Advances in animal ecology from 3D-LiDAR ecosystem mapping

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The advent and recent advances of Light Detection and Ranging (LiDAR) have enabled accurate measurement of 3D ecosystem structure. Here, we review insights gained through the application of LiDAR to animal ecology studies, revealing the fundamental importance of structure for animals. Structural heterogeneity is most conducive to increased animal richness and abundance, and increased complexity of vertical vegetation structure is more positively influential compared with traditionally measured canopy cover, which produces mixed results. However, different taxonomic groups interact with a variety of 3D canopy traits and some groups with 3D topography. To develop a better understanding of animal dynamics, future studies will benefit from considering 3D habitat effects in a wider variety of ecosystems and with more taxa.

3D ecology: the importance of structure

The 3D structure (see Glossary) of ecosystems has long been understood to have profound effects on animal communities. As early as 1935, the vertical structure of vegetation was recognised as an important factor for bird assemblages [1], with the first attempts to quantify this relation made in 1961 [2]. This early work demonstrated that, in deciduous forests, bird diversity was determined solely by vegetation structure, with plant species diversity only important when it influenced this structure. Although there has been subsequent debate on the relative importance of vegetation physiognomy compared with floristic composition and other factors (e.g., prey abundance) for animal distributions and diversity, especially for birds [3–10], it is clear that the 3D structure of ecosystems influences many aspects of animal ecology, ranging from species distributions and abundance [11–14] to behaviour [15] and patterns of predation risk [16,17]. Indeed, several studies have shown it to be the principal driver of animal diversity across different taxa (see [2,3] for birds and [14] for primates).

All animals live in a physical habitat with a 3D structure. Vegetation 3D structure is thought to influence animals through several processes (Box 1), including the availability of niches for species coexistence [11,18,19], alteration of microclimate [20,21], and providing concealment from predators [22,23]. In turn, animals also influence vegetation structure through mechanisms such as consumption [24–26] and seed dispersal [27–29]. Important feedback loops are also likely to occur because the structure of the vegetation influences the behaviour of animal populations and communities, which subsequently affects plant distribution and structure [6,30]. The dynamics of ecosystem structure are not limited to biotic components and interactions; abiotic factors such as landscape topography are also of consequence, affecting animal dynamics by altering hydrological patterns [31,32], habitat accessibility, temperature, and other microclimatic factors (Box 1) [33].

Thus, understanding ecosystem 3D structure and its biotic effects is fundamental to advancing ecological theory and understanding. However, until recently, data on 3D structure were difficult and labour intensive to collect, especially over large spatial scales. Habitat models relied on field data of limited spatial extent or passive remote sensing techniques (such as aerial photographs and satellite images) that are unable to penetrate past the uppermost portion of the canopy and characterise the vertical distribution of vegetation canopies and tissues [34]. Recent advances in remote sensing technology, particularly LiDAR (Box 2), successfully addressed these difficulties, enabling accurate measurement of the 3D structure of ecosystems across spatial scales from tree branches to entire landscapes [34,35]. Much scientific effort has gone into validating the accuracy of LiDAR measurements and exploring possibilities for their application in ecology

Glossary

Canopy cover: the extent of the canopy in 2D (*x* and *y*) horizontal space.
Canopy height: the vertical (*z* dimension) height of the canopy above the ground.
Canopy structural complexity: the amount of detail and number of components present in the canopy layer. Greater structural complexity is characterised by more branches and greater connectedness of tree canopies.
Canopy structural variability: variation in the vegetation canopy layer, encompassing vertical (canopy height and vertical distribution) and horizontal (canopy cover and extent) variation.
Canopy vertical distribution: the vertical spread of canopy components and tissues (e.g., tree branches and leaves).
Horizontal structure: structure in the *x* and *y* dimensions, including canopy cover and vegetation extent.
Light detection and ranging (LiDAR): an active remote sensing technology that emits and receives its own near-infrared light to measure 3D structure (Box 2).
Structure: the physical arrangement of individual components into a complex whole. In relation to 3D ecosystem structure, it refers to the physical arrangement of vegetation and ground elements.
Understory vegetation: any vegetation layer that is beneath the uppermost canopy.

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Box 1. Direct and indirect interactions between animals and 3D ecosystem structure

The 3D properties of vegetation and/or terrain create the habitat setting for all animals. At broad spatial and temporal scales, climate, soils, and disturbance regimes are key to determining vegetation structure at the biome scale (e.g., forest, savanna, or grassland). Within any given biome, vegetation structure modifies local-to-landscape abiotic conditions that contribute to variation in microhabitats, with direct and indirect effects on animals. Animals interact directly with vegetation structure, such as primates climbing trees and occupying the upper layers of the canopy as habitat [13]; however, vegetation structural effects are often indirect, being important in the way that they alter habitat conditions, such as the amount of light reaching the ground or lower vegetation layers, local temperature, and the relative humidity of a habitat.

Structural effects also include the 'shaping' of habitat through structural features, including canopy openings or closures, and features that might obstruct animal mobility and movement. Structure further influences the surface area and availability of niches for competing species. Habitats with increased structural complexity in the form of a higher canopy, greater canopy cover, or more vegetation layers will have a greater volume of potential habitat (including greater branch and leaf surface area) available for species to occupy, conceivably leading to greater species richness.

Vegetation structure can not only be related to the species present in a habitat (floristic composition), but also influence which species (both flora and fauna) can establish, thus influencing species diversity and composition. Such effects will regulate the availability of prey and forage, and influence ecosystem processes such as the amount and quality of nutrients in soils, thus modifying biotic interactions. Animals themselves also influence vegetation structure, shaping it through their foraging and seed dispersal activities [25,26].

Ground terrain similarly influences animals through direct effects such as the steepness of slopes [32] and indirectly through effects on hydrology [31,79] or temperature related to aspect [33,72]. Terrain can also impede animal movement at broad (e.g., mountains or ridges) and fine scales (e.g., obstacles that hinder escape from predators [17]), as well as block the line of sight of an animal [15]. Air movement can be diverted by terrain, interfering with olfactory cues and similar interactions, such as the use of scent by an animal during hunting or foraging.

[34,36], with a strong consensus that LiDAR is both accurate (often more so than ground measurements) and valuable for elucidating relations between animals and 3D ecosystem structure [37–39]. LiDAR is not the only tool available for measuring ecosystem structure; field-based methods, active radar sensors [40], and image matching [41,42] are examples of alternative techniques, yet LiDAR is arguably the most promising in terms of both accuracy and cost-effectiveness over large spatial scales that are meaningful at the ecosystem level (Box 2) [34,35,43].

With the accuracy and feasibility of LiDAR for ecological studies having been repeatedly demonstrated, a review of the knowledge gained through the application of LiDAR to animal ecology is timely and potentially transformative. Previous syntheses (e.g., [34,36,44–46]) focussed largely on the technology and its potential application to ecology, with some limited to forested environments [44,45]. There now is a need to move the science beyond verification of the remote sensing method to its application across a range of habitats, animal communities, and ecological questions, using it to further unravel observed relations between animals and ecosystem structure. Here, we synthesise the knowledge gained from recent studies using 3D-LiDAR measurements of vegetation and topography as applied to animal ecology. We divide the available literature into three broad taxonomic groups: birds and bats; nonflying mammals; and invertebrates, aiming to reduce the disparate literature into a clear and straightforward set of reductions. We also uncover current biases and gaps in the literature, and conclude with suggestions on where and how future research is likely to be most informative for advancing animal ecology.

Advances in 3D animal ecology

Flying vertebrates: birds and bats

Flying animals (birds, bats, and flying invertebrates) inherently move and live in 3D space. Therefore, vegetation structure will influence all aspects of their ecology, from habitat characteristics to movement in flight. It is not surprising then that the bulk of the literature, including the earliest vegetation structure–animal ecology studies [2], has focusses on birds.

Most of the 23 avian studies reviewed found a positive relation between bird richness and abundance (including activity or occurrence) and canopy structural variability and complexity, vertical tissue distribution, and overall height ([3,6,12,36–38,47–57], Table 1, see Box 3 for descriptions of structural metrics). Similarly, of the three published studies investigating bat responses to 3D vegetation structure [7,58,59], two reported bat activity and occurrence to increase under conditions of increasing canopy structural variability [59] and height [58,59] (Table 1). Only three avian studies recorded a negative relation between some bird species and canopy complexity [37,38,52], and none did so for bats. Moreover, within each of these three studies, not all species responded negatively. Out of 16 riparian bird species evaluated, six exhibited a neutral response to increased canopy structural complexity, whereas nine responded positively and only one species (Bullock's oriole, *Icterus bullockii*) decreased with increased complexity [52]. Similarly, out of 23 passerine species investigated [37], seven decreased in abundance with taller canopies and six increased. However, only one species (nuthatch, *Sitta europaea*, which increased with taller canopies) decreased in abundance with increasing canopy structural variability. Differences in response are also influenced by functional guild. Scrub species in temperate forests decreased in richness with increasing canopy height, whereas the richness of forest guild species increased [38]. The ecological effects of increased canopy structural complexity likely extend beyond effects on bird and bat diversity and activity. In Hawaiian habitats, for example, native birds that are adapted to the high structural variability of native tree species help prevent the spread of structurally simple invasive trees by outcompeting the non-native birds that are effective dispersers of the invasive tree [6].

Although most studies report significant relations between elements of canopy structure and birds, LiDAR has shown that patterns are not always clear-cut and consistent, even within a single species. For example, in British woodlands, great tit (*Parus major*) chick mass, an indicator of breeding success and habitat quality, increased with increasing canopy height during abnormally warm springs, but decreased in colder springs [36]. This study revealed links between habitat quality and climate that

Box 2. LiDAR: measuring structure

LiDAR is an active remote sensing technique in the sense that the sensor emits its own light (Figure I). This contrasts with traditional passive remote sensing techniques, such as satellite imagery and aerial photography, which rely on reflected radiation from the surface originating from the sun. LiDAR instruments emit short-duration laser pulses that illuminate a target and measure its location in three dimensions (*x*, *y*, and *z*). Given that the time the pulse is emitted and received back to the sensor is known, as well as the exact position of the sensor in space (including the roll, pitch, and yaw when on board an aircraft), the distance to the object can be calculated and the vertical distribution of the surface measured. LiDAR sensors emit near-infrared (NIR) light, typically between 900 and 1100 nm. In this wavelength range, vegetation foliage is partly transmissive, allowing the NIR light to pass through the canopy to the ground. With each interaction of the light with the canopy elements, such as foliage, some of the light is returned to the sensor, allowing for a digitisation of the vertical distribution of the canopy tissues. In addition, some light passes through gaps in the foliage to reach the ground.

LiDAR sensors are usually mounted on aircraft (airborne LiDAR), although ground-based systems also exist. The resolution at which the laser-return 'point cloud' data are collected, from which 3D models are built, depends on instrument specifications (e.g., scan angle and mirror rotation frequency) and the distance between the sensor and the target. The closer the sensor is to the object, the greater the point cloud density and the higher the resolution of the LiDAR data. However, the closer the distance, the smaller the area covered by the laser footprint. See [35] for additional details.

Although aspects of LiDAR data collection and analysis are expensive, it is cost-effective over large areas compared with field surveys, and it is becoming increasingly available in many regions [34]. Furthermore, because of certain fixed costs, the cost of LiDAR per hectare decreases with the area covered during a survey campaign [18,43]. Given the financial and time investment needed to collect reliable field data, such studies are often limited in their spatial extent and conducted at spatial grains that are too coarse to be relevant for management [43]. LiDAR data can address these difficulties by collecting fine-scaled, reliable data over large spatial extents. Nevertheless, LiDAR cannot easily determine floristic species composition or animal distributions, necessitating field surveys. Therefore, remote sensing facilitates, rather than impedes, field-based studies.

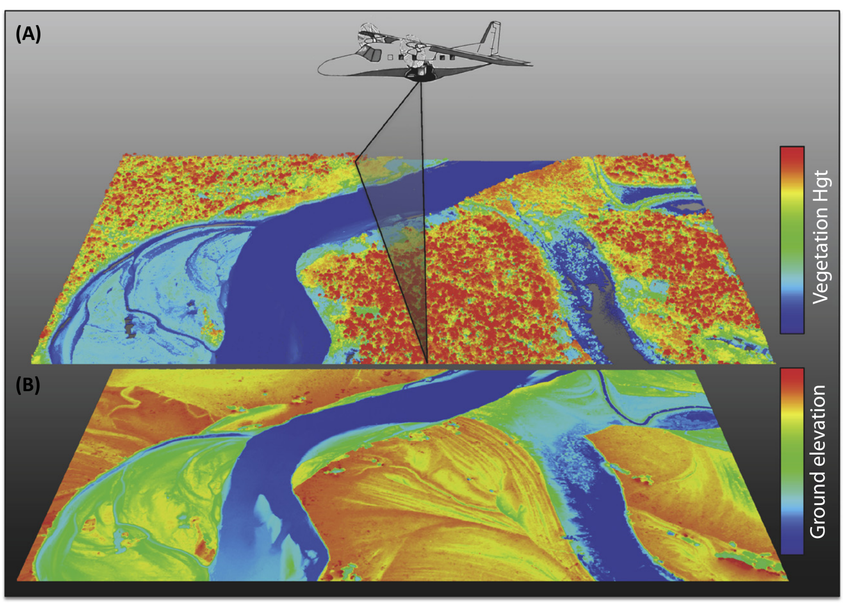

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Figure I. Example of airborne Light Detection and Ranging (LiDAR) data collected over lowland Amazonia by the Carnegie Airborne Observatory [96]. Laser pulses are sent and returned to a LiDAR sensor on board an aircraft, scanning from side to side as the plane moves forward in the air, creating a 2D spatial coverage. Each near-infrared wavelength laser beam penetrates the canopy, returning light along its pathway to the ground. This interaction is digitised by the LiDAR receiver, and is used to map vegetation height **(A)**, underlying terrain **(B)**, and the layering of the vegetation in between (not shown).

were only discovered due to the high level of accuracy inherent to LiDAR-based measurements of vegetation 3D structure. An individual bird species might also show variable responses to seemingly similar canopy structural metrics, thereby highlighting the importance of nuanced differences in structural attributes that are only discernable with LiDAR. For example, the abundance of song thrushes (*Turdus philomelos*) increased with mean canopy height in Bavarian forests, but abundance decreased with increasing maximum canopy height [37].

Canopy cover is another important measurement of vegetation 3D structure that is determined, at least in part, by both canopy structure and plant species composition. It alters environmental variables beneath the canopy, such as temperature and solar radiation, and has been shown to significantly influence bird communities (Table 1). Although overall species diversity [3,51] and native species [6] displayed positive relations with increasing cover, out of 15 individual bird species investigated in LiDAR based studies, eight increased (either in abundance, occupancy, or nest site preference) [19,20,48,49,54] and six decreased [19,54]. Therefore, avian species consistently display higher preference for vertical canopy structural complexity than they do for simple canopy cover alone. Although variation in canopy structure generates increased habitat heterogeneity, which is conducive to increased avian diversity [60,61], it is unlikely that canopy cover does the same. Increased canopy cover could well create more uniform landscapes because of

Table 1. Published LiDAR-based vegetation and topographic 3D structure studies in relation to animal ecology[a]

Taxonomic group	Structural attribute	Response	Refs
Birds and bats	Vegetation		
	Canopy heterogeneity	22 (out of 44) species occupancy increased with increasing heterogeneity	[37,47–50,52,53,57]
		Two (out of 44) species occupancy decreased	[37,52]
		Species richness increased	[51]
		Bat activity and occurrence increased	[59]
	Canopy vertical distribution	Two species (out of two) increased abundance and/or occupancy with increasing vertical distribution	[50,53]
		Species diversity increased	[3,51]
	Canopy height	Chick mass increased in blue tits, decreased in great tits, was climate dependent for great tit chick mass (increased in warm springs, decreased in cold springs) with increasing height	[36,56]
		Native to exotic species ratio increased with increasing height	[6,12]
		Species richness (forest species richness increased, scrub species richness decreased)	[38]
		21 (out of 49) species abundance and/or occupancy increased with increasing height	[37,47–50,52,54,57]
		Nine (out of 49) species abundance decreased	[37,57,66]
		Species diversity increased	[3,55]
		Bat activity and occurrence increased	[58,59]
	Canopy cover	Native to exotic species ratio increased with increasing cover	[6]
		Species diversity increased	[3,51]
		11 species (out of 23) increased abundance and/or occupancy with increased cover (horizontal extent and foliage density)	[19,20,48,49,54,57]
		Six species (out of 23) decreased abundance and/or occupancy with cover	[19,54]
	Understory density	Species diversity increased with increasing density	[3,51,55,65]
		12 (out of 34) species increased abundance and/or occupancy with increasing understory density	[19,50,53,57]
		Seven (out of 34) species decreased abundance and/or occupancy with increasing understory density	[19,37,49]
		Foraging bat abundance decreased with increasing density	[7,58]
	Horizontal structure	Two species (out of two) preferred intermediate or mixed levels of horizontal structure	[47,67]
		Species richness increased with increasing patch diversity	[51]
	Contiguous forest	Native to exotic species ratio increased with larger forest patches	[12]
		One species (out of one) preferred larger forest patches	[66]
	Topography		
	Elevation	Species richness decreased with increasing elevation	[51]
	Slope	Species richness decreased with increasing steepness	[51]
Nonflying mammals	Vegetation		
	Canopy vertical distribution	Two species (out of three) preferred increased vertical distribution, one avoided it	[13,32,72]
	Canopy height	Three species (out of five) preferred increased height, one avoided it. Moose made use of increased height (and denser canopies) during high temperatures	[13,32,70–72,92]
	Canopy cover	Three species (out of four) preferred increased cover, one avoided it. Roe deer preferred increased cover in cold weather, but avoided it when foraging	[32,70–73]
	Understory density	Two species (out of two) preferred increased density for hunting, three (out of three) for foraging. Roe deer avoided understory when resting	[15,17,70,72,73]
	Contiguous forest	One species (out of one) preferred larger forest patches	[71]
	Topography		
	Elevation	Mule deer preferred higher elevation in winter	[72]
	Aspect	Mule deer preferred warmer slopes in winter	[72]
	Ruggedness	Two species (out of two) preferred increased steep slopes for hunting, one (out of one) for nesting	[17,32]

Table 1 (*Continued*)

Taxonomic group	Structural attribute	Response	Refs
Invertebrates	Vegetation		
	Canopy variability	Arthropod diversity increased at the tree scale	[11]
		Beetle and spider species richness increased, and beetle abundance and diversity increased with increasing canopy variability	[18,43]
		Beetle and spider body size decreased with increasing variability	[18,43]
	Canopy density	Arthropod diversity increased with increasing canopy density at tree scale, but decreased at stand scale	[11]
	Canopy height	Beetle body size increased, abundance decreased with increasing height	[43]
		Three butterfly species (out of four) preferred increased height	[76]
	Canopy cover	One butterfly species (out of four) avoided increased cover	[76]
		Individual spider species responded to shade (cover), some avoided it, others preferred it	[18]
	Understory density	Insect abundance increased with increasing density	[7]
		Three butterfly species (out of four) avoided increased density	[76]
	Topography		
	Elevation	Beetle species richness and spider diversity increased with higher elevation	[18,43]
		Spider body size decreased with elevation	[18]
	Hydrology	Termite distributions were restricted to crests above seeplines	[31,79]
		Female carabid beetles preferred steep slopes with high flow accumulation	[33]
	Aspect	Female carabid beetles preferred cooler (north-facing) slopes	[33]
Other taxa	Vegetation		
	Canopy cover	Acoustic diversity decreased with increasing cover	[63]
	Understory density	Acoustic diversity increased with increasing density	[63]
	Contiguous forest	Acoustic diversity decreased with contiguous forest	[63]
	Topography		
	Ruggedness	Fish species richness and abundance increased with increased reef rugosity	[97]
		Out of four lizard species, two preferred flat areas and two were widespread. All individual lizards selected preferred sites with increased solar radiation	[98]
	Beach dynamics	Sea turtles nested on beaches within a tolerable range of topographic variables, with slope (compared with neighbouring regions) being particularly important	[99]
		Sea turtle-nesting success decreased with increased alteration of beach morphology following hurricane activity	[100]

[a]Five unique studies describing acoustic diversity [63], fish species richness, and abundance responses to 3D structure [97], lizard habitat preference in relation to topographic structure [98] and sea-turtle nesting sites [99,100] are included, but not discussed in the main text due to the limited number of studies.

increased shading and fewer canopy gaps, which are known to contribute to plant diversity and animal distributions [62,63].

Vegetation 3D structure beneath the uppermost canopy has been revealed and mapped through recent advances in LiDAR technology [64], with its importance for both birds and bats demonstrated (Table 1). Several studies found that bird diversity [3,51,55,65] and individual bird species [19,38,53,66] increased with increasing understory plant density, whereas others measured decreases [37,49]. The abundance of open-foraging bats decreased in areas of high understory plant density [7,58]. These differences in response result from differing habitat requirements. For example, open habitat-foraging bat guilds are adapted to forage in forest gaps and are unable to utilise areas of high vegetation density even when they contain higher prey abundance, whereas other bat species have more inflight manoeuvrability and are unperturbed by understory vegetation [7]. Other species, particularly within understory specialist guilds, actively seek out dense understory vegetation. For example, the reproductive success of black-throated blue warbler (*Dendroica caerulescensis*) is positively influenced by understory plant density [50].

Horizontal structure in the form of vegetation extent as well as topographic variables also influences avian ecology (Table 1). Bird species richness [51], and at least two individual species [47,67], displayed a strong preference for heterogeneous horizontal vegetation structure and patch dynamics, whereas willow warbler (*Phylloscopus trochilus)* [66] and native Hawaiian species [6] preferred

Box 3. Describing vegetation structure

LiDAR has enabled measurement of 3D ecosystem structure like never before. However, there is a plethora of terms used to describe 3D structure, with the possibility of confusion arising as to what different terms mean. This is heightened by a lack of concise definitions presented in the literature. In the broadest sense, there are differences between vertical and horizontal structure. Vertical vegetation structure refers to the arrangement of canopies and tissues in the *z* dimension (e.g., canopy height, Figure I), whereas horizontal vegetation structure refers to these arrangements in *x* and *y* [e.g., canopy cover and forest extent (including patch connectivity)]. It is possible to measure horizontal structure with passive remote sensing techniques, but vertical structure is only quantifiable with active remote sensing. Vegetation vertical structure involves the arrangement (distribution and layering) of canopy and understory elements as well as their height. Vertical structural heterogeneity refers to the variability of canopy dynamics (canopy structural variability), and incorporates variation in aspects such as canopy height and the vertical distribution of canopy layers and tissues (where in the canopy, including the vertical spread, branches and tissues are positioned). Canopy structural complexity increases when there are more components (layers and tissues) to the canopy (Figure I).

Canopy understory (vegetation beneath the uppermost stratum of the canopy) can be measured with newer LiDARs because of the high wattage of the newest lasers, and because of the transmissive nature of the NIR light emitted by the sensor (Box 2). Understory vegetation can be extracted directly from models of the 3D structure of the laser point cloud (Box 2) collected beneath the canopy, or indirectly through the penetration ratio of the emitted light. This ratio can also be used to measure the density of canopies, and serves as a proxy for microclimatic conditions (e.g., light and temperature) in the lower levels of vegetation (e.g., [3]).

Topographic structure (e.g., elevation, terrain roughness, and slope steepness) can also be measured at fine spatial resolutions with LiDAR. An advantage of LiDAR over traditional methods is that the vegetation layer can be removed through modelling techniques, revealing a 'bald' surface (Box 2). This provides a much-improved perspective on landscape topography and can be used to measure topographic features otherwise concealed by vegetation.

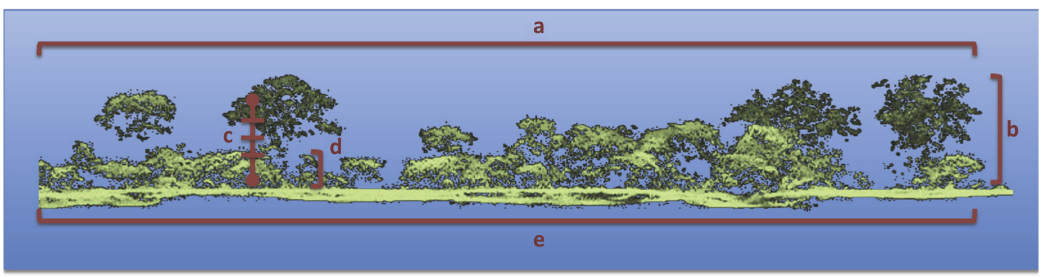

Figure I. Cross-sectional view of African savanna vegetation structure collected by the Carnegie Airborne Observatory. Different aspects of the three-dimensional vegetation structure are defined throughout the paper as: **(A)** canopy cover, **(B)** canopy height, **(C)** vertical layering or profile, **(D)** vegetation understory, and **(E)** topography. Combined, (A–E) define the structural heterogeneity and/or complexity of an ecosystem.

larger patches of contiguous forest. Only a single study investigated bird responses to topographical structure measured with LiDAR [51], finding that overall avian species richness decreased with increasing slope and elevation in North American mixed-conifer forests, but only at one of two study sites.

Although vegetation structure has long been understood to be important for birds and bats, LiDAR technology has revealed which structural metrics are most important and how even subtle structural changes matter. The degree of vertical structural heterogeneity in the canopy layer (measured as canopy structural variability, vertical distribution, and complexity; Box 3) is most conducive to increased diversity and favourable to most species. Habitat heterogeneity enables competing species to coexist and promotes species diversity through the creation of multiple niches [60,61,68,69]. Increased structural heterogeneity in the canopy layer generates a variety of habitats in 3D space, enhancing diversity and favouring most flying vertebrate species. By contrast, canopy height and cover, and the density of understory vegetation, have been shown with LiDAR to have mixed results for bird and bat diversity. This re-enforces the notion that vegetation structural heterogeneity is pivotal to increased bird and bat diversity. Responses to structural changes are further co-mediated by plant growth form and floristic composition, with these acting in concert with structural characteristics to influence bird and bat assemblages (e.g., [6]).

Nonflying mammals

Compared with bird and bat research, fewer studies (eight) have considered interactions between 3D vegetation structure from LiDAR and nonflying mammal species, but all have recorded significant relations between at least one measure of vegetation structure and habitat preference [13,15,17,32,70–73] (Table 1). Together, these studies suggest that, similar to flying vertebrates, the structural heterogeneity of the vegetation underpins population and community assembly of nonflying mammals. At least two species, Pacific fishers (*Martes pennanti*) [32] and mule deer (*Odocoileus hemionus*) [72], were shown to respond positively to increased canopy vertical heterogeneity. More importantly, however, varied responses to vegetation structural measures were exhibited by mammals, even between sexes of the same species [15], emphasising the necessity of heterogeneous landscapes for animal diversity.

Vegetation structure also influences predator–prey relations in different ways. Although open areas (less understory vegetation density) favour female lion (*Panthera leo*) hunting habits in southern African savannas, male hunting success increases in areas of denser vegetation, owing to their close-quarters, ambush style of attack compared with that of females, attesting that, in contrast to conventional wisdom, male lions are adept at hunting, but use a different strategy [15]. Across species, lynx (*Lynx lynx*) predation on roe deer (*Capreolus capreolus*) was greater in areas of dense understory vegetation, whereas human (*Homo sapiens*) hunters targeted open areas (decreased understory). This created contrasting areas of risk for roe deer and few low-risk areas [17]. Such interactions between vegetation structure and predator–prey relationships are likely ubiquitous and changing rapidly as human hunting landscapes expand at the demise of nonhuman predator densities [74,75].

Topographic 3D structure has appeared in more LiDAR habitat studies for nonflying vertebrates than for flying ones (Table 1). Being constrained to the terrestrial surface, such animals have reduced mobility and are strongly influenced by topography, demonstrated by the importance of terrain ruggedness to several species. Ruggedness was an important predictor of successful roe deer hunting for both lynx and human hunters. Steeper slopes enable hunters to get closer to deer, and deer escape routes can be more easily predicted by hunters in difficult terrain [17]. In addition to increased canopy structural complexity, Pacific fishers preferred nest sites on steeper slopes, where they have better access to water [32], providing insight for effective conservation management and planning for this species. Accordingly, these studies suggest that topographically varied landscapes are better at enabling the coexistence of predators and prey, as well as competing species with differing abilities to access rugged areas.

Invertebrates

From the eight studies available for review, variability in the canopy profile (both vertical and horizontal), or 'structural variability' (Box 3), rather than a single structural metric, was most important for invertebrate assemblages (Table 1). Beetle [43] and spider [18] species richness, as well as beetle abundance and diversity [43], increase with increasing canopy structural variability. Differences in canopy height have also been an important predictor of invertebrate prevalence, with three butterfly species preferring areas of increased canopy height [76], whereas beetle abundance decreased with canopy height [43]. Most invertebrates, because of their small size, function at small spatial scales (tens of meters), with response patterns to structural variables changing over similarly small scales. Müller *et al.* [11] found higher arthropod diversity with increased canopy structural variability and density at the tree scale, but significantly lower diversity at the stand scale, suggesting that the highest levels of arthropod diversity will be in forests with relatively open stands containing individual trees with dense crowns. Such insight was only possible because of the unique ability of LiDAR to accurately map forest structure at a fine resolution over a broad spatial extent.

Canopy cover has had mixed effects on invertebrates. One butterfly species avoided it, whereas three others were unaffected [76]. Some individual spider species showed preference for increased shading and, therefore, preferred higher canopy cover, whereas others avoided it, favouring increased levels of solar radiation [18]. The mixed responses that invertebrates display to both canopy structural variability and height, and canopy cover, imply that habitat heterogeneity is essential for their biodiversity in similar ways to birds, bats, and nonflying mammals. Different groups (overall arthropod diversity [11], spiders [18], and beetles [43]) increase in richness and abundance with increasing canopy structural variability, but results are mixed in terms of simple canopy cover.

Beyond diversity and autecology, LiDAR measurements have revealed relations between invertebrate body size and vegetation structure (Table 1). Body size has important implications for organisms through its effect on thermoregulation and energetics [77], and appears to respond to vegetation structure in directions opposite to those of diversity. Whereas beetle [43] and spider [18] species richness increased with increasing canopy structural variability in temperate forests, the body size of both groups decreased. Furthermore, beetle abundance increased with increasing canopy height, but body size decreased [43]. Body size variation has been clearly linked to climatic factors [77] and, although arthropods exhibit variable responses, European spider body size declines with temperature [78], in line with increasing canopy structural variability [18], which affects temperature and moisture regimes through opening up of the canopy. Therefore, vegetation structure, through influences on climate, can have effects not only on animal distributions and diversity, but also indirectly (Box 1) on morphological attributes.

LiDAR studies have shown that invertebrates respond to topographic 3D structure, particularly through indirect effects on hydrological dynamics. Termite mounds of the genus *Macrotermes* are clustered on crests above hydrological seeplines in savanna catenal landscapes to avoid inundation from flooding [31,79], while also occurring at higher densities on crests with higher woody cover [79]. Carabid beetles (Coleoptera, Carabidae) also respond to topographical effects on hydrology, with a higher proportion of female beetles found on steep and cool slopes that have high levels of flow accumulation, providing better access to water [33].

Current biases in 3D-habitat mapping

Most LiDAR-animal ecology studies conducted thus far are strongly biased toward birds in forested landscapes of North America and Europe (Figure 1), and have remained so since the earliest studies [34]. This is somewhat understandable given: (i) the inherent 3D nature of bird ecology; (ii) the appeal and suitability of LiDAR for mapping forested environments [80]; and (iii) the relatively greater availability of LiDAR funding resources and expertise in North America and Europe. However, this has limited the current potential of LiDAR to better understand how 3D ecosystem structure affects animal dynamics. Successful LiDAR-based studies of nonflying mammals, invertebrates, and acoustic diversity (Table 1) have been carried out in Africa and South America, and in ecosystems other than forests, with new insights gained; however, because of the paucity of studies, it is difficult to make broad statements of understanding for these taxa or regions. Moreover, even though most studies focussed on birds, none of

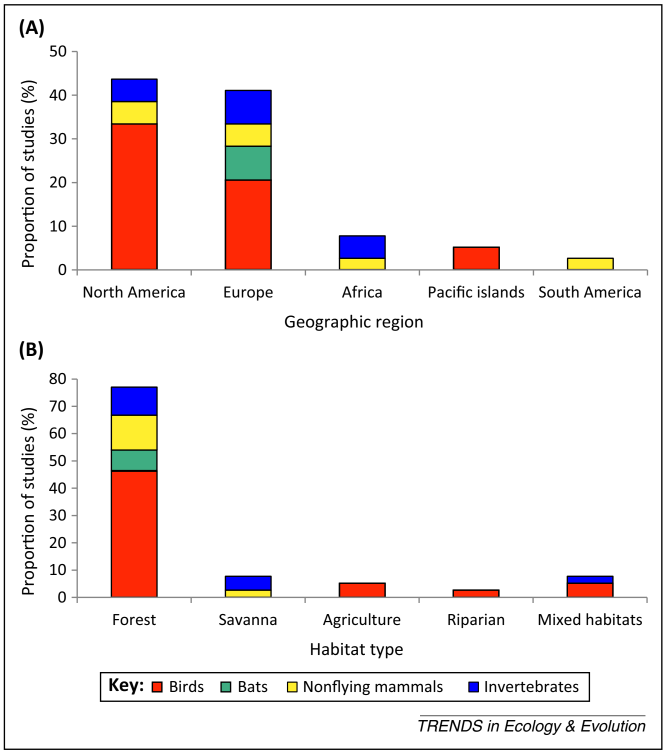

Figure 1. The proportion of studies investigating animal responses to 3D structure as measured and mapped with Light Detection and Ranging (LiDAR). The studies are reported by taxonomic group based on **(A)** geographic region and **(B)** biome type. No published studies exist in regions or biomes not presented here.

these are outside of North America, Europe, or Hawaii, and not a single LiDAR animal ecology study has been reported from either Asia or Australia.

Although forests are often perceived as harbouring high vegetation structural heterogeneity with pronounced animal responses in these environments, all biomes contain highly variable levels of vegetation and topographic structure. Any universal model describing structural effects on animals will need to consider these other biomes, as well as taxonomic groups other than birds. Several biomes are undergoing vast structural changes. In areas where deforestation and forest degradation is on-going (e.g., tropical forests [81,82]), structural complexity and heterogeneity are decreasing, whereas in other areas, bush encroachment and woody thickening are either increasing or decreasing vegetation structural complexity [83,84]. An understanding of how these vegetation changes will affect animals cannot be achieved without detailed knowledge on the interactions between animals and vegetation structure in multiple environments and across various taxonomic groups (e.g., [85]).

Synthesis

LiDAR technology has revealed strong influences of 3D ecosystem structure on animal diversity and distribution, many of which were previously indiscernible. This has revealed the importance of 3D structure relative to the more commonly measured metric of canopy cover, finding vertical structure to be more influential in predicting animal dynamics, especially for birds and invertebrates. Increased structural heterogeneity usually leads to increased richness and abundance, whereas canopy cover has mixed results. There is a strong emphasis on measuring vegetation cover as a proxy for vegetation structure and ecosystem pattern (e.g., [86]), but cover increases do not always lead to increased animal diversity. In fact, this synthesis shows that it often leads to a reduction in animal diversity, with richness and abundance positively responsive rather to 3D vertical structural heterogeneity. Given the relatively few studies to date using LiDAR to investigate animal responses to 3D structure, and the current biases in the literature, we are not yet able to construct a detailed universal model of exactly which components of 3D vegetation or topographical structure matter most for animal diversity or specific guilds. However, the literature does indicate that structural heterogeneity is most conducive to increased animal diversity, following the general heterogeneity–diversity hypothesis [60,61]. This implies that landscapes with greater structural heterogeneity (e.g., natural forests compared to plantations) are more desirable for increased animal diversity. Moreover, the studies that do exist on a great variety of taxa and ecosystems demonstrate that LiDAR has the potential to yield insights across taxa and, if applied more broadly, will further advance our understanding of the relations between animal ecology (diversity, distributions, and behaviour) and vegetation structure.

Although structural heterogeneity leads to a general increase in diversity by promoting species coexistence, differences in response across taxonomic groups suggest that different components of 3D structure matter more to different groups. Flying vertebrates respond to 3D vertical structure, canopy cover, and understory density (Figure 2), but species richness and abundance (and/or occupancy) increase more consistently with 3D vertical structural heterogeneity. Responses to canopy cover and understory density are mixed, being positive for some species and negative for others. Being constrained to the surface and smaller scales, topographic structure has been found to be more consequential for nonflying mammals and invertebrates than for flying vertebrates (Figure 2B). Canopy cover has also been shown to have positive effects on nonflying mammal species, whereas understory vegetation density influences predator hunting habits. Vertical structural heterogeneity has had mixed results for this group. Giving their diverse range of life forms, invertebrates respond to various 3D structural components, including vertical heterogeneity, understory density, and topographic structure, but less so to canopy cover (Figure 2).

Despite the importance of 3D structure for animal ecology, vegetation growth form and floristic composition still have profound impacts on animal communities. There is long-standing debate on the relative importance of each for animals [3–9,14], with strong cases argued for both structure and floristic composition. In reality, they are likely to work in concert with species composition, affecting structure by dictating the persistence of specific growth forms, species, or plant communities. For example, floristic composition and vertical structure were indistinguishable and equally important in predicting avian abundance in Hawaiian habitats [6]. Structure might or might not be determined by the species composition, but where it is,

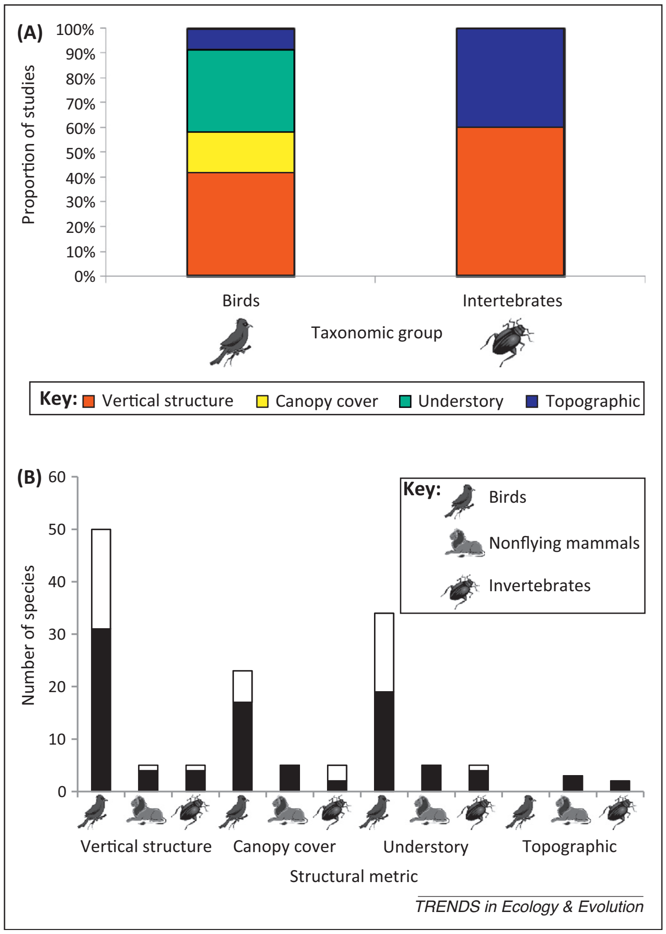

Figure 2. Interactions between animal groups and the three major components of 3D vegetation and topographic structure (Box 3) measured with Light Detection and Ranging (LiDAR). **(A)** Proportion of published studies recording an increase in species richness and/or diversity with each major structural metric. **(B)** The number of published studies recording a significant (either positive or negative; black bars) or neutral response (open bars) on animal abundance. No published studies on nonflying mammal richness were found.

these two aspects of plant communities will have profound effects on animals and, thus, they need to be considered together. Given that LiDAR cannot easily detect variation in plant composition, field-based studies or other remote sensing approaches are necessary, complementing LiDAR structural data. Such studies provide an opportunity to disentangle the relative importance of physiognomy and composition for animal ecology (e.g., [3]) across taxonomic groups and geographical regions, where responses are likely to differ [87]. Before the advent of LiDAR, such studies were difficult to conduct because measurements of vegetation structure were severely restricted, both in precision and spatial extent.

Concluding remarks and future directions

Much of the application of LiDAR to date has focussed on investigation of already known or suspected ecological relations, such as increased heterogeneity leading to increased animal diversity. Potential exists to make use of the technology and its ability to measure ecosystem complexity and heterogeneity to unravel the mechanistic underpinnings and finer details of such broad relations. Simple positive relations between heterogeneity and diversity have recently been challenged [88,89] and the shape of the relation shown to differ between habitats and the measures of heterogeneity used [90]. Many studies investigating heterogeneity–diversity have suffered from not being able to accurately measure 3D vegetation structure (an important component of heterogeneity) accurately or over large spatial extents [90]. LiDAR is capable of providing such data and should be used to decipher such relations.

In conjunction with GPS telemetry data [91], LiDAR provides an excellent opportunity to assess how animal movement is affected by vegetation and topographic structure. New insights and finer details about how animals make decisions based on habitat structure, from activities as diverse as hunting [15,17] and thermoregulation [92], have been achieved with LiDAR data. Such insight can lead to a deeper understanding of how animals interact with their environment and each other, including how competing species might spatially avoid each other and coexist through use of ecosystem structure.

Future animal ecology studies will benefit by including structural aspects shown to be important in this synthesis in their analyses, and by placing higher priority on metrics produced by LiDAR that address these more directly, such as measurements related to vertical structural heterogeneity and complexity, as well as topographical features. Helpful reviews of the more useful metrics available from LiDAR are provided by [45,46,93]. Furthermore, although structural heterogeneity is most favourable for increased diversity, exactly which structural elements should display the most heterogeneity for increased diversity, and whether these components are consistently important across taxa and biomes, warrant further investigation.

The use of LiDAR data should be extended beyond only taxonomic diversity to investigate how ecosystem structural components, relative to species composition, affect functional diversity and ecosystem services. Given the current rapid loss of biodiversity and its impacts on ecosystems [94,95], such understanding will be imperative and inform which structural components are necessary to sustain ecosystem functioning and prevent further losses. Multitrophic interactions in relation to ecosystem structure are another avenue of research that is currently lacking. Presently, only two studies exist using LiDAR ([15,17]), both demonstrating influences of vegetation structure on predation success, and highlighting the need for heterogeneous landscapes to facilitate biodiversity and species coexistence. LiDAR holds tremendous promise for deepening our knowledge and understanding of structural effects on animal dynamics, providing habitat information that is otherwise unattainable, and should be applied with greater vigour to unravel the nuances of plant–animal relations at ecosystem to global scales.

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References

1 Dunlavy, J.C. (1935) Studies on the phyto-vertical distribution of birds. *Auk* 52, 425–431
2 MacArthur, R.H. and MacArthur, J.W. (1961) On bird species diversity. *Ecology* 42, 594–598
3 Müller, J. *et al.* (2010) Composition versus physiognomy of vegetation as predictors of bird assemblages: the role of lidar. *Remote Sen. Environ.* 114, 490–495
4 Fleishman, E. and Mac Nally, R. (2006) Patterns of spatial autocorrelation of assemblages of birds, floristics, physiognomy, and primary productivity in the central Great Basin, USA. *Divers. Distrib.* 12, 236–243
5 Anderson, S.H. and Shugart, H.H., Jr (1974) Habitat selection of breeding birds in an east Tennessee deciduous forest. *Ecology* 55, 828–837
6 Boelman, N.T. *et al.* (2007) Multi-trophic invasion resistance in Hawaii: bioacoustics, field surveys, and airborne remote sensing. *Ecol. Appl.* 17, 2137–2144
7 Müller, J. *et al.* (2012) Aggregative response in bats: prey abundance versus habitat. *Oecologia* 169, 673–684
8 Rotenberry, J. (1985) The role of habitat in avian community composition: physiognomy or floristics? *Oecologia* 67, 213–217
9 Robinson, S.K. and Holmes, R.T. (1984) Effects of plant species and foliage structure on the foraging behavior of forest birds. *Auk* 101, 672–684
10 Wilsey, C.B. *et al.* (2012) Performance of habitat suitability models for the endangered black-capped vireo built with remotely-sensed data. *Remote Sen. Environ.* 119, 35–42
11 Müller, J. *et al.* (2014) Airborne LiDAR reveals context dependence in the effects of canopy architecture on arthropod diversity. *Forest Ecol. Manag.* 312, 129–137
12 Flaspohler, D.J. *et al.* (2010) Long-term effects of fragmentation and fragment properties on bird species richness in Hawaiian forests. *Biol. Conserv.* 143, 280–288
13 Palminteri, S. *et al.* (2012) LiDAR measurements of canopy structure predict spatial distribution of a tropical mature forest primate. *Remote Sens. Environ.* 127, 98–105
14 Gouveia, S.F. *et al.* (2014) Forest structure drives global diversity of primates. *J. Anim. Ecol.* http://dx.doi.org/10.1111/1365-2656.12241 Published online 27 May 2014
15 Loarie, S.R. *et al.* (2013) Lion hunting behaviour and vegetation structure in an African savanna. *Anim. Behav.* 85, 899–906
16 Tambling, C.J. *et al.* (2013) Elephants facilitate impact of large predators on small ungulate prey species. *Basic Appl. Ecol.* 14, 694–701
17 Lone, K. *et al.* (2014) Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos* 123, 641–651
18 Vierling, K.T. *et al.* (2011) Spinning a laser web: predicting spider distributions using LiDAR. *Ecol. Appl.* 21, 577–588
19 Swatantran, A. *et al.* (2012) Mapping migratory bird prevalence using remote sensing data fusion. *PLoS ONE* 7, e28922
20 García-Feced, C. *et al.* (2011) LiDAR as a tool to characterize wildlife habitat: California spotted owl nesting habitat as an example. *J. Forestry* 109, 436–443
21 Suggitt, A.J. *et al.* (2011) Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* 120, 1–8
22 Valeix, M. *et al.* (2011) Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biol. Conserv.* 144, 902–912
23 Seibold, S. *et al.* (2013) Forest vegetation structure has more influence on predation risk of artificial ground nests than human activities. *Basic Appl. Ecol.* 14, 687–693
24 Levick, S.R. *et al.* (2009) The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. *Biol. Conserv.* 142, 1693–1700
25 Asner, G.P. and Levick, S.R. (2012) Landscape-scale effects of herbivores on treefall in African savannas. *Ecol. Lett.* 15, 1211–1217
26 Asner, G.P. *et al.* (2009) Large-scale impacts of herbivores on the structural diversity of African savannas. *Proc. Natl. Acad. Sci. U.S.A.* 106, 4947–4952
27 Lengyel, S. *et al.* (2010) Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: a global survey. *Perspect. Plant Ecol. Evol. Syst.* 12, 43–55
28 Côrtes, M.C. and Uriarte, M. (2013) Integrating frugivory and animal movement: a review of the evidence and implications for scaling seed dispersal. *Biol. Rev.* 88, 255–272
29 Schupp, E.W. *et al.* (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytol.* 188, 333–353
30 Terborgh, J. (1992) Maintenance of diversity in tropical forests. *Biotropica* 24, 283–292
31 Levick, S.R. *et al.* (2010) Regional insight into savanna hydrogeomorphology from termite mounds. *Nat. Commun.* 1, 65
32 Zhao, F. *et al.* (2012) Characterizing habitats associated with fisher den structures in the Southern Sierra Nevada, California using discrete return lidar. *Forest Ecol. Manag.* 280, 112–119
33 Work, T.T. *et al.* (2011) Response of female beetles to LIDAR derived topographic variables in Eastern boreal mixed wood forests (Coleoptera, Carabidae). *Zookeys* 147, 623–639
34 Vierling, K.T. *et al.* (2008) Lidar: shedding new light on habitat characterization and modeling. *Front. Ecol. Environ.* 6, 90–98
35 Lefsky, M.A. *et al.* (2002) Lidar remote sensing for ecosystem studies: Lidar, an emerging remote sensing technology that directly measures the three-dimensional distribution of plant canopies, can accurately estimate vegetation structural attributes and should be of particular interest to forest, landscape, and global ecologists. *BioScience* 52, 19–30
36 Bradbury, R.B. *et al.* (2005) Modelling relationships between birds and vegetation structure using airborne LiDAR data: a review with case studies from agricultural and woodland environments. *Ibis* 147, 443–452
37 Müller, J. *et al.* (2009) Using airborne laser scanning to model potential abundance and assemblages of forest passerines. *Basic Appl. Ecol.* 10, 671–681
38 Goetz, S. *et al.* (2007) Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. *Remote Sens. Environ.* 108, 254–263
39 Garabedian, J.E. *et al.* (2014) Quantitative analysis of woodpecker habitat using high-resolution airborne LiDAR estimates of forest structure and composition. *Remote Sens. Environ.* 145, 68–80
40 Waring, R.H. *et al.* (1995) Imaging radar for ecosystem studies. *Bioscience* 45, 715–723
41 Zarco-Tejada, P.J. *et al.* (2014) Tree height quantification using very high resolution imagery acquired from an unmanned aerial vehicle (UAV) and automatic 3D photo-reconstruction methods. *Eur. J. Agron.* 55, 89–99
42 Nurminen, K. *et al.* (2013) Performance of dense digital surface models based on image matching in the estimation of plot-level forest variables. *ISPRS J. Photogrammetry Remote Sens.* 83, 104–115
43 Müller, J. and Brandl, R. (2009) Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. *J. Appl. Ecol.* 46, 897–905
44 Hill, R. *et al.* (2014) Assessing habitats and organism-habitat relationships by airborne laser scanning. In *Forestry Applications of Airborne Laser Scanning* (Maltamo, M. *et al.*, eds), pp. 335–356, Springer Netherlands
45 Müller, J. and Vierling, K. (2014) Assessing biodiversity by airborne laser scanning. In *Forestry Applications of Airborne Laser Scanning* (Maltamo, M. *et al.*, eds), pp. 357–374, Springer Netherlands
46 Merrick, M.J. *et al.* (2013) Into the third dimension: benefits of incorporating LiDAR data in wildlife habitat models. *USDA Forest Service Proc.* 67, 389–395
47 Smart, L.S. *et al.* (2012) Three-dimensional characterization of pine forest type and red-cockaded woodpecker habitat by small-footprint, discrete-return lidar. *Forest Ecol. Manag.* 281, 100–110
48 Vogeler, J.C. *et al.* (2013) Lidar-derived canopy architecture predicts brown creeper occupancy of two western coniferous forests. *Condor* 115, 614–622
49 Hagar, J.C. *et al.* (2014) Modeling marbled murrelet (*Brachyramphus marmoratus*) habitat using LiDAR-derived canopy data. *Wildlife Soc. Bull.* http://dx.doi.org/10.1002/wsb.407 Published online February 12 2014
50 Goetz, S.J. *et al.* (2010) Lidar remote sensing variables predict breeding habitat of a Neotropical migrant bird. *Ecology* 91, 1569–1576
51 Vogeler, J.C. *et al.* (2014) Terrain and vegetation structural influences on local avian species richness in two mixed-conifer forests. *Remote Sens. Environ.* 147, 13–22
52 Seavy, N.E. *et al.* (2009) Riparian bird response to vegetation structure: a multiscale analysis using LiDAR measurements of canopy height. *Ecol. Appl.* 19, 1848–1857

53 Vierling, L.A. *et al.* (2013) Using satellite and airborne LiDAR to model woodpecker habitat occupancy at the landscape scale. *PLoS ONE* 8, e80988

54 Tattoni, C. *et al.* (2012) Can LiDAR data improve bird habitat suitability models? *Ecol. Model.* 245, 103–110

55 Lesak, A.A. *et al.* (2011) Modeling forest songbird species richness using LiDAR-derived measures of forest structure. *Remote Sens. Environ.* 115, 2823–2835

56 Hinsley, S.A. *et al.* (2006) The application of lidar in woodland bird ecology: climate, canopy structure, and habitat quality. *Photogrammetric Eng. Remote Sens.* 72, 1399–1406

57 Eldegard, K. *et al.* (2014) Modelling bird richness and bird species presence in a boreal forest reserve using airborne laser-scanning and aerial images. *Bird Study* 61, 204–219

58 Müller, J. *et al.* (2013) From ground to above canopy: bat activity in mature forests is driven by vegetation density and height. *Forest Ecol. Manag.* 306, 179–184

59 Jung, K. *et al.* (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

60 Tews, J. *et al.* (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31, 79–92

61 Stein, A. *et al.* (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* 17, 866–880

62 Brokaw, N. and Busing, R.T. (2000) Niche versus chance and tree diversity in forest gaps. *Trends Ecol. Evol.* 15, 183–188

63 Pekin, B. *et al.* (2012) Modeling acoustic diversity using soundscape recordings and LIDAR-derived metrics of vertical forest structure in a neotropical rainforest. *Landscape Ecol.* 27, 1513–1522

64 Asner, G.P. *et al.* (2008) Invasive plants transform the three-dimensional structure of rain forests. *Proc. Natl. Acad. Sci. U.S.A.* 105, 4519–4523

65 Clawges, R. *et al.* (2008) The use of airborne lidar to assess avian species diversity, density, and occurrence in a pine/aspen forest. *Remote Sens. Environ.* 112, 2064–2073

66 Bellamy, P.E. *et al.* (2009) Willow warbler *Phylloscopus trochilus* habitat in woods with different structure and management in southern England. *Bird Study* 56, 338–348

67 Graf, R.F. *et al.* (2009) Habitat assessment for forest dwelling species using LiDAR remote sensing: capercaillie in the Alps. *Forest Ecol. Manag.* 257, 160–167

68 Tilman, D. and Kareiva, P. (1997) *Spatial Ecology: the Role of Space in Population Dynamics and Interspecific Interactions*, Princeton University Press

69 Palmer, T.M. (2003) Spatial habitat heterogeneity influences competition and coexistence in an African *Acacia* ant guild. *Ecology* 84, 2843–2855

70 Melin, M. *et al.* (2013) Assessing and modeling moose (*Alces alces*) habitats with airborne laser scanning data. *Int. J. Appl. Earth Observ. Geoinformation* 23, 389–396

71 Nelson, R. *et al.* (2005) Locating and estimating the extent of *Delmarva* fox squirrel habitat using an airborne LiDAR profiler. *Remote Sens. Environ.* 96, 292–301

72 Coops, N.C. *et al.* (2010) Assessing the utility of lidar remote sensing technology to identify mule deer winter habitat. *Can. J. Remote Sens.* 36, 81–88

73 Ewald, M. *et al.* (2014) LiDAR remote sensing of forest structure and GPS telemetry data provide insights on winter habitat selection of European roe deer. *Forests* 5, 1374–1390

74 Berger, J. *et al.* (2001) A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecol. Appl.* 11, 947–960

75 Estes, J.A. *et al.* (2011) Trophic downgrading of planet earth. *Science* 333, 301–306

76 Hess, A.N. *et al.* (2013) Employing lidar data to identify butterfly habitat characteristics of four contrasting butterfly species across a diverse landscape. *Remote Sens. Lett.* 4, 354–363

77 Gardner, J.L. *et al.* (2011) Declining body size: a third universal response to warming? *Trends Ecol. Evol.* 26, 285–291

78 Entling, W. *et al.* (2010) Body size–climate relationships of European spiders. *J. Biogeogr.* 37, 477–485

79 Davies, A.B. *et al.* (2014) Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. *Ecography* 37, 852–862

80 Maltamo, M. *et al.* (2014) *Forestry Applications of Airborne Laser Scanning: Concepts and Case Studies*, Springer

81 Asner, G.P. *et al.* (2009) A contemporary assessment of change in humid tropical forests. *Conserv. Biol.* 23, 1386–1395

82 Achard, F. *et al.* (2014) Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. *Global Change Biol.* http://dx.doi.org/10.1111/gcb.12605 Published online May 30 2014

83 Archer, S. *et al.* (1995) Mechanisms of shrubland expansion: land use, climate or CO^2? *Climatic Change* 29, 91–99

84 Myers-Smith, I.H. *et al.* (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ. Res. Lett.* 6, 045509

85 Broadbent, E.N. *et al.* (2008) Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol. Conserv.* 141, 1745–1757

86 Harvey, C.A. *et al.* (2006) Patterns of animal diversity in different forms of tree cover in agricultural landscapes. *Ecol. Appl.* 16, 1986–1999

87 Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*, Cambridge University Press

88 Allouche, O. *et al.* (2012) Area–heterogeneity tradeoff and the diversity of ecological communities. *Proc. Natl. Acad. Sci. U.S.A.* 109, 17495–17500

89 Kadmon, R. and Allouche, O. (2007) Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. *Am. Nat.* 170, 443–454

90 Bar-Massada, A. and Wood, E.M. (2014) The richness–heterogeneity relationship differs between heterogeneity measures within and among habitats. *Ecography* 37, 528–535

91 Cagnacci, F. *et al.* (2010) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philos. Trans. R. Soc. B: Biol. Sci.* 365, 2157–2162

92 Melin, M. *et al.* (2014) Moose (*Alces alces*) reacts to high summer temperatures by utilizing thermal shelters in boreal forests – an analysis based on airborne laser scanning of the canopy structure at moose locations. *Global Change Biol.* 20, 1115–1125

93 Bergen, K.M. *et al.* (2009) Remote sensing of vegetation 3-D structure for biodiversity and habitat: Review and implications for lidar and radar spaceborne missions. *J. Geophys. Res. Biogeosci.* 114, G00E06

94 Cardinale, B.J. *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature* 486, 59–67

95 Hooper, D.U. *et al.* (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, 105–108

96 Asner, G.P. *et al.* (2012) Carnegie Airborne Observatory-2: Increasing science data dimensionality via high-fidelity multi-sensor fusion. *Remote Sens. Environ.* 124, 454–465

97 Kuffner, I. *et al.* (2007) Relationships between reef fish communities and remotely sensed rugosity measurements in Biscayne National Park, Florida, USA. *Environ. Biol. Fish.* 78, 71–82

98 Sillero, N. and Gonçalves-Seco, L. (2014) Spatial structure analysis of a reptile community with airborne LiDAR data. *Int. J. Geogr. Info. Sci.* 28, 1709–1722

99 Yamamoto, K.H. *et al.* (2012) Using LiDAR to quantify topographic and bathymetric details for sea turtle nesting beaches in Florida. *Remote Sens. Environ.* 125, 125–133

100 Long, T.M. *et al.* (2011) LiDAR-derived measures of hurricane- and restoration-generated beach morphodynamics in relation to sea turtle nesting behaviour. *Int. J. Remote Sens.* 32, 231–241