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Using airborne laser scanning to model potential abundance and assemblages of forest passerines

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Abstract

Modelling and forecasting of the distribution and abundance of organisms using environmental variables is a major focus of applied ecological research. High-resolution airborne laser scanning is a recently developed remote-sensing method that provides data that can be used as surrogates for the vertical structure of the vegetation. These data can be used for modelling the occurrence and abundance of species or species assemblages. Until now, few studies evaluated the potential of these data for use in such models, or compared the suitability of data obtained by airborne systems with data gained by alternative methods. To fill part of this gap, we used forest passerine bird species to evaluate airborne laser scanning data for statistical modelling of potential bird abundances and composition of assemblages. Birds were counted in a mixed montane forest, on 223 1-ha plots along four transects. In the same period, these areas were scanned using Light Detection And Ranging (LiDAR) to characterise canopy structure. Additionally, we used visual interpretations of aerial photographs and field measurements on the same plots to derive habitat variables for comparison. We found clear correlations between the LiDAR variables and the other two variable sets using canonical correlation analysis. With a few exceptions, predictive power of the LiDAR data set for modelling abundances of single species, with up to 40% explained variance, was superior to that of the other two data sets. Models agreed with existing ecological knowledge for these species. For modelling of species composition with redundancy analysis, LiDAR was also superior to the other two data sets with more than 20% unique contribution to the explained variance. Our results clearly showed that LiDAR provides valuable data for describing and modelling single species as well as assemblages of forest organisms.

Zusammenfassung

Die Modellierung und Vorhersage der Verbreitung und Abundanz von Organismen ist ein Schwerpunkt in der angewandten Ökologie. Neue entwickelte Anwendungen von Lasern aus Flugzeugen liefern Daten, die sich zur Charakterisierung der Vegetation eignen. Mit diesen Daten lassen sich Vorkommen und Häufigkeit von Arten in Wäldern modellieren. Bis heute haben aber nur wenige Arbeiten das Potential solcher Daten für den Gebrauch in Habitatmodellen geprüft oder die Eignung der Daten mit Parametern aus anderen Quellen verglichen. Um diese Lücke zumindest teilweise zu schließen, haben wir die Abundanz von Sperlingsvögeln und sowie die Artenzusammensetzungen verwendet, um die Eignung von solchen durch Fernerkundung gewonnene Charakterisierung der

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Vegetationsstruktur für statistische Modellierung zu evaluieren. In einem Bergmischwald wurden auf 223 Ein-Hektar Quadranten entlang von vier Transekten Vögel standardisiert erfasst. Parallel dazu wurde die Fläche mit Hilfe von Light Detection And Ranging (LiDAR) aus der Luft erfasst. Darüber hinaus wurden Luftbilder interpretiert und auch Strukturvariablen im Gelände erhoben. Kanonische Korrelationsanalysen Analysen zeigten eine klare Korrelation der drei verschiedenen Datensätze. Mit wenigen Ausnahmen zeigten die aus LiDAR abgeleiteten Umweltdaten die beste Vorhersagekraft bei der Modellierung der Abundanz einzelner Arten und erreichten eine Varianzerklärung von 40%. Darüber hinaus standen die Ergebnisse auch im Einklang mit dem bestehenden Wissen zur Ökologie der Vogelarten. Auch bei Modellierung der Artenzusammensetzung mit Hilfe einer Redundanzanalyse zeigten die aus LiDAR abgeleiteten Variablen mit 20% unabhängiger erklärter Varianz den größten unabhängigen Erklärungsbeitrag. Unsere Ergebnisse unterstreichen das Potential von LiDAR-Daten für die Modellierung von Arten und auch Artengemeinschaften in Wäldern.

Keywords: Aerial photography; Breeding birds; LiDAR; National park "Bavarian Forest"; Temperate montane forest; Species-abundance models

Introduction

As early as 1935 the term phyto-vertical distribution was introduced for the vertical occurrence of birds in plant communities (Dunlavy 1935). During the golden age of community ecology commencing in the 1950s and 1960s, ecologists recognised that vertical distributions differ between phylogenetically closely related species, e.g. within the genus *Dendroica* (MacArthur, 1958; see also Morrison, Ralph, Verner, & Jehl 1990; Shaw, Freeman, & Flick 2002) and that diversity increases with increasing complexity of vegetation structure (MacArthur & MacArthur 1961; Recher 1969). These patterns were interpreted as resulting from competitive interactions (Levine 1976). Although ecologists are nowadays reluctant to ascribe patterns of bird–vegetation relationships solely to competition (Hinsley, Hill, Gaveau, & Bellamy 2002; Shaw & Flick 1999), the analysis and understanding of these relationships is still important in predicting species responses to management (Stork, 2001). However, the measurement of vegetation structure is not without problems, particularly in forests: first, the direct measurement of vegetation characteristics is time consuming, leading to a trade-off between intensity and extent of sampling. Therefore many studies rely on point measurements in small areas. Second, for logistical reasons it is difficult to measure the crown structure, because methods such as canopy cranes provide only access to crowns within a restricted area (Nadkarni & Cushing 2002).

During the last decades the increasing sophistication of remote sensing offered the possibility of measuring vegetation structure of even large and remote areas (Mason et al. 2003). One example is the use of Light Detection And Ranging (LiDAR) data obtained by airborne laser scanning (Lefsky, Cohen, Parker, & Harding 2002; Vierling, Vierling, Gould, Martinuzzi, & Clawges 2008). LiDAR is a technology that offers the ability to measure vegetation height with a high vertical resolution across large areas and the resultant data fulfil the twin requirements of adequate resolution and sufficient area coverage required in statistical modelling of animal–vegetation relationships. Although other remote-sensing technologies also provide large-scale information, LiDAR seems to be particularly effective (Bradbury et al. 2005). Forest authorities already started to use this method to estimate timber production (Naesset 2004). During the last decade ecologists also recognised that LiDAR provides valuable information for modelling relationships between vegetation structure and birds, mammals and plants (Bongers 2001; Mason et al. 2003; Turner et al. 2003).

First studies using LiDAR were conducted on the habitat structure of breeding territories and breeding success of tit species in broadleaf forests (Broughton, Hinsley, Bellamy, Hill, & Rothery 2006; Hill, Hinsley, Gaveau, & Bellamy 2004; Hinsley, Hill, Bellamy, & Balzter 2006). In temperate forests LiDAR data have been used for predicting bird species richness of various functional groups (Clawges, Vierling, Vierling, & Rowell 2008; Goetz, Steinberg, Dubayah, & Blair 2007). However, few studies have evaluated the power of LiDAR in comparison to other methods that allow measurement of the vegetation structure for predicting density using general linear or general additive models and assemblages of forest species using canonical ordinations. Using forest birds as an example we show that LiDAR data provide a valuable basis for modelling the relationship of birds and vegetation within forests. We used not only standardised bird counts together with LiDAR data, but also aerial photos and field measurements to explore two questions:

1. Do canopy characteristics provided by LiDAR allow modelling habitat relationships of forest birds at the species and assemblage level?
2. Does LiDAR provide a database, which is more efficient for predicting densities of single species and assemblages than do aerial photography and field measurements?

Material and methods

Study site and bird sampling

We estimated the densities of bird species across the montane zone of the Bavarian Forest National Park in southeast Germany using quantitative grid mapping (Moning & Müller 2008). This zone is dominated by mixed montane forests consisting of spruce (*Picea abies*), beech (*Fagus sylvatica*) and fir (*Abies alba*). Due to extensive infestation by bark beetles (mainly *Ips typographus*) in the southern part of the National Park, the structure of the canopy varies widely from open forests dominated by dead wood to more or less dense stands. We established four transects (see Moning & Müller 2008). Each transect was divided into plots of 100 m × 100 m, resulting in 223 plots.

Each plot was visited on five dates in 2007: end of March, in mid-April, at the beginning and at the end of May, and at the beginning of June. Observations were conducted from sunrise till 11 a.m. Each of 3–4 experts visited a section of around 3.0 km length at one morning, so that each observation campaign could be completed within 3 days. For 10 min in each plot, the locations of all bird individuals seen or heard were recorded with an accuracy of about 5 m on a field map. We restricted our analyses to passerines, because plot size was not sufficient for mapping non-passerines with territories much larger than 1 ha. The sum of all observations per plot and species was used as a surrogate for bird abundance. Our measure of abundance integrates across the migratory and breeding period. The importance of the migratory and breeding period for our abundance measure differs between bird species and it is not possible to compare densities among species (for further discussions see Moning & Müller 2008).

Environmental variables sets

Full waveform canopy data were gathered by digital airborne LiDAR using a Riegl LMS-Q560 scanner with a flight height of 400 m, as reviewed by Bradbury et al. (2005). After leaf flush in May 2007 data were collected with an average point density of 25 m^{-2}. On the basis of this data a digital surface model and a digital terrain model were calculated (for methods see Axelsson 2000). The digital crown model was then derived by subtracting the digital terrain model from the digital surface model. Finally, for each plot the mean canopy height (MeanCH), the standard deviation of MeanCH (SDCH), and the maximum height of canopy (MaxCH) were calculated.

MeanCH provides a measure of the vegetation height, but is also a strong surrogate for density (see Appendix A). SDCH is an index of vertical variation of canopy height (Table 1).

Table 1. Summary of the environmental variables extracted from LiDAR data, aerial photographs and field measurements.

Environmental variables	Mean	Min.	Max.	Skewness	Kurtosis
LiDAR					
Mean canopy height—MeanCH (m)	14.6	**1.75**	**28.6**	−0.336	−0.242
Standard deviation of canopy height—SDCH (m)	8.29	2.87	**12.4**	−0.286	−0.110
Maximum canopy height—MaxCH (m)	37.7	22.6	51.7	0.261	−0.0276
Penetration rate 5–1 m above ground—Pen5 (%)	71.3	35.1	93.5	−0.593	−0.508
Penetration rate 10–2 m above ground—Pen10 (%)	63.5	21.1	76.3	−0.367	−0.523
Aerial photographs					
Gaps without regeneration (m^2)	272	0.00	7376	5.48	36.1
Young broadleaf forest, height 0–6 m (m^2)	801	0.00	8799	2.59	6.18
Young coniferous forest, height 0–6 m (m^2)	446	0.00	9108	4.03	16.7
Middle aged broadleaf forest, height 6–12 m (m^2)	1114	0.00	8641	1.97	3.39
Mature broadleaf forest. height above 12 m (m^2)	2568	0.00	9620	0.751	−0.577
Mature coniferous forest. height above 12 m (m^2)	3051	0.00	10,000	0.824	−0.428
Edge length of patches (m)	568	0.00	1257	0.048	−0.381
Field measurements					
Number of tree species	2.71	1	6	0.855	2.23
Number of cavity trees	1.66	0	12	1.93	3.49
Volume of snags ($m^3\,ha^{-1}$)	37.6	0.00	411	2.86	9.03
Maximal diameter in breast height (cm)	57.6	8.00	130	0.57	1.08
Age of the oldest tree (years)	131	0	400	2.16	6.92

For LiDAR variables the abbreviations used throughout the paper are also given. The canopy surface models for the values in bold are shown in Appendix A.

Plots with a uniform tree height exhibit a small SDCH, plots with a mixture of small and large trees a larger SDCH. MaxCH provides information about the occurrence of the tallest tree canopy within a single 1.0 ha plot. Additionally, we calculated penetration rates for two different lower canopy layers: first, we calculated the sum of all laser echoes below 2 m above ground divided by the sum of all laser echoes below 10 m above ground (= Pen10). Second, as an estimator for the shrub and regeneration layer we calculated the penetration ratio between 5 and 1 m above ground (= Pen5).

For comparison we used data from aerial photography and field measurements collected on the same plots (Table 1). We used the ERDAS stereo analyst to analyse infra-red aerial photographs from 2007, with a spatial resolution of 40 cm. The whole area of a plot was divided into conifers and broadleaf trees and height categories by visual 3D inspection. We measured edge length as the length in metres of the classified vegetation patches. For the field measurements, conducted in 2007, we selected characteristics that were often used in ornithological studies (Chambers, McComb, & Tappeiner 1999; Clawges et al. 2008; Goetz et al. 2007; Hinsley et al. 2006; James & Wamer 1982) and characteristics with the potential to explain the abundance of a wide array of forest species (Bradbury et al. 2005; James & Wamer 1982; Swallow, Gutierrez, & Howard 1986). The number of cavity trees was counted in all plots. The volume of snags per hectare and the diameter of the largest tree at breast height were measured in a 0.1 ha plot. At the centre of the plot, we recorded the number of tree species in all canopy layers, while the age of the oldest tree within each plot was taken from National Park field inventories (for more details see Appendix A).

Statistical analysis

To investigate the multivariate relationships between the data sets gained by LiDAR, aerial photography and field measurements, we used canonical correlation analysis provided by 'vegan' within R. Our bird data are counts and accordingly we used Poisson regression to analyse the relationships of the abundance of single bird species, occurring in 20 or more plots, with the five variables extracted from the LiDAR data (Everitt & Hothorn 2006; Quinn & Keough 2002). To obtain comparable estimators, all predictors were standardised. Due to our transect design we expected some spatial autocorrelation between. Therefore we used Bayesian semiparametric spatial generalised linear models, in which spatial autocorrelation is alleviated by including a spatial surface in the regression model. Assuming asymptotic normality of the estimated regression coefficients, confidence bands and p-values can be computed based on the standard deviations obtained from the expected Fisher information matrix as implemented in 'BayesX' (Brezger, Kneib & Lang 2005).

Preliminary detrended correspondence analysis indicated that linear ordination techniques were appropriate for summarising our bird data. Therefore we extracted the main patterns of bird assemblages, including bird species occurring in at least five plots, using partial principle component analysis (PCA) on the covariance matrix to consider space as a covariable with the terms X, Y, $X \times Y$. In an ordination using the covariance matrix the result is dominated by the common species. Therefore we used square root transformation to downweight this influence. Subsequently, LiDAR data were fitted to the ordination and the significance of the relation between LiDAR data and plot scores tested with 1000 permutations.

As a simple metric for evaluating the predictive power for single species we used the mean-squared multiple regression coefficient R^2 calculated by cross-validation using 200 randomly selected training and test data sets. Training sets consisted of 123 plots; the remaining 100 plots were used to calculate R^2 by correlating observed versus predicted abundances. These simulations also permit the construction of confidence limits. We considered only species occurring in at least 20 plots and calculated for each species the predictive power for each of the three environmental data sets as well as space based on all plots. Furthermore, we calculated the unique contribution of each environmental data set x to the total predictive power across all three data sets x,y,z:

$$\text{Unique contribution of set } x = R^2_{x,y,z} - R^2_{y,z}$$

To compare the explanatory power of different environmental data sets for bird assemblages we used variance partitioning implemented in 'vegan', again with square root transformed density data. Bootstrapping was used to estimate the error of our variance components (Roff 2006).

Results

The canopy surface models used to extract forest stand characteristics with LiDAR exhibited rich patterns, sometimes with obvious differences between plots (see Appendix A). Compared with aerial photography and field measurements, the skewness and kurtosis of our variables extracted from LiDAR data indicated that the latter were often close to normal distributions (see Table 1). Canonical correlation analysis showed a clear relationship of the first roots extracted from LiDAR

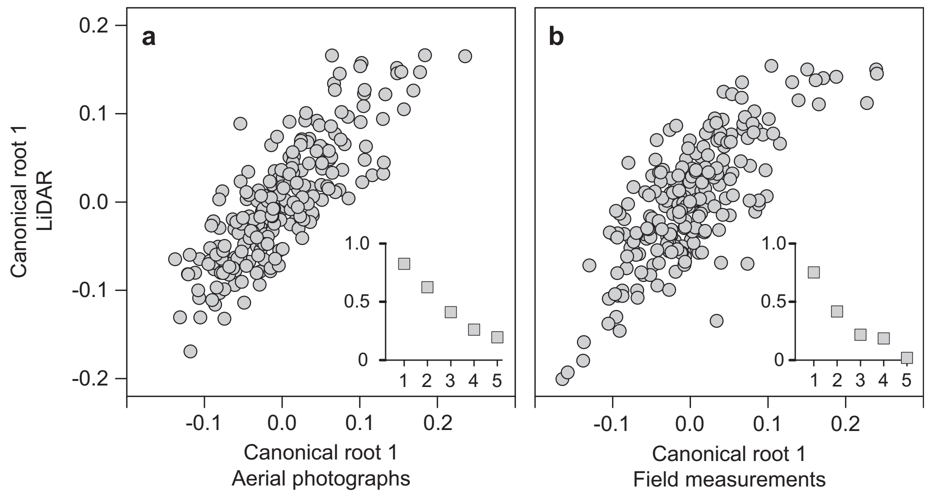

Fig. 1. Canonical correlations between the first roots extracted to maximise the correlation between the data sets using variables derived form LiDAR and aerial photographs (A) as well as from LiDAR and field measurements (B). The insets show the decrease of correlation coefficients for the first five roots of each pair of data sets.

Table 2. List of bird species occurring in at least 5 of 223 plots and results of spatial GLM for species occurring in at least 20 plots (rare species are indicated by #).

	Species	Frequ.	MeanCH	SDCH	MaxCH	Pen5	Pen10
#	Grey Wagtail *Montacilla cinerea*	7					
	Wren *Troglodytes troglodytes*	153	−0.37***	0.29***			
	Dunnock *Prunella modularis*	63	−1.13***	0.67***	−0.39*	−0.47*	
	European Robin *Erithacus rubecula*	198					
#	Redstart *Phoenicurus phoenicurus*	5					
	Blackbird *Turdus merula*	142	0.22*	0.17*			−0.28**
	Song Thrush *Turdus philomelos*	135	0.47*	0.19*	−0.27*	0.25*	−0.24*
	Mistle Thrush *Turdus viscivorus*	76					
	Blackcap *Sylvia atricapilla*	157	−0.37***	0.20*		−0.27*	
#	Wood Warbler *Phylloscopus sibilatrix*	19					
	Chiffchaff *Phylloscopus collybita*	98	−0.94***	0.48***		−0.42**	
	Willow Warbler *Phylloscopus trochilus*	36	−1.70***			−0.53*	
	Goldcrest *Regulus regulus*	143		0.19*			
	Firecrest *Regulus ignicapillus*	65	0.53*				−0.44*
#	Red-breasted Flycatcher *Ficedula parva*	6					
#	Long-tailed Tit *Aegitalos caudatus*	11					
	Marsh Tit *Parus palustris*	30					
#	Willow Tit *Parus montanus*	13					
	Crested Tit *Parus cristatus*	100					
	Coal Tit *Parus ater*	212	0.19**				
	Blue Tit *Parus caeruleus*	30					
	Great Tit *Parus major*	85					
	Nuthatch *Sitta europaea*	119	0.24*	−0.18*	0.40**	−0.40**	
	Common Treecreeper *Certhia familiaris*	115		0.36***			
	European Jay *Garrulus glandarius*	87					
#	Nutcracker *Nucifraga caryocatactes*	6					
	Chaffinch *Fringilla coelebs*	222	0.15***	0.09**			
	Eurasian Siskin *Carduelis spinus*	127	−0.27**	0.37***			
	Common Crossbill *Loxia curvirostra*	132	−0.80***	0.16*			
	Northern Bullfinch *Pyrrhula pyrrhula*	38					
#	Hawfinch *Coccothraustes coccothraustes*	9					

We show only significant estimators and in order to compare estimators, the independent variables were zero mean—unit variance standardised. Species are listed in taxonomical order. Significance levels: *$p<0.05$, **$p<0.01$, ***$p<0.001$.

with those from aerial photographs (Fig. 1A). The canonical correlations between LiDAR and field measurements were also compelling, but with a lower canonical correlation coefficient (Fig. 1B inset). Thus, there were similarities between the structural variables extracted by all three methods, although the correlation coefficients between pairs of variables from two data sets were always less than 0.5.

Forest birds and LiDAR

Twenty three passerine species were found in at least 20 plots, and 31 in at least five (Table 2; for a list of all species see Moning & Müller 2008). Spatial general linear models using density of individual bird species as the independent variable and the five LiDAR variables as predictors detected a significant influence of at least one predictor for 15 of the 23 species (Table 2). The most frequent significant variable (for explanation of abbreviations see Table 1) was MeanCH (13), followed by the SDCH (12), the Pen5 (6), the Pen10 (3) and the MaxCH (3).

The first two axes of a partial PCA with space as a covariable explained 20% of total variance (Fig. 2). After fitting the LiDAR data to this ordination the first axis can be interpreted as a gradient from open to dense stands (Table 3, Fig. 2). The second axis was correlated with MaxCH and SDCH and therefore represents a gradient from homogenous to highly structured forest stands.

Predictive power of LiDAR data

Predictive power of the best single species-abundance model reached values of almost 40% for LiDAR and aerial photography (Fig. 3A). The predictive power of the aerial photographs was in most cases close to the lower boundary of the 95% confidence intervals constructed for the predictive power of LiDAR data, although aerial photographs had seven variables compared with five in the LiDAR data set. In more than 50% of our analysed species LiDAR had the highest unique contribution to the predictive power (Fig. 3B).

The three environmental data sets together with space explained in total slightly more than 20% of the variation in the bird assemblage, much more than expected by randomising bird densities across plots (Fig. 4). Setting the total explained variance to 100%, the unique contribution of LiDAR to the predictive power of the environmental variable sets and space was

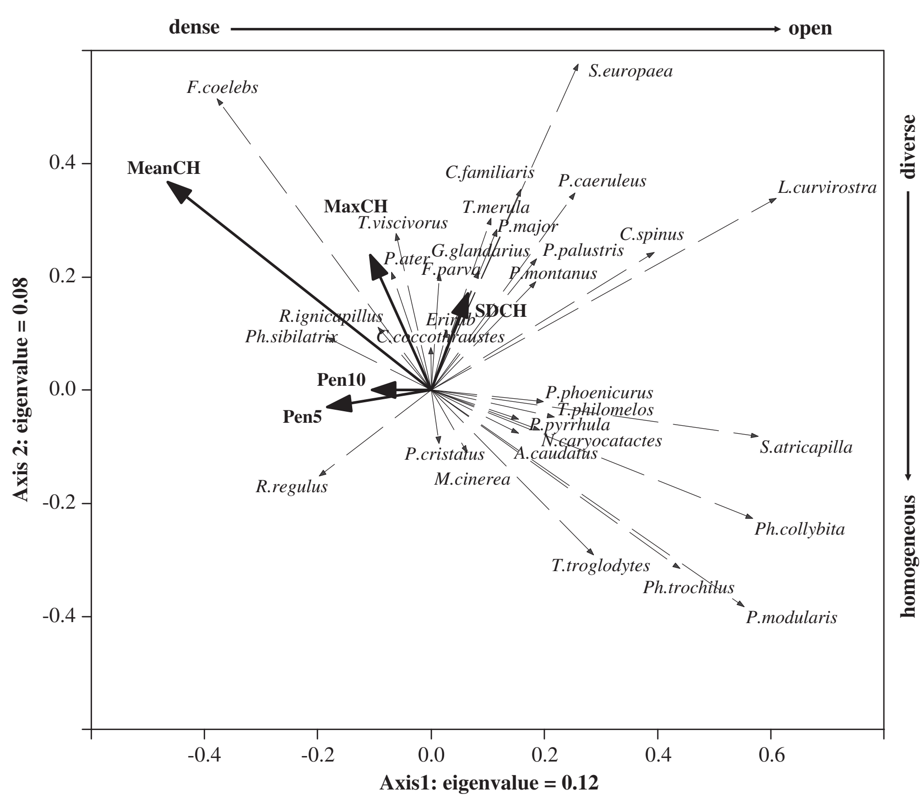

Fig. 2. Partial PCA ordination, considering space as covariable, of the square root abundance of 31 passerine bird species occurring in at least 5 plots. LiDAR variables were fitted on the ordination space. For statistical tests see Table 3. Sum of all eigenvalues standardised to one. Therefore eigenvalues present the percentage of explained variance.

Table 3. Individual correlations of LiDAR variables with the plot scores of the first two ordination axes extracted by partial PCA with space as covariate.

LiDAR variables		PC 1	PC 2	R^2	p
Mean canopy height	MeanCH	−0.46	0.37	0.35	<**0.001**
Standard deviation of canopy height	SDCH	0.068	0.17	0.033	**0.018**
Maximum canopy height	MaxCH	−0.11	0.24	0.069	**0.001**
Penetration rate from 5 to 1 m above ground	Pen5	−0.18	−0.031	0.034	**0.028**
Penetration rate from 10 to 2 m above ground	Pen10	−0.10	−0.0027	0.011	>0.3

R^2 measures the correlation with both axes (sum of the squared values of the correlation coefficients in PC1 and PC2), p-value for this coefficient was estimated with 1000 permutations.

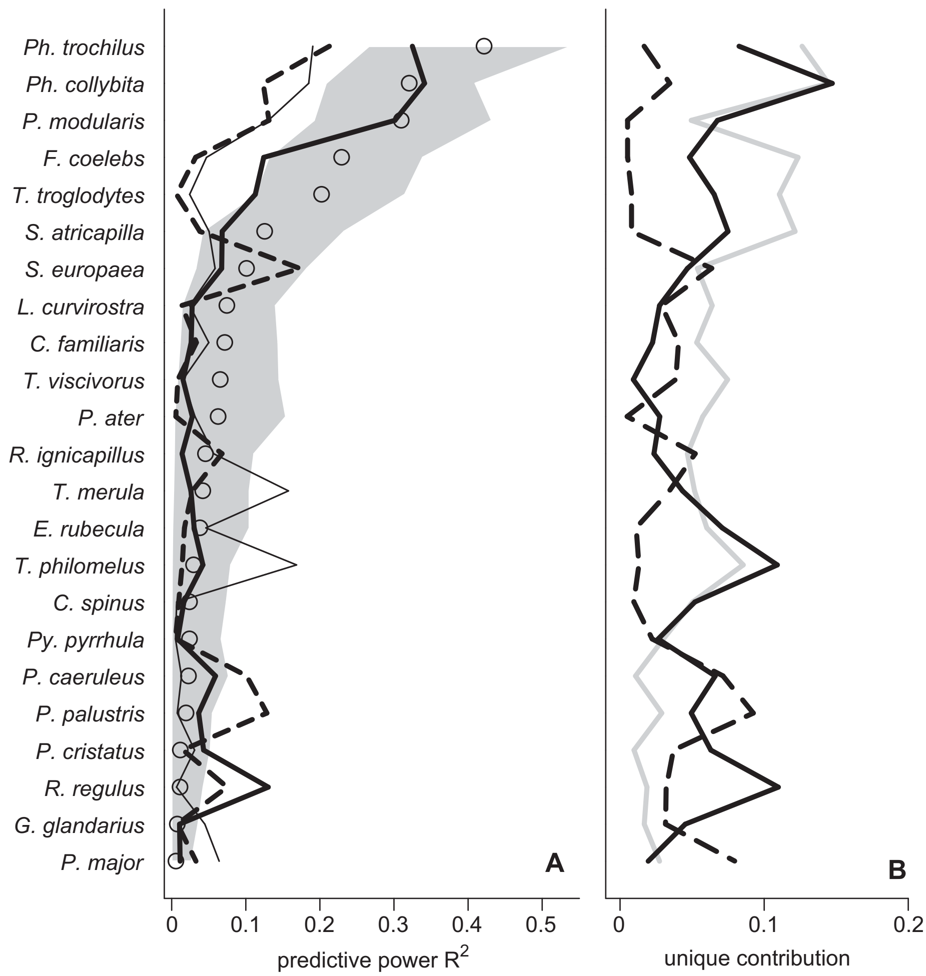

Fig. 3. (A) Predictive power expressed by the squared multiple correlation coefficients (R^2) between abundance of 23 species as dependent variable and three sets of environmental variables and space as independent variables. Species are ranked by decreasing R^2 of LiDAR (open circles). The gray area gives the approximate 95% confidence band for these circles. The other three variable sets are plotted without symbols: black line—aerial photography; dashed line—field measurements; hairline—space). (B) Unique contribution of the three environmental data sets (gray line—LiDAR data; black line—aerial photographs; dashed line—field measurements).

21% (95% CF 16.7–25.5%). The respective values for the other sets are only between 5% (95% CF 2.1–8.5%) and 16% (95% CF 11.7–19.8%). Note that the joint effect of LiDAR and aerial photographs (unique contribution 14%, 95% confidence limits 9.9–17.5%) is almost 15% (Fig. 4).

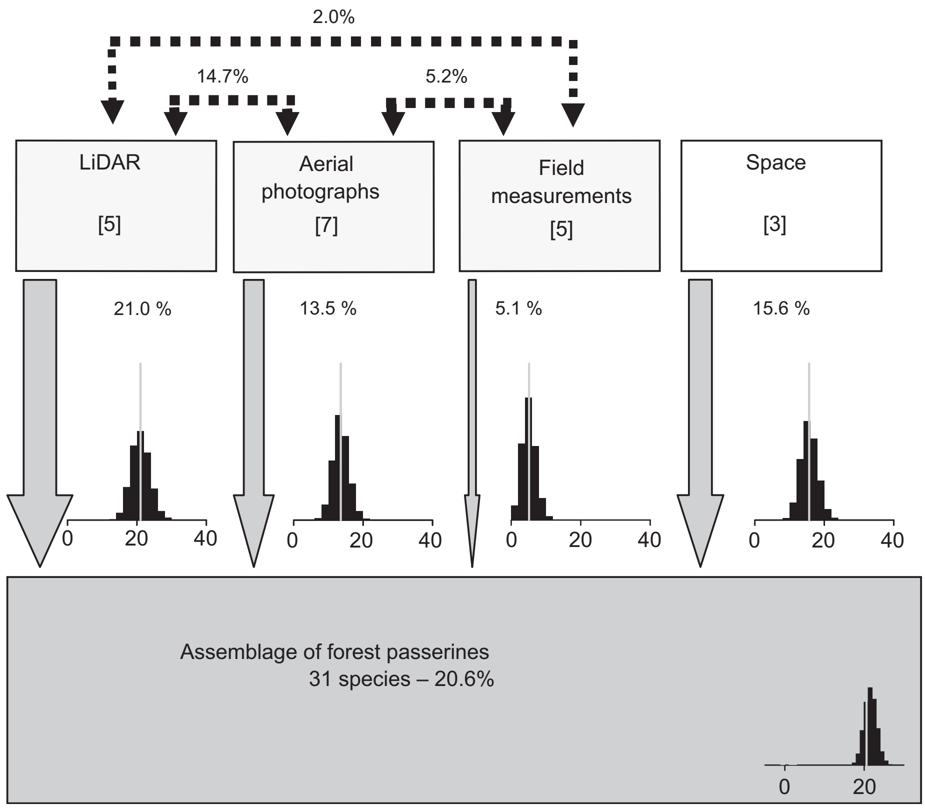

Fig. 4. Percentages of explained variances of breeding bird assemblages (abundances of 31 species across 223 plots) by three environmental sets and space using redundancy analysis. Abundance values of species are the combined counts from five sampling campaigns (see also Material and Methods). These data were square-root transformed to down weight the influence of common species. The number of variables in each data set is given in brackets. The histograms give the distribution of the bootstrap values with the mean indicated by gray lines. The variance partitions were standardised by setting the total explained variance to 100%. Note that for clarity not all joint effects are given. The plot with the two histograms gives the distribution of bootstrap values of the total explained variance as well as the explained variance for communities, generated by randomising species across plots (histogram around zero).

Discussion

Our results showed that LiDAR is a useful method for reducing the complexity of the canopy structure to a few ecologically meaningful variables. Furthermore, these LiDAR variables allowed the construction of statistical models of the abundance of species, which were often more powerful than the models derived from the aerial photography or field measurements used in this study.

Measuring forest canopy structure

Of course, one can always achieve a high predictive power of statistical models by increasing the number of independent variables. To achieve high predictive ability the aim is to use as few independent variables as possible with the incorporation of habitat variables that reflect the habitat selection of the species. Habitat selection is, however, a complex behavioural process and only time-consuming experimental methods for a small number of species can reveal the decision chains of animals in habitat selection (e.g. Thaler, 1986). However, our aim was to compare variable sets consisting of variables with some implication for as many bird species as possible, although the direct ecological process linking each variable to the abundance of a species is far from obvious. From the conservation perspective, statistical species-abundance models for many species are needed to predict changes in biodiversity resulting from habitat change (Turner et al. 2003). Such applications are also possible with models based on phenomenological relationships, particularly at larger spatial scales. Field measurements are often too time consuming, but the array of available remote-sensing methods offers alternatives to derive surrogates (Bradbury et al. 2005; Goetz et al. 2007; Hinsley et al. 2006; Lefsky et al. 2002; Turner et al. 2003).

Although more expensive than aerial photography (for costs see Appendix A), the main advantage of LiDAR is that it allows sampling habitat characteristics across large areas, including underlying canopy layers, with a high resolution even in remote regions with rough terrain or otherwise restricted access. Finally, the variables derived from the LiDAR data are statistically well behaved (e.g. symmetric distribution, few outliers) compared with variables obtained by the other methods, which is an important advantage for statistical modelling (for more details see Appendix A).

Modelling abundance of forest species

The main objectives of our study were not only to show that LiDAR is a cost-effective method of characterising complex habitat structures like forest canopies in large areas, but also to show that the variables extracted from LiDAR data are to a certain extent ecologically meaningful. For this purpose, we used birds as an example. Especially in Central Europe, the ecology of birds is well understood, which allows checking of our statistical models against generally accepted knowledge. For example, the most common and widely distributed bird in the sampled area, the chaffinch, is positively correlated with MeanCH (Table 2) and has an extreme position on the left-hand side along the first axis of our ordination space. This indicates that this species prefers dense, mature high forests. Of course the chaffinch occurred almost everywhere along the transects, but its abundance varied considerably. In contrast, the dunnock is negatively correlated with MeanCH, with an extreme position on the right side of the first axis, indicating high abundance in open forests. In one of the many handbooks dealing with birds one finds ''chaffinches maybe found breeding … where ever there are trees or bushes. The densest population occur in major broadleaf woodlands.'' (Sharrock 1976). For the Dunnock the habitat is described as ''choosing glades and edges away from tall trees and among scrub coniferous growth, dwarf heath, alder *Alnus* or willow *Salix* bushes'' (Cramp, Simmons, & Perrins 1977–1994). Clearly, the statistical models derived from LiDAR data match these descriptions.

However, habitat variables derived from LiDAR are not always successful in predicting the abundance of certain species (Fig. 3). This may have several mutually non-exclusive reasons. First, some species have no clear habitat preference. Second, the habitat variables may not include the important habitat characteristics for the species. Third, estimated densities may not be reliable. The breadth of the habitat niche of a species can vary considerably (Brändle & Brandl 2001). For example, the great tit may be considered to have a broad habitat niche, as this species occurs in considerable densities in all types of habitats with at least some shrubs or trees. Therefore, we were not surprised that we failed to find significant relationships between density and our LiDAR variables (and even the other variable sets) for this species. Our LiDAR variable set also had a low predictive power for the goldcrest. This species illustrates the second condition. The goldcrest is adapted to and prefers conifers in habitat choice experiments (Thaler 1986). In contrast to our variables extracted from the aerial photographs, the LiDAR data do not directly estimate occurrence of particular tree species in a plot. Consequently, the predictive power derived from the aerial photographs was higher than for LiDAR. Note that the goldcrest showed a significant relation to SDCH, a LiDAR variable, which is partly influenced by tree species composition (see discussion above). Finally, low predictive power of species density models may be the result of a low precision of the abundance data. Density cannot be reliably estimated for all species during only a few short visits, leading to considerable statistical noise in the data (Boulinier, Nichols, Sauer, Hines, & Pollock 1998). Furthermore, some species show considerable variation in density between years, influenced by weather conditions and/or mast years of beech or spruce (Scherzinger 2006).

Conclusions

Using birds as an example, we have shown that LiDAR has the potential to provide habitat data with considerable predictive power for modelling potential abundances of single species as well as assemblages. Predictive power was similar to that of aerial photography and superior to that of field measurements. Thus for large areas it seems to be the method of choice in measuring habitat characteristics. As already recommended by Bradbury et al. (2005), LiDAR data should increasingly be integrated into ecological projects. We only want to mention two applications for LiDAR data in conservation ecology. First, LiDAR data may create new opportunities for deriving key structures for species under conservation focus (e.g. the capercaillie: Graf, Mathys, & Bollmann 2009). Second, forest science has developed high-quality models for tree and stand growth for evaluation of management strategies in forests, allowing connection of tree growth models with LiDAR data. In the long run this offers the possibility of modelling distribution and abundance of forest species in relation to management strategies.

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Appendix A. Supporting Information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2009.03.004.

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