



# Composition versus physiognomy of vegetation as predictors of bird assemblages: The role of lidar

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## ABSTRACT

Whether diversity and composition of avian communities is determined primarily by responses of species to the floristic composition or to the structural characteristics of habitats has been an ongoing debate, at least since the publication of MacArthur and MacArthur (1961). This debate, however, has been hampered by two problems: 1) it is notoriously time consuming to measure the physiognomy of habitat, particularly in forests, and 2) rigorous statistical methods to predict the composition of bird assemblages from assemblages of plants have not been available. Here we use airborne laser scanning (lidar) to measure the habitat (vegetation) structure of a montane forest across large spatial extents with a very fine grain. Furthermore, we use predictive co-correspondence and canonical correspondence analyses to predict the composition of bird communities from the composition and structure of another community (i.e. plants). By using these new techniques, we show that the physiognomy of the vegetation is a significantly more powerful predictor of the composition of bird assemblages than plant species composition in the field and as well in the shrub/tree layer, both on a level of  $p < 0.001$ . Our results demonstrate that ecologists should consider remote sensing as a tool to improve the understanding of the variation of bird assemblages in space and time. Particularly in complex habitats, such as forests, lidar is a valuable and comparatively inexpensive tool to characterize the structure of the canopy even across large and rough terrain.

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## 1. Introduction

More than 70 years ago, field biologists recognized that the vertical structure of vegetation is an important factor for the composition of assemblages of birds and ecological separation of species (Dunlavy, 1935). The first quantitative approach to analyse the relationship of bird assemblages in relation to plant assemblages was published by MacArthur and MacArthur (1961). The strong correlation between foliage height diversity and bird diversity was interpreted to be the result of an increase of potential niche space with an increase of physiognomic diversity of the vegetation. Plant species *per se* or plant species diversity were thought to have limited importance for the niche space, although physiognomy and composition of the vegetation are positively related (Mac Nally et al., 2002). Since these early studies, there has been an ongoing debate about the relative importance of species composition *versus* physiognomy of the vegetation for the diversity and composition of bird assemblages, with equivocal results (Anderson & Shugart, 1974; Fleishman & Mac Nally, 2006; MacArthur et al., 1966; Recher, 1969; Robinson &

Holmes, 1984; Rotenberry, 1985; Tomoff, 1974; Wiens & Rotenberry, 1981).

The debate has been complicated by two methodological problems. First, it is difficult to quantify the physiognomy of the vegetation (Wiens & Rotenberry, 1981). This is particularly true for forests. Time-consuming field methods for measuring vegetation physiognomy constrained the available data sets to at best moderate sample sizes, often collected across a limited spatial extent (Anderson & Shugart, 1974; Mac Nally, 1990; MacArthur et al., 1966). The issue of measuring the structure of the vegetation across a broad extent with fine grain was solved, however, by the rapid development of several high-resolution remote-sensing techniques within the last 15 years (Lefsky et al., 2002; Vierling et al., 2008; Goetz et al., 2007). One of these methods is light detection and ranging (lidar), which measures vegetation heights and characteristics of the vegetation in the sense of MacArthur and MacArthur's foliage profile without limitations to the extent (Goetz et al., 2007).

The second methodological problem is a statistical problem: a comparison of the predictions of the composition of one assemblage (i.e. bird species) based on the composition of another assemblage (i.e. plant species) with a prediction based on the vegetation structure (i.e. physiognomy of the vegetation). The composition of an assemblage can be predicted from environmental data using canonical correspondence analyses (Jongmann et al., 1995). However, the

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problem of predicting one community matrix from another was only recently solved by [Ter Braak and Schaffers \(2004\)](#) by developing a procedure called co-correspondence analysis. The number of relevant axes for comparing the predictions can be selected by using the number of axes providing the best cross-validated fit or by using the significant axes for each of two ordinations. In earlier studies, the problem regarding the relationship between bird assemblages and vegetation was bypassed either by using certain surrogates representing characteristics of the two communities [i.e. species richness, diversity; e.g. [MacArthur and MacArthur \(1961\)](#)], by using Procrustes superimposition of independent ordinations of the two matrices, or by using matrix correlation ([Mac Nally, 1990](#)). Reducing the composition of an assemblage to a vector, i.e. species richness, reduces much of the information in the community composition to single numbers. When Procrustes superimposition is used, the same number of axes of the ordination of bird and plant data must be used to evaluate the similarity in the configurations ([Ter Braak & Schaffers, 2004](#)); this selection of the number of axes is often arbitrary, and the relevant axis of each ordination may not capture the essentials of the joint information. Matrix correlations require the input of a similarity index between bird assemblages and the vegetation, and these are plotted against each other (for a comparison of matrix correlation and Procrustes superimposition, see [Peres-Neto & Jackson, 2001](#)). The plethora of similarity and dissimilarity coefficients leads to arbitrary decisions in the selection of appropriate coefficients. Matrix correlations as well as Procrustes rotations are by definition correlative rather than predictive.

The combination of variables derived from high-resolution lidar data with predictive statistical methods now provides the methodological basis for a rigorous test of the differences in the power of plant species composition *versus* structure of the vegetation to predict the composition of bird assemblages, i.e. the relative abundance of each species.

## 2. Methods

### 2.1. Study area

We sampled the composition of bird and plant assemblages in the Bavarian Forest National Park in southeast Germany along four transects ([Bässler et al., 2008](#); [Müller et al., 2009a,b](#)). These transects are part of a long-term monitoring project of biodiversity and climate changes (for a map and further discussion about spatial effects see [Bässler et al., 2008](#); [Müller et al., 2009a](#); [Müller & Brandl, 2009](#)). The elevation ranges from 650 to 1420 m above sea level and is dominated by mixed montane forests consisting of spruce (*Picea abies*), beech (*Fagus sylvatica*), and fir (*Abies alba*). At higher elevations, spruce is the dominant tree species. Owing to natural disturbances during the last decades (wind throw, bark beetle attack; [Müller et al., 2008](#)), the canopy structure within all transects varies from open to closed, independent of altitude. Owing to the acidic soil, the field layer at higher elevations with an open canopy is dominated by *Vaccinium* sp., and the field layer in the beech-dominated stands is species poor. In open stands, grass species, in particular *Calamagrostis villosa*, dominate the vegetation (for an illustration, see [Appendix Fig. S1](#)).

### 2.2. Bird and vegetation data

Along each transect, plots were arranged in 100 m intervals. We counted birds within 100 m × 100 m grids around each plot centre for 10 min during five visits at the end of March, in mid-April, at the beginning and at the end of May, and at the beginning of June in 2007. The sum of all registrations of a species was used as a surrogate for the abundance of this species within the plot and was arranged in a matrix of bird composition by site ([B]). Our measure of abundance integrates across the migratory and breeding season. Although the

probabilities of registering migratory and breeding species differ, this measure is nevertheless a fair representation of the usage of a plot by the bird assemblage from spring to autumn (for more details and discussion of methods, see [Möning & Müller, 2008](#); [Müller et al., 2009b](#)).

The plant species composition was mapped by *rélevees* (excluding mosses and lichens) covering 0.5 ha in the centre of each plot. Cover-abundance of species was noted for four strata following [Braun-Blanquet \(1964\)](#): herb layer, shrub layer up to 5 m, tree layer 1 from > 5 to 20 m, and tree layer 2 from > 20 m. From these raw data, we generated two matrices characterizing the composition of the plant assemblages as well as cover-abundance of each species (for an example, see Appendix material [Tables S1, S2](#)): First, we summarized the cover-abundance of species among the shrub and tree layers ([T]). Second, we formed a similar matrix only for the plant species recorded in the field layer ([F]).

### 2.3. Airborne laser scanning (lidar)

Canopy data were gathered by digital airborne lidar using a Riegl LMS-Q560 scanner installed on a helicopter at a flight height of 400 m. The pulse at half maximum lasted 4 ns and the laser wavelength was 1550 nm. Full waveform data were collected in May 2007 after leaf flush, with an average point density of 25 m<sup>-2</sup> and a vertical error of 15 cm, on an approximately 400 m wide strip along the transects. The lidar points were derived from the full waveform data, with one to 11 discrete points generated per laser shot. On the basis of these data, a digital surface model and a digital terrain model were calculated. To calculate the digital surface model, the raw data points were sorted into a rectangular array of cells (0.25 m × 0.25 m). When sorting these data into the grid, some cells may contain more than one value. From these points, only the cell with the highest elevation value was used. The cells not covered by laser data points were filled by bilinear interpolation.

The digital terrain model was developed in three steps according to the method described by [Axelsson \(2000\)](#). First, during the automatic classification, where the appropriate suitable estimation area of 60 m × 60 m was defined step-wise, the lowest data points were located, classified as ground points, and connected by a triangulated irregular network. This network was then refined by an iterative addition of lidar points and therewith new triangles, until no further points could be found. Second, the automatically classified digital terrain model was checked visually, and incorrectly classified points (< 1 % of all points) were manually assigned to the correct classes. Third, the raster digital terrain model was created by interpolation of the height values generated by the previous steps to obtain values for the centres of the digital terrain model cells with a spatial resolution of 1.0 m ([Axelsson, 2000](#)). The digital crown model was then derived by subtracting the digital terrain model from the digital surface model, providing a canopy model with a spatial resolution of 0.25 m.

Finally, for each 100 m × 100 m plot, we calculated six parameters characterizing the canopy structure (after [MacArthur & MacArthur, 1961](#)). The mean canopy height, the standard deviation of mean canopy height, and the maximum height of canopy were calculated from the digital crown model. Mean canopy height provides a measure of the vegetation height. The standard deviation of vegetation height is an index of vertical variation of canopy height: plots with a uniform tree height exhibit a small standard deviation, and plots with a mixture of small and large trees exhibit a larger standard deviation. The maximum height of canopy provides information about the occurrence of the tallest tree canopy within a single 1.0 ha plot. To characterize the openness of the canopy, we calculated the penetration ratio at 2 m above ground, dividing the sum of all laser echoes below 2 m by the sum of all laser echoes below 50 m, and the penetration ratio at two different lower canopy layers.

The sum of all laser echoes below 2 m above ground divided by the sum of all laser echoes below 10 m above ground (including those of below 2 m) represents an estimate of the proportion of intermediate trees (mid-storey) of the forest stands in our region, with a regular height up to 30–40 m. The ratio of the sum of echoes below 1 m above ground divided by the sum of all laser echoes below 5 m in the same way is an estimator particularly for the shrub and regeneration layer, with high values in plots having a low density of shrubs and regeneration (for further discussion of the ecological interpretation of these parameters, see Müller et al., 2009b). Overall, we characterized the structure (physiognomy) of the vegetation by a matrix of six variables derived from lidar across sites ([P]). We deliberately did not derive topographic parameters from the terrain model in this application because the aim of this study was to compare only the predictive power of physiognomy and plant species composition on bird species assemblages. However, the elevation gradient has some influence on both the physiognomy and the plant species composition (see above). Furthermore, none of our species under focus was restricted by elevation *per se*. A quantification of the influence of altitude in predictive power can be found in Müller and Brandl (2009) and Müller et al. (2009b).

#### 2.4. Statistical methods

The trees at some sites were too densely grown for any plants to occur in the herb layers on the plots; other sites were open plots lacking tree or shrub species after bark beetle infestation (see Appendix Fig. S1). For these latter plots, the column sums in [T] and [F] were zero. Therefore, for all statistical analyses, we used only plots with at least one record in [T] and [F]. Overall, 254 plots passed these two criteria. To test the correlation of bird composition [B], floristic composition ([T], [F]), and vegetation characteristics [P], we used matrix correlation (Mantel test) with a Bray–Curtis distance for all matrices with bird and plant species ([B], [T], [F]) and Euclidian distance for structural characteristics [P]. These two indices are widely used in ecology for that purpose (e.g. Magurran, 2004; Wolda, 1981). The significance of the matrix correlation was evaluated by 999 permutations in the first matrix. To test for differences between two matrix correlations, we compared the difference between two matrix correlations with the differences calculated during the permutations using a two-sided test.

To predict the composition of the bird assemblages from the structural characteristics, we used a predictive version of canonical correspondence analysis (CCA); to predict [B] from [T] and [F], we used the recently developed (predictive) co-correspondence (CoCA) analysis, which allows the prediction of an assemblage by a second highly complex assemblage. In the analyses, we included only bird and plant species that occurred in at least five plots. To reduce the effect of very abundant bird species, the counts were square-root transformed. To determine the number of relevant axes, we used “leave-one-out” cross-validation (see Ter Braak & Schaffers, 2004). The number of relevant axes is the number of axes that minimizes the squared prediction error. We followed the method of Ter Braak and Schaffers (2004) and reported the cross-validated fit:

$$\text{Cross-validated fit} = 100 \left( \frac{1 - \text{ssp}_n}{\text{ssp}_0} \right),$$

where  $\text{ssp}_n$  is the sum of squared prediction error using  $n$  axes, and  $\text{ssp}_0$  is the sum of the squared prediction errors if rows and columns of the response matrix are independent. The cross-validated fit may even become negative ( $\text{ssp}_0 > \text{ssp}_n$ ), which indicates that the prediction using the mean abundance of species is already better than the statistical models. We also report the significance of axes determined by permutations using functions available in the add-on package *vegan* for CCA analyses (Oksanen et al., 2006) and *cocorresp*

for CoCA (Ter Braak & Schaffers, 2004). Finally, the significance of pair-wise differences in the cross-validated fit was tested by a randomization test suggested by van der Voet (1994). This test randomizes the residuals of the predictions between the two prediction methods and therefore can cope with a different number of relevant axes selected for the two methods. All analyses were conducted in R 2.8.1 (R Core Development Team, 2008).

### 3. Results

Our final data set comprised 35 bird species in [B], 83 plant species in [F], and 6 plant species in [T]. In our analyses, the use of presence/absence of species in [F] and [T] produced consistently better relationships to [B] irrespective of whether we used matrix correlation or ordination methods. Furthermore, the matrix correlation analyses as well as the predictive co-correspondence and canonical correspondence analyses agreed very well (Table 1); we will only discuss the results of the latter two methods in detail. Cross-validated fit was more than 10% for [P] and almost 8% for [F] (Fig. 1, Table 1). Although the shrub/tree layer provides the main habitat for most of our forest birds, [T] showed only a weak power for predicting bird assemblages (<2.5%). Permutation tests showed that only the first and third axes of [F] and only the first axis of [T] were significant, while the first four axes of [P] were significant. A two-sided permutation test indicated that the difference between [P] and [F] as well as between [P] and [T] was highly significant. Therefore, [P], the physiognomy of the vegetation, is the most appropriate predictor of [B], the quantitative composition of the bird assemblages.

### 4. Discussion

#### 4.1. Footprint size, full wave form and lidar-derived variables

For many current ecological applications, particularly in Europe, only discrete return, small footprint lidar data are available for analysis. In our study, we used a lidar density of about 25 shots  $\text{m}^{-2}$  and a footprint size of 25 cm, which is a high spatial sampling density even for small footprint laser data. Other discrete return small footprint lidar applications to studies of birds used lower shot densities of 1–4 shots  $\text{m}^{-2}$  (i.e. Clawges et al., 2008; Hill et al., 2004), but were also able to model bird and physiognomy relationships with sufficient accuracy and ecologically meaningful results. In addition, Goetz et al. (2007) were able to predict bird species richness in forests using full waveform lidar data collected at a footprint size of nominally 12 m in diameter. In our study, however, we collected a high density of shots  $\text{m}^{-2}$  for a number of reasons. First, such a high information density is required for the detection of single trees,

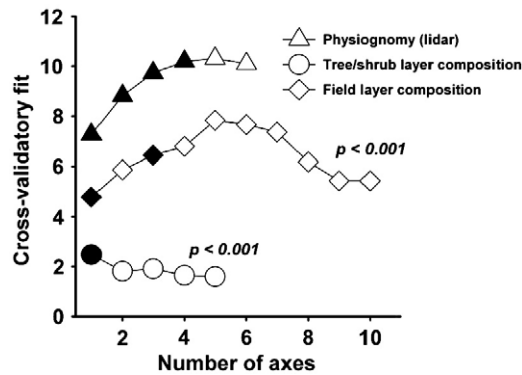
**Table 1**

Comparison of matrix correlations with the maximum cross-validated fits (number of axes given in parentheses) between the different matrices of bird species composition, physiognomy, and plant species composition in the field and shrub/tree layers.

Independent matrix	Dependent matrix	Mantel correlation	<i>P</i>	Cross-validated fit (number of axes)
Physiognomy [P]	Field layer [F]	0.27	<0.001	6.80 (5)
Physiognomy [P]	Shrub/tree layer [T]	0.28	<0.001	10.7 (5)
Field layer [F]	Shrub/tree layer [T]	0.14	<0.001	3.64 (5)
Physiognomy [P]	Birds [B]	0.44 <sup>b</sup>	<0.001	10.3 <sup>b</sup> (5)
Field layer [F]	Birds [B]	0.11 <sup>b</sup>	<0.001	7.83 <sup>a</sup> (5)
Shrub/tree layer [T]	Birds [B]	0.16 <sup>b</sup>	<0.001	1.91 <sup>a</sup> (1)

For the matrix correlations, we used the Bray–Curtis distance for species  $\times$  site matrices using presence/absence information and Euclidian distance for structure  $\times$  sites matrices. Significant differences between the three matrix correlations and between the three cross-validated fits are coded by letters.





**Fig. 1.** Cross-validated fit of the avian community composition. The cross-validated fit is plotted against the number of ordination axes for the three sets of predictor variables: canopy structure and physiognomy of the vegetation, plants species composition of the shrub/tree layer, and plant species composition of the field layer. The filled symbols indicate significant axes using permutation tests. To test for differences in the cross-validated fit between two data sets, we permuted residuals between data sets (see van der Voet, 1994) using the number of axes with the maximum of predictive power (five for physiognomy and field layer composition; one for the tree/shrub layer). The significance of axis is shown as additional information. The  $p$  values for the comparison of physiognomy and each of the two plant composition matrices are indicated; the difference in the predictive power between field and tree/shrub layer composition was not significant ( $p = 0.43$ ).

particularly of smaller trees. Second, we wanted to capture characteristics also of the understory, which is difficult to measure with lower resolution lidar data in broadleaf stands during the growing season, because understory vegetation provides important habitat for birds as well as for other groups of organisms. Indeed, in our study area we have previously shown that variables describing the understory can be important in characterizing the bird community (Müller et al., 2009b).

Our aim to collect small footprint, discrete return lidar data at a very fine spatial resolution to characterize the vegetation canopy is consistent with studies that have utilized larger footprint full waveform lidar data. In contrast to first-last pulse and even to multiple-return, full waveform data records substantial amounts of energy as returned from throughout the vertical profile of the canopy (including more reflections in the tree crowns, which can be critically in bird habitat modelling (Graf et al., 2009)) and allows one to derive a broad set of habitat variables (Goetz et al., 2007). By using small footprint, discrete return data collected at a high density and averaging the returns over a larger area (i.e., similar in size of a large footprint system), it is possible to derive “simulated” waveforms to characterize vegetation structure (e.g. Falkowski et al., 2009) that may assist our future data analyses.

However, the question remains if a density 25 of shots  $m^{-2}$  is necessary. In this respect, we also tested our ability to model the relationships of organisms with a much smaller body size than birds, i.e. beetles (see Müller & Brandl, 2009), with the expectation that we would find greater importance particularly of fine scale information as the organisms decrease in size. In general, the question of resolution decreases in importance with increasing plot size. Our recent study on the predictability of beetle assemblages as a typical small-body-sized species group showed a higher predictive power of lidar variables when we integrated the data across 1.0 ha around the trap stations than when we integrated the data across 0.1 ha (Müller & Brandl, 2009). Considering these results, we expect that even lidar data with a lower shot density in small footprint data or much lower resolution of Satellite-borne large footprint waveform lidar data, when more broadly available in the future, have enormous potential for modelling assemblages of birds or other organisms and remove spatial restrictions. A rigorous investigation of the required resolutions and spatial scales is

urgently needed in order to assess the appropriate scales at which similar relationships can be modeled. We need to compare the relationships of habitat variables derived by remote sensing and ecological data using environmental data of different resolution and ecological data of organisms differing in body size and dispersal propensity. Only a few steps have been taken in this direction (e.g. for skylark, Mason et al., 2003).

The first applications of lidar used only the canopy height as parameter in modeling forest bird response (Hinsley et al., 2006). The rapid increase of applications in the last three years resulted in a wide set of different variables derived, which evokes the question, of whether the use of other variables could have improved our results. We attempted to quantify the cover of the typical layers in temperate forests, which may be useful in characterizing habitats for bird species according to the literature (Glutz von Blotzheim & Bauer, 1991). We aimed to measure important variables which can be directly interpreted. Nevertheless, the usefulness of such variables may differ between species as well as habitats. Clawges et al. (2008) derived not the same but similar variables capturing different vegetation layers as well as the diversity of layers. Furthermore they combined the information with multispectral data which clearly will improve the information beyond physiognomy if tree species can be identified and taken into account. However, this was not the aim of our study, as we restricted the information to physiognomy only following the idea of MacArthur and MacArthur (but see also previous analysis in our study using aerial photography; Müller et al., 2009b). Goetz et al. (2007) successfully developed an index of the vertical distribution of the vegetation independent from height using full waveform data. We included only the standard deviation of height as a measurement of vertical distribution, but we have to be aware that many of the different variables are clearly correlated. Therefore we would not expect a much better result using different parameters in our analysis. At present there is no standard set of variables derived from lidar to characterize the physiognomy of the vegetation (i.e. for birds see Bradbury et al., 2005; Clawges et al., 2008; Goetz et al., 2007; Vierling et al., 2008). A systematic evaluation of the different possible ways to measure single habitat characteristics with lidar in bird studies and their ecological interpretation across organisms and ecosystems would be helpful.

#### 4.2. Statistical methods

Beyond the availability of meaningful physiognomic data, the development of co-correspondence analyses and the first applications of this technique by Schaffers et al. (2008) paved the road for studies comparing the predictive power of the vegetation structure and of the plant species composition for the community composition of birds and other organisms. Such a predictive approach seems to be more powerful and rigorous than the comparison of matrix correlations (Legendre et al., 2005; Ter Braak & Schaffers, 2004). In the ecological literature, one finds some discussion about the conceptual differences between the two approaches (Pélissier et al., 2008; Tuomisto & Ruokolainen, 2006). Nevertheless, in our study (Table 1), the matrix correlations between the data sets did not statistically differ, whereas the predictive power showed clear significant differences. Beyond the advanced possibilities of testing predictive ordinations, these methods also maintain information about species identity. This may turn into a disadvantage, however, when data with very different species compositions are used. A further advantage of co-correspondence analyses and canonical correspondence analysis is the visual inspection of the relationship of species or variables in the dependent and independent matrices (for an example, see Appendix Figs. S2, S3), which is also possible for Procrustes superimpositions (Peres-Neto & Jackson, 2001; see also Müller et al., 2009b).

#### 4.3. Physiognomy versus plant species composition

The main aim of MacArthur and MacArthur's classic 1961 study, and of our study, was to compare the predictive power of plant species composition and physiognomy for forest bird assemblages. In an analysis of insect assemblages along road verges, Schaffers et al. (2008) demonstrated that plant species composition had more predictive power than the physiognomy of the vegetation. This result was attributed to the integrative character of the plant assemblages for characterizing the environmental condition, which in turn determines the occurrence of insects. Our results for bird assemblages contrast with this recent finding for insect assemblages. In our study, the structure of the vegetation was a significantly more powerful predictor for birds than plant species composition. Even if the majority of the bird species in our study have mostly shrubs and trees as habitat (for the species list, see Appendix Table S3), the species composition of the field layer had more predictive power than the species composition of the shrub/tree layer (see Table 1). The density and cover of the shrub layer influences foraging and resting behaviour. Nevertheless, the structure of the shrub/tree layer, like the canopy in general, also determines the composition of the field layer, which leads to a positive matrix correlation and cross-validated fit of physiognomy and field layer (Table 1): below an open canopy, plant species composition differs between open and closed habitats. Our results suggest that for birds the lidar-derived variables characterize the physiognomy of the shrub/tree layer in a more meaningful way than the plant species composition of the field layer.

A number of published studies using matrix correlations have shown that plant species composition is more closely correlated to bird species composition than a similarity matrix constructed from physiognomic data (Mac Nally, 1990; Wiens & Rotenberry, 1981). This was not the case in our study, where the correlation coefficients were higher between physiognomy and community composition of birds than between plant composition and birds (Table 1). Furthermore, matrix correlation and the new statistical methods generated almost similar results, which indicate that the difference in the conclusions between our study and previous studies is not due to different statistical methods. We argue that the different results are a matter of spatial scale (Mac Nally, 1990). Studies favouring the importance of physiognomy use sites spread across a larger geographical range and with a greater diversity of habitat types than in our study. In contrast, studies favouring the composition of the plant community use fewer and less diverse sites (Mac Nally, 1990).

#### 4.4. Remote sensing opens new doors for ecology

As demonstrated, lidar-derived variables provide elegant possibilities to test the long-standing hypothesis about the relationship between vegetation and assemblages of organisms. Clearly, remote-sensing techniques allow the collection of data of the vegetation across large spatial extents and with a small grain. In the extremes, lidar can identify single trees (Popescu et al., 2003) and can also provide information across continents. Although several review articles on the potential of lidar for habitat modelling have appeared, the number of applications that approach basic ecological questions is still small (for an overview, see Bradbury et al., 2005; Clawges et al., 2008; Vierling et al., 2008). As Turner et al. (2003) point out, this probably stems from the persistent false impression among scientists that there is a mismatch between the supposed coarse resolution of remote sensing versus the fine scale of environmental response of small organisms (e.g. arthropods). If an expanding number of biodiversity studies can show that there is a strong correlation with a causal link between environmental parameters derived with remote sensing and the distribution of an organism (e.g. Lassau et al., 2005a,b; Müller & Brandl, 2009), the remote-sensing revolution could be the key to obtain wide spatial coverage of biodiversity estimators, without

sacrificing data resolution. Even in aquatic habitats, there are several ecological applications of lidar for modelling fish diversity in coral reefs (Kuffner et al., 2007) or salmon nesting patterns in rivers (McKean et al., 2008).

#### 5. Conclusions

Our study shows that airborne laser scanning (lidar), a comparatively inexpensive remote-sensing technique, provides statistically well-behaved data on plant physiognomy in a complex habitat, i.e., forest. This technique enabled us to better test the long-standing hypothesis on the relationship between vegetation structure and assemblages of birds. The physiognomy of the vegetation was clearly a better predictor than plant species composition. The initial sampling of detailed information on the vegetation structure, even across large areas, allows the application of powerful statistical methods, such as co-correspondence analysis. Therefore, ecologists should consider lidar as an important remote-sensing tool to test ecological theories and to improve the understanding of the variation of assemblages in space and time, even across large areas and rough terrain.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rse.2009.10.006.

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