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Assessing biodiversity in forests using very high-resolution images and unmanned aerial vehicles

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Summary

1. Structural diversity and niche differences within habitats are important for stabilizing species coexistence. However, land-use change leading to environmental homogenization is a major cause for the dramatic decline of biodiversity under global change. The difficulty in assessing large-scale biodiversity losses urgently requires new technological advances to evaluate land-use impact on diversity timely and efficiently across space.

2. While cost-effective aerial images have been suggested for potential biodiversity assessments in forests, correlation of canopy object variables such as gaps with plant or animal diversity has so far not been demonstrated using these images.

3. Here, we show that aerial images of canopy gaps can be used to assess floristic biodiversity of the forest understorey. This approach is made possible because we employed cutting-edge unmanned aerial vehicles and very high-resolution images (7 cm pixel⁻¹) of the canopy properties. We demonstrate that detailed, spatially implicit information on gap shape metrics is sufficient to reveal strong dependency between disturbance patterns and plant diversity (R^2 up to 0.74). This is feasible because opposing disturbance patterns such as aggregated and dispersed tree retention directly correspond to different functional and dispersal traits of species and ultimately to different species diversities.

4. Our findings can be used as a coarse-filter approach to conservation in forests wherever light strongly limits regeneration and biodiversity.

Key-words: biodiversity, coarse-filter approach, forest understorey, gap shape complexity index, unmanned aerial vehicles

Introduction

The devastating loss of biodiversity requires sustained investment in coherent biodiversity monitoring and its integration into broad-scale land-use planning (Butchart *et al.* 2010). At the same time, surveying methods need to be cost-effective to provide a framework of practical feasibility (Gardner *et al.* 2008).

While it is known that land-use change is the most prominent driver of current global changes in biodiversity (Sala *et al.* 2000), the response of biodiversity to varying land-use intensities is so far little understood (Fischer *et al.* 2010). This is particularly true for the temperate forest biome with timber-oriented management, often leading to simplified, species-poor forest structure and in combination with climate

change increasing susceptibility to insect attacks, fire disasters and storm events (van Vuuren, Sala & Pereira 2006; Lindner *et al.* 2010).

Empirical and theoretical studies have shown that tree thinning and resultant changes in canopy gap structure strongly affect woody regeneration and biodiversity of understorey plants (Whitney & Foster 1988; Coates *et al.* 2003). Hence, management prescriptions that increase within-stand variability can provide important habitat features across multiple scales to enhance biodiversity in forests (Wilson & Puettmann 2007). Creating spatially variable sizes and shapes of forest gaps at the local plot scale thus bears the potential to optimize land-use intensities in favour of high biodiversity. This causal link between so-called 'higher-level' structures and dependent 'lower-level' processes is also well known from landscape-scale analysis where habitat fragmentation such as the shape complexity of larger forest patches may be related to biodiversity (Saura & Carballal 2004). For example, it has been shown for

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the tropics that the degree of patch convolution is positively correlated with woody plant species diversity (Galanes & Thomlinson 2009).

Remote sensing based on satellite or aerial images is ideal to identify and functionally link the spatial configuration of forest patches to biodiversity at the coarse landscape scale because the resolution of such images is sufficient to correlate diversity with shape metrics of larger patches (Newton *et al.* 2009). However, at the local plot scale, the resolution of image sensors is commonly not high enough to permit very accurate spatial quantifications of fine-scale canopy objects. For example, with conventional aerial or satellite images, it is hardly possible to correctly record small gaps of < 10 or 20 m² size (Fujita *et al.* 2003; Turner *et al.* 2003). This is probably the reason why so far no study has yet successfully correlated plant or animal diversity of the forest understorey with canopy gaps as detected in aerial images. We consider this as a major research gap because such fine-scale correlations with biodiversity are a crucial key for assessing specific land-use intensities in managed forests. This is because actual tree thinning as a disturbance happens at the fine scale within continuous areas or large patches of forest.

Investigating the hypothesis that gap information on aerial images can be principally used for the ecological assessment of plant diversity in forests is a major scientific achievement for the following reasons:

1. Airborne imagery reflects two-dimensional measures of gap distribution in horizontal space. Such indirect optical approaches 'hold the promise of not only getting better estimates of species distributions and richness levels, but of also shedding light on the processes underlying them' (Turner *et al.* 2003). For example, the spatial characteristics of gaps determine the balance of neighbourhoods between different plant functional types (clonal spread vs. seed dispersal; shade-tolerant vs. shade-intolerant species) or between invader and native species (Koukoulas & Blackburn 2004; Li, Bogaert & Nijs 2005).
2. Aerial images are very cost-effective and therefore routinely used by most forest administrations for recurrent monitoring purposes of large areas. This makes them particularly suitable for practical decision support (Morgan, Gergel & Coops 2010; Pasher & King 2010). While expensive 3D airborne laser scanning can be used to predict biodiversity in forests (Turner *et al.* 2003), the cost-saving concept of a coarse-filter approach (Beier & Brost 2010) is more competitive when a minimum set of explanatory variables is used, such as with 2D images (Gardner *et al.* 2008; Proulx & Parrott 2008).
3. Since the emergence of digital photography, airborne optical image sensors are subject to rapid improvement in resolution. Consequently, path-breaking methodologies and results from pilot studies using very high-resolution images will be applicable to monitoring processes in the very near future (Clark *et al.* 2004; Morgan, Gergel & Coops 2010).
4. As a new technology itself, unmanned aerial vehicles (UAV) will soon be an important commercial tool for monitoring purposes. So far, 'we have only seen the tip of the

iceberg of what is achievable'; however, 'unmanned aircraft begin to take on almost any traditional role that is performed by a piloted aircraft' (Stafford 2007). UAV applications in surveys have a number of advantages over established remote-sensing methods. They provide extremely fine sub-25-cm resolutions and thus allow the identification of previously undetected object details, and images are rarely affected by cloud cover because flying altitudes are usually low, flight missions can be timed very flexibly, and owing to low fixed charges, they are very cost-effective (Dunford *et al.* 2009; Rango *et al.* 2009; Watts *et al.* 2010).

Until now, UAV applications in ecology are still rare. In the following, we demonstrate how high-resolution images and unmanned aircraft may be used to assess understorey biodiversity in forests.

Materials and methods

STUDY SITES

Our study sites were located within beech-dominated deciduous and mixed deciduous/coniferous forests of the so-called Biodiversity Exploratories in Germany. These exploratories are long-term research platforms to investigate the effects of varying land-use intensities on functional biodiversity response (Fischer *et al.* 2010). We selected 20 1-ha plots of mature and mainly single-layered stands in the exploratory 'Hainich-Dün' in central Germany and similarly 16 plots in the 'Schwäbische Alb' about 300 km away in south-western Germany. These exemplary study plots represent different land-use intensities such as unmanaged near-natural ($N = 13$), selection-cutting ($N = 6$) and traditionally managed age-class forest ($N = 17$) with varying thinning patterns. Mean annual precipitation in the Hainich is 500–800 mm and in the Alb 700–1000 mm. Soils of the Hainich have a loamy texture and are dominated by Luvisols and Stagnosols on loess. Soils of the Alb are rich in clay and are dominated by Cambisols and Leptosols on limestone. Our chosen study sites were located on relatively level topography with only a few plots in the Schwäbische Alb having some moderate slopes.

Within each plot, we recorded the vascular plants (herbs, grasses, ferns, woody plants ≤ 1.5 m) in seven randomly spread 10×10 m² subplots. Random spreading of subplots was performed to account for various local light conditions within the 1-ha plot and thus to get a representative sample of shade-tolerant and light-demanding species. The plant data were used to correlate species richness, Shannon index (H), Shannon evenness (E) and beta diversity (β_{sim}) of understorey plants in each 1-ha plot with canopy objects from aerial image analysis. Thereby, Shannon evenness was calculated as $E = H/H_{max}$ with H being the observed species diversity and H_{max} the species diversity under conditions of maximal equitability (Krebs 1994). Beta diversity was calculated as 1–Simpson's similarity index ($\beta_{sim} = 1 - S_{sim}$). This measure was chosen because β_{sim} performed best overall out of 24 tested indices of beta diversity (Koleff, Gaston & Lennon 2003). The four measures of biodiversity are commonly used in ecological surveys and should thus be suitable for comparative studies.

AERIAL IMAGES

Very high-resolution RGB images (≈ 7 cm pixel⁻¹) were taken at the end of the summer in 2008 and 2009 with the UAV 'Carolo P200' above the centres of the 1-ha forest plots at flying altitudes of



Fig. 1. Start of the unmanned aerial vehicle Carolo P200. Initially, the UAV gets manually started. Once it has reached the desired height, it can fly automatically along any predefined spline-based trajectory.



Fig. 2. Very high-resolution image. The aerial image shows an intensively managed, beech-dominated age-class forest of the region Hainich-Dün. The resolution permits accurate identification of gap objects up to a minimal size of 1 m². After orthorectification, only the central 1-ha square of the image is used for gap analysis.

≈250 m (Figs 1 and 2; Figs S1 and S2 in Supporting information). This state-of-the-art UAV was recently developed by the Institute of Aerospace Systems/TU Braunschweig in conjunction with the Andromeda-Project (Chmara 2010). The UAV has a wing span of 2 m and weighs 6 kg. It can fly automatically along any predefined spline-based trajectory for a time span of 60 min and makes every 3-s an image. All images were orthorectified based on data recording of the internal UAV orientation, GPS position and a digital terrain model. Orthophotos were converted into binary images, and gap polygons were manually segmented to create shapefiles (a geospatial vector data format digitized with ArcGIS-9.3 software) as accurate as possible.

VARIABLE SELECTION

Owing to the very high-resolution image, we were able to segment small gaps of a minimal size of up to 1 × 1 m². Inclusion of such gap properties is a prerequisite for any analysis of the potential importance of smallest gaps for driving understorey plant diversity. For each gap, we calculated eight different patch (gap) metrics that are predominantly used in landscape-scale analyses for correlations with biodiversity and in forest applications. The first three gap metrics area

(A), perimeter (P) and perimeter/area ratio (P/A) are very basic measures. Then, circularity (C) was calculated as $4\pi A/P^2$, with values of 1.0 describing a perfect circle and values approaching 0.0 indicating increasingly elongated shapes. The gap shape complexity index (GSCI) = $P/\sqrt{4\pi A}$ is an important measure of forest gaps (Koukoulas & Blackburn 2004). It is the ratio of a gap's perimeter to the perimeter of a circular gap of the same area. A value of 1.0 describes a perfect circle while increasing values indicate increasing shape complexity. For example, values of 1.40 and 2.60 have 40% and 160% complexity, respectively. The last three gap metrics are the patch fractal dimension (PFD) = $2\ln(P)/\ln(A)$ (Moser *et al.* 2002), the fractal dimension (FD) = $2\ln(P/4)/\ln(A)$ (Salvador-Van Eysenrode *et al.* 1998) and the fractal dimension index (FDI) = $2\ln(P/\sqrt{4\pi})/\ln(A)$ (Saura & Carballal 2004). These three metrics are nonlinearly related, and especially for small gaps with $A < 10$ m², PFD may attain higher values than FDI that, in turn, attains higher values than FD. Thus, all eight patch metrics emphasize different nuances of two-dimensional gap properties that may be potentially important for linking image-detected higher-level structures to dependent lower-level processes of the biota.

For each patch metric, we calculated the total sum (Tot), mean (M), median (Mdn), standard deviation (SD) and coefficient of variation (CV) for all segmented polygons including the smallest 1-m² gaps. We also calculated these same statistics once for only the 10 largest gaps (measured by area), once for the nine, eight, seven and so on largest gaps. This gives a total of 50 variables per patch metric. For the two largest gaps, we skipped the median, and for the single largest gap, we just used the patch metric as such. For example, the abbreviated gap variable 'Mdn_GSCI_3' is the median of the gap shape complexity index of the three largest gaps of a 1-ha plot. All 50 variables of all patch metrics were applied to all 1-ha plots.

The direct relationship between understorey light and biodiversity may be affected e.g. by soil condition (Lalanne *et al.* 2010). Therefore, we included the four additional covariates pH, bulk density (BD), organic carbon concentration (OC) and organic carbon stock (C_{stock}) in subsequent analyses to judge their relative importance for the biodiversity assessment based on aerial image analysis. Soil samples were taken approximately at the centre of each 1-ha plot (for details see Fischer *et al.* 2010; Data S3 in Supporting Information). The soil data used in this analysis originate from the upper 10 cm because this layer is most influential on understorey vegetation such as herbs, grasses or ferns. The four soil parameters were measured as continuous variables with e.g. OC measured in g kg⁻¹ or C_{stock} in kg m⁻².

STATISTICAL ANALYSES

Several statistical analyses were applied to evaluate the dependency between image-based variables (or soil covariates) and understorey biodiversity. In Analysis 1, we used all gap variables based on the eight patch metrics for linear correlations with biodiversity as measured by Pearson's *r*. This initial data screening allowed us to get an overview on the systematic importance of certain patch metrics for correlation with understorey diversity. To avoid the likelihood that our meaningful R^2 values ≥ 0.25 could have arisen just by chance, we tested the significance of each correlation coefficient using 9999 permutations following the procedure by Legendre & Legendre (1998). Following Møller & Jennions (2002), we have chosen a value of $R^2 \geq 0.25$ as 'meaningful' because a predictor variable causes a large effect if 25% or more of the variance is explained.

In Analysis 2, we used at first only the gap variables with highest correlation with biodiversity for univariate linear regressions.

Afterwards, multiple linear regressions were fitted to judge the relative importance of soil covariates for modelling our four biodiversity measures species richness, Shannon H, evenness E and beta diversity β_{sim} . For this purpose, our single most important gap variable and the four soil covariates pH, bulk density, organic carbon concentration and organic carbon stock were simultaneously forced into stepwise forward regression modelling in the form of $Y = B_0 + B_1 \times X_1 + B_2 \times X_2 + B_3 \times X_3 + B_4 \times X_4 + B_5 \times X_5 + E$. The outcome of stepwise inclusion of the five variables is based on goodness-of-fit measures (multiple R^2).

In Analysis 3, we investigated whether 'region' as a covariate does have a significant effect on the image-based assessment of biodiversity given that one and the same gap variable is used for the combined data of the regions Alb and Hainich together. This was tested with analysis of covariance (ANCOVA) where we took the best image-based predictor, showing strongest correlation with biodiversity as continuous variable and region as a factor with the two categorical levels Alb and Hainich.

All statistical analyses were performed using R-2.11 software (<http://www.R-project.org/>).

Results

In Analysis 1, we searched for a single best predictor variable to evaluate biodiversity based on linear correlations with gap properties. The highest R^2 (0.74) we found here was for correlating species richness of the region Hainich with the median of the GSCI of the three largest gaps (Fig. 3). Generally, species richness was the best response measure to assess biodiversity from image analysis (Table 1). Overall, there was a systematic response of biodiversity to the eight patch metrics. For example, summarized over all three separate correlations (regions Hainich, Alb and data of Hainich + Alb locations combined), variables of the GSCI were in 93% positively correlated with species richness and caused in 68% a large effect with an $R^2 \geq 0.25$ (Table 1). This systematic suitability of the GSCI for image-based assessments of understorey diversity is also indicated by the following fact: Among the 20 variables causing

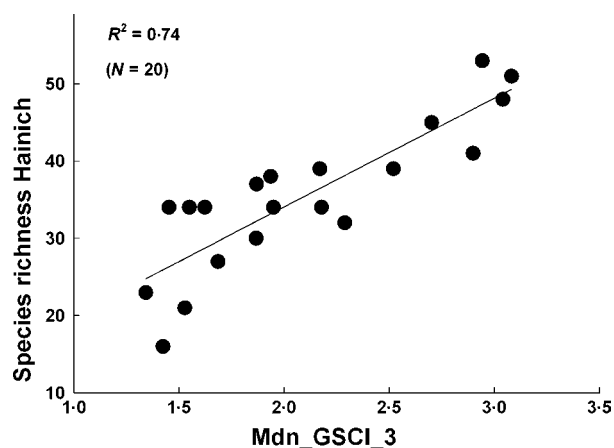


Fig. 3. Example of a strong correlation between information from gap objects and biodiversity of the understorey in the region Hainich. The independent predictor variable Mdn_GSCI_3 is the median of the gap shape complexity index of the three largest gaps per 1-ha plot.

Table 1. Summarized percentages of positive correlations with biodiversity

Gap metric	Species richness	Shannon	Evenness	Beta diversity
A	75 (40)	69 (25)	35 (5)	38 (0)
P	85 (55)	69 (25)	31 (2)	83 (0)
P/A	35 (3)	28 (0)	68 (2)	54 (0)
C	41 (17)	47 (0)	58 (3)	39 (0)
GSCI	93 (68)	81 (21)	25 (0)	97 (0)
PFD	35 (1)	27 (0)	71 (1)	39 (0)
FD	89 (33)	73 (1)	38 (1)	89 (8)
FDI	63 (9)	51 (0)	72 (2)	58 (10)

Gap metrics are area (A), perimeter (P), perimeter/area ratio (P/A), circularity (C), gap shape complexity index (GSCI), patch fractal dimension (PFD), fractal dimension (FD) and fractal dimension index (FDI). Each number reflects the total proportion of positive correlation coefficients (Pearson) summarized over all 3×50 variables per metric in the three separate correlations (Hainich, Alb and data of Hainich + Alb combined). The difference to 100% is thus negative correlations with biodiversity. Numbers in braces reflect the total percentages of positive correlations with $R^2 \geq 0.25$.

highest positive correlations with species richness in the Hainich ($R^2 = 0.64$ – 0.74), 15 variables were based on the GSCI. Likewise, among the 20 variables causing highest positive correlations with species richness for combined data of the Hainich and Alb together ($R^2 = 0.35$ – 0.47), 13 variables were based on the GSCI.

Also, Analysis 2 demonstrated that species richness is a highly suitable response variable for image-based evaluations of biodiversity. All univariate regression results were very highly significant with P values < 0.001 and R^2 values ranging from 0.47 to 0.74 (Table 2). All other univariate regressions with gap measures were significant, too, except for the Shannon index in the Alb where the variable Tot_PFD was close to significance at 0.05 level ($P = 0.058$). These results underline the high suitability of gap-based variables for remotely sensed assessments of understorey biodiversity.

Multiple regressions revealed that gap-based predictor variables always made the strongest contribution to explain variation in the four biodiversity measures. This is evident from the sorting order of the five included predictors with gap variables being always placed at first position (B_1) right after the intercept (B_0). In contrast, the effects of soil variables were relatively low. In the Hainich, none of the four soil variables made any significant contribution to the regression model, and in the Alb, only organic carbon stock had a significant effect on beta diversity (Table 2). For the combined analyses of Hainich and Alb together, organic carbon stock had a significant effect on species richness and beta diversity and bulk density had a significant effect on evenness.

In Analysis 3, one and the same gap variable was used for the combined data of the regions Alb and Hainich together. ANCOVA indicated that 'region' as a covariate did have a significant effect on the assessment of species richness and evenness (Table 3). Hence, the predictability of these two biodiversity measures from aerial image analysis was affected by differences

Table 2. Results of univariate and multiple linear regression modelling

	Species richness				Shannon				Evenness				Beta diversity						
	B	SE (B)	Multiple R ²	P value	B	SE (B)	Multiple R ²	P value	B	SE (B)	Multiple R ²	P value	B	SE (B)	Multiple R ²	P value			
Univ. regres.																			
Intercept	5.86	4.31			Intercept	2.32	0.29			Intercept	0.73	0.03			Intercept	0.14	0.05		
Mdn_GSCI_3	14.10	1.98	0.74	0.000	CV_P	0.01	0.00	0.36	0.005	CV_A_10	0.00	0.00	0.37	0.004	CV_FD_5	0.02	0.01	0.22	0.035
Multi. regres.																			
Intercept	23.19	22.91			Intercept	3.10	1.57			Intercept	0.87	0.35			Intercept	-0.04	0.30		
Mdn_GSCI_3	14.32	2.20	0.74	0.000	CV_P	0.01	0.00	0.36	0.005	CV_A_10	0.00	0.00	0.37	0.004	CV_FD_5	0.03	0.01	0.22	0.035
BD	-21.79	21.03	0.76	0.276	BD	-0.51	1.53	0.41	0.241	pH	-0.04	0.04	0.40	0.333	C_stock	-0.10	0.10	0.26	0.402
C_stock	1.77	7.63	0.78	0.245	pH	-0.03	0.18	0.42	0.629	C_stock	0.07	0.12	0.43	0.374	pH	0.05	0.04	0.38	0.086
pH	4.18	2.49	0.81	0.149	C_stock	0.37	0.55	0.42	0.841	OC	-0.00	0.01	0.45	0.461	OC	0.01	0.01	0.39	0.645
OC	-0.61	0.79	0.81	0.450	OC	-0.04	0.06	0.43	0.529	BD	-0.06	0.34	0.45	0.863	BD	0.11	0.29	0.40	0.722
Alb (N = 16)																			
Univ. regres.																			
Intercept	23.97	4.02			Intercept	2.54	0.21			Intercept	0.64	0.03			Intercept	-2.20	0.60		
CV_C_4	0.59	0.13	0.58	0.000	Tot_PFD	0.00	0.00	0.23	0.058	SD_PFD	0.00	0.00	0.33	0.019	M_FDI_10	1.81	0.45	0.54	0.001
Multi. regres.																			
Intercept	5.12	20.14			Intercept	3.41	1.32			Intercept	1.20	0.29			Intercept	-1.00	0.59		
CV_C_4	0.58	0.13	0.58	0.000	Tot_PFD	0.00	0.00	0.23	0.058	SD_PFD	0.01	0.00	0.33	0.019	M_FDI_10	1.11	0.39	0.54	0.001
OC	0.50	0.16	0.68	0.064	C_stock	-0.25	0.17	0.40	0.078	C_stock	-0.05	0.04	0.47	0.082	BD	-0.06	0.09	0.63	0.102
C_stock	-5.71	2.70	0.72	0.208	pH	-0.13	0.12	0.46	0.259	BD	-0.33	0.23	0.57	0.140	C_stock	-0.05	0.02	0.79	0.011
BD	28.68	15.18	0.79	0.075	OC	0.01	0.01	0.47	0.709	OC	-0.00	0.00	0.59	0.460	OC	0.00	0.00	0.82	0.143
pH	-1.59	1.88	0.81	0.416	BD	0.44	1.07	0.48	0.689	pH	-0.00	0.03	0.59	0.886	pH	-0.02	0.01	0.88	0.056
Hainich + Alb (N = 36)																			
Univ. regres.																			
Intercept	26.87	2.27			Intercept	2.82	0.12			Intercept	0.70	0.03			Intercept	0.15	0.03		
SD_GSCI_4	31.61	5.72	0.47	0.000	Mdn_P_3	0.00	0.00	0.16	0.015	SD_P/A_10	0.29	0.10	0.21	0.005	SD_FD_4	1.26	0.47	0.18	0.010
Multi. regres.																			
Intercept	12.82	12.91			Intercept	2.71	0.68			Intercept	0.66	0.18			Intercept	0.24	0.13		
SD_GSCI_4	35.10	5.60	0.47	0.000	Mdn_P_3	0.00	0.00	0.16	0.015	SD_P/A_10	0.29	0.10	0.21	0.005	SD_FD_4	1.30	0.47	0.18	0.010
OC	0.36	0.14	0.53	0.061	pH	-0.12	0.10	0.23	0.085	BD	0.16	0.14	0.32	0.029	C_stock	-0.06	0.02	0.27	0.042
C_stock	-7.19	2.16	0.62	0.008	BD	0.91	0.52	0.25	0.369	C_stock	-0.03	0.03	0.34	0.266	OC	0.00	0.00	0.35	0.058
BD	12.30	8.57	0.64	0.174	OC	0.01	0.01	0.28	0.313	OC	0.00	0.00	0.35	0.728	pH	0.00	0.02	0.36	0.584
pH	2.35	1.83	0.66	0.208	C_stock	-0.16	0.14	0.31	0.256	pH	-0.00	0.03	0.35	0.906	BD	0.01	0.09	0.36	0.888

Image-based variables used for univariate regressions are those that showed the highest correlation with measures of biodiversity (for abbreviations, see Materials and methods section). These measures were subsequently used for multiple regression modelling to assess the relative importance of the four soil covariates pH, bulk density (BD), organic carbon concentration (OC) and organic carbon stock (C_stock). All five variables were simultaneously forced into stepwise forward regression modelling, and the order of the regression coefficients B₁ to B₅ reflects the importance of the five variables for explaining variation in understorey biodiversity (multiple R²). Numbers were rounded to two digits after the comma for B, the standard error (SE) of B and multiple R². P values were not rounded but given to three digits after the comma to indicate very highly significant cases with P < 0.001. All significant contributions (at least P < 0.05) of variables are given in bold numbers.

between both regions. However, regional effects had no significant influence on regressions with the Shannon index or beta diversity.

Discussion

Our results are based on two independent temperate forest regions in Germany that are located several hundred kilometres apart from each other. While we have demonstrated this method for a limited number of exemplary forest plots in both regions, we controlled for sampling error using permutation tests (Legendre & Legendre 1998). All R² values showing large effects were not the result of chance or sampling error but constitute significant correlations. Consequently, the excellent predictability of biodiversity we found in this study is based on a systematic suitability of some specific gap metrics such as the GSCI that may be used to assess understorey diversity based on aerial images. These results provide strong evidence for the dependency between spatial disturbance structures and plant diversity in

forests because high correlations were found in both regions and even when data of the two regions were combined.

With multiple regressions, we have shown that soil variables had a relatively small effect on our gap-based assessments of biodiversity, at least if regions are considered separately. Still, ANCOVA revealed that regressions with species richness or evenness for combined data have been significantly affected by regional differences. This could have arisen because of dissimilarities in site characteristics such as parent material and associated soil texture, which are also reflected in bulk densities and carbon stocks. Indeed, the median of organic carbon stock was 4.2 kg m⁻² for all 16 plots of the Alb but 3.2 kg m⁻² for the 20 plots of the Hainich. We also found a median of three major tree species in our investigated plots in the Alb but only of two tree species in the Hainich. This could have affected our regressions because overstorey composition may influence understorey vegetation (Barbier, Gosselin & Balandier 2008). Also, climatic differences may impair our regressions and cause lower R² values for combined regional data. For example,

Table 3. Results of analysis of covariance (ANCOVA) for the combined data of the regions Hainich and Alb

Species richness					Shannon				Evenness				Beta diversity						
Hainich + Alb (N = 36)	B	SE (B)	T value	P value		B	SE (B)	T value	P value		B	SE (B)	T value	P value		B	SE (B)	T value	P value
ANCOVA																			
Intercept	34.58	4.08	8.48	0.000	Intercept	2.48	0.21	11.74	0.000	Intercept	0.56	0.05	11.60	0.000	Intercept	0.11	0.04	2.58	0.014
SD_GSCI_4	31.98	5.42	5.90	0.000	Mdn_P_3	0.00	0.00	2.33	0.025	SD_P/A_10	0.19	0.09	2.12	0.041	SD_FD_4	1.16	0.47	2.48	0.018
Region effect	-5.04	2.26	-2.23	0.032	Region effect	0.23	0.12	1.91	0.065	Region effect	0.10	0.03	3.28	0.002	Region effect	0.03	0.02	1.44	0.159
F _{2,33} = 19.50, P = 0.000					F _{2,33} = 5.32, P = 0.009				F _{2,33} = 11.17, P = 0.000				F _{2,33} = 4.81, P = 0.014						

Image-based gap measures used as continuous predictor variables are those that showed the highest correlation with measures of biodiversity for combined data of the two regions (for abbreviations, see Materials and methods section). ‘Region’ was treated as a factor with the two categorical levels Hainich and Alb. All numbers were rounded to two digits after the comma, except for *P* values that were not rounded but given to three digits after the comma to indicate very highly significant cases with $P < 0.001$. All significant contributions (at least $P < 0.05$) of variables are given in bold numbers.

the higher annual precipitation of the Schwäbische Alb (Fischer *et al.* 2010) could have been an intrinsic factor in our ANCOVA. We, therefore, recommend that similar future studies should explicitly investigate the regional effects on remotely sensed assessments of biodiversity in forests.

Overall, the study has demonstrated a high potential for predicting biodiversity in forests from high-resolution aerial images. Gaps created by natural tree death or man-made thinning seem to be a major driver of understorey plant diversity in deciduous forests because light distribution is strongly limiting for understorey species that vary in their optimal light requirement. Although we do not know the exact causal mechanisms, as a major limiting resource, ‘understorey light can be used as a single synthetic factor grouping less apparent microclimatic variations’ (Barbier, Gosselin & Balandier 2008), making this coarse-filter approach to the assessment of biodiversity a highly efficient tool.

Here, we emphasize that it is the spatially implicit information on gap shape measures of several gaps per hectare that is necessary to cause strong correlations with biodiversity. Several gaps per hectare with their shape complexity function as higher-level structures and partition essential resources such as understorey light into various quantities and qualities. This structural filter then determines biodiversity by providing many niches for the survival and reproduction of different species with different competitive strength, shade tolerance and dispersal mode. Hence, the spatial characteristics of gaps like perimeter or shape are important because they determine the competitive or facilitative relationships of plant species in the understorey (Li, Bogaert & Nijs 2005). As understorey structure provides microhabitat niches that may function as shelter or food resource, cascading feedbacks may directly affect the diversity of faunistic taxa such as insects, mammals or reptiles as well (Bouget & Duelli 2004). Indeed, a test-wise correlation analysis that we undertook for data of the Hainich (results not shown) revealed also a significant and strong dependency of arthropod species richness on a measure with the gap shape complexity index. The result that measures based on the GSCI strongly positively correlate with biodiversity may be ascribed to the fact that high shape complexities provide various aggregated niches to sustain coexistence of many species. This agrees with theoretical findings where highest biodiversity emerged at highly correlated disturbances (Banitz *et al.* 2008).

In our study species richness has been the best response variable of all four biodiversity measures. The gap shape

complexity index is a highly suitable predictor of species richness because gaps with one and the same high GSCI value may differ widely in area (Saura & Carballal 2004). Thus, GSCI is not a direct indicator of the magnitude of disturbance or the quantity of total light influx. For example, in the Hainich region, the traditionally managed selection-cutting forests had about a 20% higher Mdn_GSCI_3 value and 10% higher species richness than the conventionally managed age-class forests, but the total gap fraction of selection-cutting forests was even smaller. In other words, the species richness detected via gap shape complexity is not necessarily biased towards ruderal species with high light demands, which may possibly obscure the presence of more forest-characteristic specialists.

In agreement with previous studies, here we emphasize that in terms of biodiversity-friendly forest management it is also the quality in the fine-scale spatial distribution of light that is beneficial to species richness and biodiversity in general (Coates *et al.* 2003; Wilson & Puettmann 2007). Obviously, the type of tree retention achieved with selection cutting allows for more irregularly shaped gaps, thus fostering high understorey biodiversity. This indicates that species richness may be actively controlled by the spatial quality, and not just quantity, of tree harvesting and likewise that the ecological value of this thinning action may be assessed via gap analysis in aerial surveys.

From a technical point of view, these findings suggest that remotely sensed biodiversity assessments using object-based image analysis of segmented gaps such as performed in this study may have certain advantages over coarse-filter approaches that rely on more abstract spectral indices or texture-based analysis. While it has been shown that image texture may be used for correlation with bird species richness (St-Louis *et al.* 2006) or spectral indices for correlation with ant species richness (Lassau *et al.* 2005), spatially implicit quantification of real objects such as gaps in forests allows for more direct insight into the dependent ecological, lower-level processes of plant or animal taxa.

In conclusion, we have shown that very high-resolution images can be used to effectively assess biodiversity in temperate forests. These results may also hold for other global forest biomes wherever strong limitations of light occur. For example, in neotropical rainforests, gap shape is an important factor that determines microclimatological effects, subsequent ecological processes and ultimately plant composition

(Salvador-Van Eysenrode *et al.* 1998). We, therefore, strongly encourage future studies to test this method of biodiversity assessment in various forest regions of the world.

Our application of UAV technology in ecological studies could serve as an inspiration for combining innovative high-tech with the need for practical decision support. Unmanned aerial vehicles are increasingly being used in environmental science such as for monitoring anthropogenic pollution (Roberts *et al.* 2008), rangeland condition (Rango *et al.* 2009) or riparian forest (Dunford *et al.* 2009). Even light detection and ranging (LIDAR) systems may nowadays be mounted to UAVs to get three-dimensional forest scans (Lin, Hyypää & Jaakkola 2011). We hope that our study proposing a new method for biodiversity assessments in forests may be seen as another path-breaking inspiration for the interplay of biology and technology (Fields 2001).

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Supporting Information

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

Fig. S1. Very high-resolution image of a near-natural forest in the Hainich Nationalpark.

Fig. S2. Very high-resolution image of a selection-cutting forest of the region Hainich-Dün.

Data S3. Soil sampling methods.

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