (20) and ecomorphological traits (8) of 11 bat species to identify the trait-environment relationships that underpin diverse bat responses to below-canopy vegetation structure (i.e. structure of the vegetation understorey). We used bat acoustic surveys, trait measurements for individual species and TLS to test for bat community relationships with vegetation structure at the overall level (total activity and foraging activity), the species level and the trait level. We predicted total bat activity and foraging would decrease with clutter, measured by vegetation density, cover and gap volume. We also predicted that variability in these relationships would be driven by diverse ecomorphological traits of the bat community.

2. Methods

2.1. Study area

We surveyed bats in Koondrook, Perricoota and Campbells Island State Forests in south-eastern Australia, on the River Murray (144.36° E, 35.72° S, Fig. 1) where long-term mean daily maximum and minimum air temperatures were 22.3 °C ± 2.6 (SE) and 9.0 °C ± 1.9, respectively (1957–2014, Echuca Aerodrome station, Australian Bureau of Meteorology, BOM, 2014). Average annual rainfall was low but highly variable (429 mm ± 95, 1914–2013, BOM, 2014). The large natural forest of predominantly flood-dependent river red gum *Eucalyptus camaldulensis* (~36,000 ha) was surrounded by a cropped and grazed agricultural landscape (Fig. 1). Forest structure, growth and recruitment is highly dependent on flooding from the Murray River, affected by nearly a century of river regulation (Stefano, 2002) and timber harvesting since the 1800s. This disturbance regime has created a mosaic of forest ages and structures, useful for examining the relationship between bats and forest structure. We surveyed insectivorous bats and forest structure when the forest was dry, after extensive inundation (2–3 weeks before), and so we assumed flooding uniformly affected bats and their insect prey across the study area (Blakey et al., 2016).

2.2. Bat surveys

We recorded echolocating bats at 47 sites using Anabat acoustic recorders (Titley Scientific, Columbia, MO, USA), from 10th December 2012 to 10th January 2013. Sites were stratified across four thinning categories (unthinned regrowth (14), recently thinned (10), medium-term thinned (12) and reference forest (11)) to provide a range of forest structures by incorporating stands with a variety of logging histories. Sites were previously described (Blakey et al., 2016) except for one unthinned site and one recently thinned site, which could not be accessed with the TLS. We replaced these with two unthinned sites to increase the number of cluttered sites. We did not use thinning categories in the analysis, given that forest structure was more important than time since thinning (Blakey et al., 2016). Acoustic detectors were calibrated to detect a frequency of 40 kHz at 15 m, using a bat chirper (Nevada Bat Technology, Las Vegas, USA) to minimise recording calls from bats flying above the canopy. Ultrasonic microphones were placed 1 m above ground, protected from the weather within S-bend PVC pipes, and pointed vertically at a 45° angle toward small vegetation gaps to reduce sound attenuation from vegetation clutter (Patriquin and Barclay, 2003). Detectors recorded from dusk to 1 h after dawn, for 2–6 nights at each site, outside full moon periods (±3 days). We did not sample during rainfall or strong winds, with sampling when mean nightly temperatures averaged 23.0 °C (16.2–30.6 °C). Number of nights varied between sites due to site accessibility and equipment failure. Average distance between sites was 822 m (384–1492 m).

We analysed bat calls (separate calls were call files comprising a sequence of pulses), using automated call identification software *Anascheme* (Adams et al., 2010), with a local identification key and a filter to identify bats calling with alternating frequencies. The identification key separated bat calls from noise files, allowing specification of species or genus. The key produced <1% misclassifications when tested against independent reference calls (Blakey et al., 2016). We grouped two genera with similar calls among species: *Nyctophilus* and *Mormopterus*. Feeding buzzes of bats, produced when honing in on prey, were identified using a filter in *Anascheme*, as rapid sequences of short, linear pulses. These buzzes were unlikely to be drinking calls,