CHAPTER 12

The challenge of pollen-based quantitative reconstruction of Holocene plant cover in tropical regions: A pilot study in Cameroon

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ABSTRACT: Quantitative pollen-based reconstruction of Holocene plant abundance has not been attempted in the tropics so far. Tropical vegetation is characterized by a large number of entomophilous species and pollen-vegetation modelling for such plants is widely considered too problematic. However, there is a pressing need for quantitative reconstructions of Holocene plant cover in tropical regions to better assess climate- and human-induced environmental crises over time. Of particular note is the environmental crisis at the end of the ‘African Humid Period’ (*c.* 3 thousand years before present [ka BP]) which remains unquantified. Here, we present results from a pilot study in the Cameroon highlands including estimates of relative pollen productivity (RPP) for major taxa of the Afromontane forests and grasslands using the Extended R-Value (ERV) model, and the first reconstructions of past regional and local Holocene plant cover using the Landscape Reconstruction Algorithm (LRA). RPP estimates were obtained for 12 taxa. We found that *Celtis*, *Alchornea*, *Syzygium*, *Macaranga/Mallotus*, *Nuxia* type, and *Schefflera* have RPPs larger than Poaceae, and Moraceae, Combretaceae/Melastomataceae, *Prunus africana/Rubus pinnatus*, Cyperaceae, and *Podocarpus* lower RPPs than Poaceae. The LRA was applied to three Holocene pollen records from Cameroon (Bambili, Mbi, Mbalang) and one from Nigeria (Tilla). The results confirm the abruptness of the forest collapse in Cameroon at 3 ka BP, and suggest that it was faster and of larger magnitude than earlier anticipated. The LRA reconstruction also indicates that the regional landscape in the mountain region was more open than uncorrected pollen percentages alone suggest. Moreover, it supports the earlier interpretation of a dense forest at Bambili 11–3.5 ka BP and the local occurrence of Afromontane forest taxa at Mbalang in the Mid-Holocene.

12.1 INTRODUCTION: THE CHALLENGE

A way to anticipate the impact of current and future anthropogenic climate change on the environment, in particular in relation to the ongoing ‘6th extinction’ (Barnosky *et al.* 2011), is to study past crises as accurately as possible. Tropical Africa experienced a major climate-driven environmental crisis at the end of the Holocene (Lézine *et al.*, this volume, and references therein). This crisis affected all natural tropical African ecosystems. Near the equator this resulted in the collapse of Afromontane forests and the expansion of grasslands and woodland grasslands. While in the Sahara and Sahel tropical species disappeared. This crisis is well documented by numerous pollen records acquired over the last decades in western Africa (e.g. Hély *et al.* 2014; Vincens *et al.* 1999). However, the resulting land-cover change remains difficult to quantify because of the wide variety of pollen productivity and dispersal mechanisms of tropical plant species (Lézine *et al.* this volume; Bouimethraan *et al.*, this volume); which implies unexpected and variable representation of the surrounding vegetation by pollen in studies of modern pollen-vegetation relationships (e.g. Gajewski *et al.* 2002; Julier *et al.* 2019). The Intergovernmental Panel on Climate Change (IPCC) pointed out that proxy-based climate reconstructions in Africa were too limited to support regional climate change assessments (Masson-Delmotte *et al.* 2013). In this

context pollen-based quantification of past land-cover change is essential for climate modelling and the understanding of past land cover-climate interactions (e.g. Gaillard *et al.* 2010) as they can be used to evaluate Dynamic Vegetation Model simulations (e.g. Lu *et al.* 2018) and Anthropogenic Land Cover Change scenarios (Kaplan *et al.* 2017; Li *et al.* 2020), and help to better evaluate carbon storage over time and its impact on climate.

Quantitative pollen-based reconstruction of Holocene plant abundance have not been attempted in the tropics so far. However, some studies have estimated Relative Pollen Productivity (RPP) of major taxa in tropical and subtropical regions of the world (e.g. Jiang *et al.* 2020; Wan *et al.* 2020), including two studies in South Africa (Duffin and Bunting 2008; Hill *et al.*, this volume) and one study in Namibia (Tabares *et al.* 2021). Here we present results from a pilot study in Cameroon testing methods and models previously used and validated in the northern Hemisphere, i.e. the Extended R-Value (ERV) model (Parsons and Prentice 1981; Prentice and Parsons 1983) and the Landscape Reconstruction Algorithm (LRA; Sugita *et al.* 2007a and 2007b). The aim was to obtain first estimates of RPPs for major plant taxa and reconstruct their cover over the Holocene at both regional and local spatial scale on the Adamawa Plateau and in the montane/sub-montane regions of Cameroon (Figure 1). Reconstruction of the relationship between the cover of woodland and open land over the 3 ka BP Holocene environmental crisis in Cameroon (e.g. Lézine *et al.* 2013) is of particular interest and represents a first attempt to quantify the crisis effect on the vegetation cover. We present major results of the study to illustrate the potential of using the ERV model and the LRA in tropical areas, and to highlight major methodological issues and possible improvements.

12.2 MATERIALS AND METHODS

12.2.1 Study Region And Study Sites

The 30 sites selected for collection of modern soil pollen and related vegetation surveys for the RPP study are distributed at altitudes between 432 and 2990 m asl. in the montane/submontane and Guineo-Congolian sectors, except one sample at the southern border of the Sudano-Guinean sector (Figure 1, Table S1). A stratified random distribution of sites was chosen to ensure a good representation of the major taxa occurring in the Holocene vegetation history of the study region. However, site distribution was also influenced by logistical issues related to the number and season of the project's field expeditions and other limitations due to local circumstances.

The Holocene pollen sites used for the LRA reconstructions fall within the geographical range of the modern sites and are located at different elevations in the volcanic mountain range of Cameroon, at 2000–2200 m asl. in the Afromontane forest sector (Bambili, Lézine *et al.* 2013; and Mbi, Lézine *et al.* 2021), and at 1110–1260 m asl. in the Guineo-Sudanian wooded grasslands (Mbalang, Vincens *et al.* 2010) (Figures 1, 2; Table S3). An additional pollen site (Tilla, Salzmann *et al.* 2002) from the Sudanian wooded grassland at 690 m asl. in Nigeria was selected for the REVEALS reconstruction of regional vegetation needed to apply the LOVE model for reconstruction of the local vegetation around Mbalang (Figure 1; Table S3). For further details on the choice of sites, please see Supporting Online Material (SOM) section 12.2.4. Henceforth, all dates are given in calibrated ^{14}C yrs before present (CE 1950) (abbreviated ka BP).

12.2.2 Pollen And Vegetation Data

The collection of soil samples and vegetation surveys for the RPP study were performed in February 2010, October 2012, and April 2015. The pollen-vegetation dataset includes data from 4 sites in semi-deciduous forests, 10 sites in mountain forests, and 16 sites in savannahs (Figure 1;

Figure 1. Location of sites for the study of relative pollen productivities (surface soil samples and vegetation surveys) and fossil pollen records used for the application of the Landscape Reconstruction Algorithm. Simplified vegetation map of Cameroon (from Letouzey (1985) and White (1983), modified). Small map, lower right corner: I. Guineo-Congolian centre of endemism; XI. Guineo-Congolian/Sudanian transition zone; III. Sudanian centre of endemism; XVI. Sahelian transition zone. XVII. Saharan transition zone. Abbreviations: modern samples: MF montane forest; SA savannah; SDF semi-deciduous forest; fossil pollen sites: Bb Bambili; Mb Mbi; Mg Mbalang; Ti Tilla.

Table S1). For further details on the methods used for collection of the pollen samples and vegetation surveys, pollen analysis, vegetation data handling, and on data access please see Supplementary Online Material, SOM-12.1.

Figure 2. Altitudinal distribution of plant taxa discussed in the text (from Verlhac *et al.* 2018; modified). The altitudinal distribution of the main vegetation types (from Letouzey 1985) is shown on the left, while the altitudinal occurrence of Poaceae as a dominant taxon in wooded and open grasslands is indicated on the right. The colours refer to those in Figure 1 (except for Poaceae) and Figures 3, 5 and 6. The altitudinal location of pollen sites used for the LRA reconstructions is shown on the right, and the Nigerian site (Tilla) on the left. * indicates that the site Tilla belongs to another grassland system than the Cameroon sites (Figure 1).

12.2.3 The Erv Model and Erv Analysis

Detailed overviews of the underlying theory and assumptions of the ERV model and its developments can be found in Gaillard *et al.* (2008) and Bunting *et al.* (2013). Details on models and methods used for calculation of RPPs, and the computer programme for the ERV analysis are provided in SOM-12.1.4.

In this study, we used the three ERV sub-models developed by Parsons and Prentice (1981), Prentice and Parsons (1983), and Sugita (1994). The application of the ERV sub-models requires the following inputs:

- Pollen data: pollen % of taxon *i* at site *k*. In this study the maximum number of taxa analysed is 26 and *k* is a soil sample from a 1 m² area, for 30 sites (SOM-12.1, Table S2)
- Radius of the sedimentary basin: distance in m. In this study this is the radius of the area from which soil was collected, i.e. 0.5 m.
- Reference taxon: the RPP of the reference taxon is set to 1, and the RPP of all other taxa included in the analysis are related to that reference taxon. In this study Poaceae is used as the reference taxon.

- Vegetation data: Non-distance-weighted vegetation abundance of taxon *i* around site *k*. In this study percentage cover is used, from 0.5 to 3000 m in 5 m-concentric rings working out from the sampling location.
- Z_{max} : distance within which most pollen comes from. In this study estimated to be 200 km (see SOM-12.1.4).

The ERV model also requires that vegetation data is distance-weighted. We used three alternative models, 1/d (Prentice and Webb 1986), ‘Prentice’s model’ for bogs (uses a Gaussian plume diffusion model (P-GPM) and assumes pollen deposition at one point; Prentice (1985)), and the Lagrangian Stochastic Model (LSM) (Kuparinen 2006; Kuparinen *et al.* 2007). P-GPM and LSM describe dispersion and deposition of pollen in different ways (e.g. Theuerkauf *et al.* 2013). For the application of these two models, additional inputs are needed:

- Fall speed of pollen (FSP) (m/s) of each taxon used in the analysis; FSP was calculated for the 26 taxa that were used in the ERV ‘start run’ (Table S2; see SOM-12.1 for details on the ERV analysis strategy and methods to calculate fall speed of pollen).
- Wind speed (m/s), in this study 3 m/s.; this wind speed is widely used in the RPP studies performed in the Northern Hemisphere; it is also close to the modern average 10-m wind speed over land in Europe and China (e.g. Grassi *et al.* 2015), and the global average 10-m wind speed over land (3.28 m/s (class 1), Archer and Jacobson 2005).

The ERV analysis estimates the RPPs and their standard errors (SEs) using the maximum likelihood method (Stuart and Ord 1994) and quantifies the best ‘linear fit’ between pollen percentages and distance-weighted plant abundances using the likelihood function score (LFS, Prentice and Parsons 1983) or log likelihood (log L; e.g. Li *et al.* 2017) over distance (see SOM-12.1 for details). Beyond the distance at which the best linear fit is achieved, the curve of LFSs and log Ls reach an asymptote, i.e. do not decrease, respectively increase with distance.

The main outputs of one ERV analysis using the three ERV sub-models and the three distance-weighting models, i.e. nine runs of ERV analysis in total are:

- Vegetation dispersion with distance (a measure of vegetation stationarity, see SOM-12.1.3) (Figure 3A),
- Mean plant composition with distance for each taxon used in the analysis (Figure 3A),
- Adjusted pollen proportions (submodels 1 and 2) or relative pollen loading (submodel 3) and vegetation proportions (1, 2) or absolute vegetation abundance (3) as calculated by the maximum likelihood method; empirical modern pollen data are expressed in percentages, which implies a non-linear pollen-vegetation relationship that would not have any algebraic solution for the RPPs and the ‘background pollen’ in the ERV model equation. The pollen-vegetation relationship needs therefore to be linearized (Figure 4) (see SOM-12.1.4 for details),
- LFS and log L with distance (Figure 3A),
- RSAP (*sensu* Sugita 1994) calculated with the moving-window regression approach developed by S. Sugita (*in* Gaillard *et al.* 2008); RSAP is Z_{RSAP} in the ERV model equation, i.e. the distance beyond which the ‘background pollen’ (second term in the ERV model’s equation, ω_i) is constant between sites within a region characterized by stationary vegetation; it is also the distance at which the linearity of the pollen-vegetation relationship is best and does not improve with distance (see SOM-12.1.4 for details); stationary vegetation implies that any area (e.g. 10 km × 10 km) has the same species composition as any other such area within the study region,
- RPP and their standard errors (SEs) with distance for each taxon used in the analysis (Figure 3B).

Details on the ERV analysis strategy are provided in SOM-12.1.4. The first ERV analysis run used the 26 taxa with both pollen and vegetation data in ≥ 5 sites (Table S2). Based on plots

Figure 3. Examples of results from the ERV analysis of pollen and vegetation data from 30 sites in Cameroon (see Figure 1 for site distribution). This analysis used 12 taxa, ERV submodel 2 and the Prentice's Gaussian Plume Model for distance weighting of vegetation (see Methods and SOM-12.1.4 for details). (A) Log likelihood, vegetation dispersion, and mean taxa composition (in proportion) over distance from the pollen sample points; note that the scale for Poaceae is on the right of the diagram. (B) Relative Pollen Productivities (RPPs) with distance from the pollen sample points for seven taxa. The colours relate to those in Figures 1, 2, 5 and 6; the five shades of red (dark brownish red to light pink) relate to the red colour in Figures 1 and 2 and to the five shades of red in Figures 5 and 6; the three shades of green relate to Figures 1 and 2 two shades of green together and to the three shade of green in Figures 5 and 6.

of adjusted pollen percentages and vegetation proportions (Figure 4), the taxa with the best linear relationships were selected for the next runs of ERV analysis. In this paper, we present the results of the ERV analysis that produced the curve of log L closest to the theoretically correct curve (increases and reaches an asymptote at a certain distance; SOM-12.1.4), which was obtained with 12 taxa, ERV sub-model 2, and P-GPM for distance weighting of vegetation (Figure 3A; Table 1A).

12.2.4 Landscape Reconstruction Algorithm (LRA)

Details on the LRA and its assumptions are found in SOM-12.2.3. LRA comprises two models, REVEALS (REgional VEgetation Abundance from Large Sites) (Sugita 2007a) and LOVE (LOcal VEgetation Estimates) (Sugita 2007b). Both models reduce biases due to inter-taxonomic differences in pollen productivity and basin size. REVEALS estimates the mean regional vegetation composition of plant taxa in proportion (dimensionless) for a large region (minimum 100 km × 100 km; Hellman *et al.* 2008) using pollen records from large lakes. REVEALS assumes that no plants are growing on the deposition basin (Sugita 2007a). Therefore, model

Figure 4. Examples of ERV-corrected pollen-vegetation relationships for six taxa from the ERV analysis using the full pollen-vegetation dataset (30 sites), 12 taxa, ERV submodel 2 and the Prentice's Gaussian Plume Model for distance weighting of vegetation (see Methods and SOM-12.1 for details). The coefficient of determination (R^2) is provided as a measure of linearity, the higher the value the more linear the relationship.

estimates from pollen assemblages in large bogs will be biased by pollen coming from the surface of the bog. LOVE estimates 'background pollen' using REVEALS estimates of regional vegetation, and subtracts 'background pollen' to derive local vegetation cover within the RSAP (see ERV model above and SOM-12.1). The RSAP represents the smallest spatial scale of the LOVE reconstruction. Both REVEALS and LOVE provide estimates of plant abundance/cover with their SEs. Note that the plant abundance estimated by LOVE is distance weighted.

The application of the LRA requires a minimum of two pollen records from the same vegetation/landscape type, one from a large lake for a REVEALS-based reconstruction of the regional plant cover, and one from a small lake for a LOVE reconstruction of the local plant cover. However, calculation of the RSAP of small sites requires pollen records from several sites (see SOM-12.2.3 for further explanations). Due to the small number of pollen records appropriate for a LRA in the study region, we made the following assumptions:

- (1) Pollen of Cyperaceae are primarily of local origin, growing on the swamp (Mbi) or at lake shores (Bambili, Tilla, Mbalang), and Cyperaceae are the dominant plants in these biotopes,
- (2) The RSAP of the small sites is 2 km (SOM-12.2.3),
- (3) The pollen record (Cyperaceae excluded) from Mbi and Tilla represent the mean regional vegetation cover around Bambili and Mbalang, respectively.

Possible departures from these assumptions are described in SOM-12.2.3. A local origin of most pollen from Cyperaceae is supported by the analysis of > 1000 modern pollen samples from Africa, Madagascar and Arabia (Gajewski *et al.* 2002) suggesting that Cyperaceae pollen is related primarily to humid regions and habitats in Africa.

Table 1. Habitus, pollination, Fall Speed of Pollen (FSP) and Relative Pollen Productivities (RPP) with their standard errors (SE) for 12 major taxa in: (A) Cameroon (this study), (B) from other studies in South Africa (Hill *et al.*, this volume); Namibia (Tabares *et al.* 2021); Bolivia (Whitney *et al.* 2018); Brazil (Piraquive Bermúdez *et al.* 2019); and (C) from other studies in Subtropical China: left (Fang *et al.* 2020), centre (Jiang *et al.* 2020), right (Chen *et al.* 2019); Tropical China (Wan *et al.* 2020). ^ FSP from Jiang *et al.* (2020). Reference taxon (Poaceae=1): * indicates that Poaceae is the reference taxon used in the analysis. ** indicates that other taxa were used as reference and RPP values were converted to Poaceae=1. Abbreviations: H herb, S shrub, T tree; Pollinat Pollination; A anemophilous, E entomophilous; (A) and (E) indicate that the one type of pollination is less common than the other.

(A) Cameroon (this study)

Taxa	Habitus	Pollinat.	FSP (m/s)	RPP	SE
<i>Alchornea</i>	S/T	E/A	0.012	4.00	0.188
<i>Celtis</i>	T	E/A	0.010	7.00	0.270
Combretaceae/Melastomataceae	T/H	E	0.012	0.50	0.039
Cyperaceae	H	A/(E)	0.022	0.23	0.045
<i>Macaranga</i>	T	E/(A)	0.013	1.70	0.054
Moraceae	T	A/E	0.006	0.60	0.070
<i>Nuxia</i> type	T	E	0.003	1.40	0.397
Poaceae	H	A	0.035	1.00*	0.000
<i>Podocarpus</i>	T	A	0.017	0.06	0.018
<i>Prunus africana</i> / <i>Rubus pinnatus</i> (Rosaceae)	T	E	0.013 (0.021)^	0.40	0.037
<i>Schefflera</i>	T	E	0.009	1.80	0.164
<i>Syzygium</i>	T	E	0.003	2.20	0.107

(B) Other studies:

	S Africa	Namibia	Bolivia	Brazil				
Taxa	RPP	RPP	SE	RPP	RPP	SE	RPP	SE
<i>Alchornea</i>								
<i>Celtis</i>								
Comb./Mel.		0.217	0.014					
Cyperaceae					0.48	0.11	0.63	0.33
<i>Macaranga</i>								
Moraceae				0,25				
<i>Nuxia</i> type								
Poaceae	1.00*	1.00*	0.00	1.00**	1.00**	0.00	1.00**	0.00
<i>Podocarpus</i>	6.50							
<i>P. africana</i> / <i>R. pinnatus</i> (Rosaceae)								
<i>Schefflera</i>								
<i>Syzygium</i>								

(Continued)

Table 1. Continued

(C) Other studies:		Subtropical China				Tropical China		
Taxa	RPP	SE	RPP	SE	RPP	SE	RPP	SE
<i>Alchornea</i>								
<i>Celtis</i>								
Comb./Mel.								
Cyperaceae								
<i>Macaranga</i>							2.21	0.08
Moraceae					0.50	0.35	6.52	0.08
<i>Nuxia</i> type								
Poaceae	1.00*	0.00	1.00**	0.00	1.00**	0.00	1.00*	0.00
<i>Podocarpus</i>								
<i>P. africana</i> /R. <i>pinnatus</i>								
(Rosaceae)	0.41	0.28	0.84	0.045	1.00	0.45		
<i>Schefflera</i>								
<i>Syzygium</i>								

Relying on the three assumptions above, we used the pollen records from Mbi and Tilla (large lake sites) for REVEALS reconstructions of the regional plant abundance, and from Bambili and Mbalang (small lake sites) for the LOVE reconstructions of the local plant abundance around each lake. We excluded Cyperaceae from the pollen records and used the 11 taxa for which we have RPP estimates (Table 1A). In addition, we tested alternative RPP values for *Podocarpus*, i.e. the mean RPPs of *Pinus* (6.38) and *Picea* (2.62) in Europe, to evaluate their effect on the reconstructions and discuss them in the light of the existing knowledge on the dispersal and deposition of *Podocarpus* pollen. Only one additional RPP value is available for *Podocarpus* to date, i.e. 6.54 (related to Poaceae) from a study in South Africa (Duthie 2015; Hill *et al.*, this volume) (Table 1B). *Pinus*, *Picea* and *Podocarpus* all belong to coniferous plants for which large pollen productivity is common. Note also that Hill *et al.*'s value is very close to *Pinus* mean RPP in Europe. The REVEALS and LOVE reconstructions were performed for continuous 500-year time windows over the last 12 ka years, except for Mbalang (last 6 ka years). Z_{max} was set to 200 km and wind speed to 3 m/s (see 12.1.4, above, and SOM-12.1.4). We used the computer programme LRA.REVEALS.v6.2.4.exe and LRA.LOVE.v6.2.3.exe (Sugita, unpublished) to calculate the REVEALS estimates of regional plant cover at Mbi and Tilla and LOVE estimates of local plant cover within 2 km-radius areas around Bambili and Mbalang. See SOM-12.2.3 for details on access to the computer programmes.

12.3 RESULTS

12.3.1 ERV analysis and RPP estimates

Vegetation dispersion and mean plant cover over distance from the pollen sample points (Figure 3A) based on the collected vegetation dataset (SOM-12.1.3) indicate that the ERV model's assumption of stationary vegetation is violated in the study region. Both vegetation dispersion and mean plant cover increase with distance until maximum values at c. 50–100 m and then decrease until c. 600 m instead of reaching an asymptote. The values of mean plant cover for *Alchornea*, *Macaranga*, *Celtis*, Moraceae and Poaceae indicate that these taxa have a more stable

composition already from *c.* 200 m. The log likelihood curve shows a similar pattern as vegetation dispersion, although with a much less prominent ‘overshoot’ of the curve at 50 m. From 600 m, the values of mean plant cover remain relatively constant for all plant taxa. This distance also corresponds to the RSAP (585 m) as calculated from the log L curve (Figure 3A) with the moving-window regression method. An attempt to analyse forest and savannah sites separately to decrease vegetation dispersion did not improve the results; instead, the log L curves diverged from the theoretically correct curve even more (results not shown).

Most curves of RPPs plotted against distance from the pollen sample point deviate from the expected behaviour (increase to reach an asymptote at a certain distance), but the RPP values are relatively constant from *c.* 1500 m for all taxa except *Celtis*. The RPPs of *Podocarpus* exhibit more or less constant values over 3 km. The RPPs of Combretaceae/Melastomataceae and *Schefflera* reach maximum values at very short distances, decrease abruptly, and maintain relatively constant values from a few metres. The RPPs of *Alchornea* and *Celtis* increase to maximum values at *c.* 200 m and then decrease gradually until 1500 m and 3000 m, respectively. The RPPs of Moraceae and *Syzygium* increase until 200 m where they reach an asymptote, although the values of Moraceae are very unstable. Because RPPs still decrease after the calculated RSAP distance (585 m), we selected the final RPP values at the distance for which they stabilize for all taxa, i.e. 1500 m (Table 1A).

Figure 4 presents examples of ERV model-corrected pollen-vegetation relationships for six of the 12 taxa. *Schefflera*, Poaceae and *Syzygium* exhibit the most linear relationships with coefficients of determination (R^2) of 0.63, 0.54 and 0.58, respectively. Moraceae and Combretaceae/Melastomataceae have weaker linear relationships with R^2 values of 0.42 and 0.26, respectively. A R^2 value of 0.14 indicates a very weak linearity for *Podocarpus*. Combretaceae/Melastomataceae, *Schefflera*, and *Syzygium* are strongly overrepresented, Poaceae is slightly overrepresented, and *Podocarpus* strongly underrepresented by pollen. The pollen-vegetation relationship of Moraceae clearly indicates either overrepresentation or underrepresentation by pollen depending on the site.

12.3.2 Landscape Reconstruction Algorithm (LRA): Regional and local plant cover

The REVEALS reconstructions represent regional plant abundance in an area of *c.* 100 km $\times$ 100 km around Mbi and Tilla, and the LOVE reconstructions the local plant abundance in an area of minimum 2 km radius around Bambili and Mbalang (see Methods and SOM-12.2.4). The REVEALS and LOVE estimates with their SEs for the 11 taxa are provided for Mbi and Bambili in Figures S2–S5) and highlight the effect of the RPPs’ SEs on the reconstructions. *Podocarpus*, *Nuxia*-type, Moraceae, and *Prunus africana/Rubus pinnatus* have the largest SEs in relation to their RPP value (Table 1A). These taxa also exhibit the largest SEs of LRA reconstructions. When RPP 0.06 is used for *Podocarpus*, SEs are very large for *Podocarpus* and relatively large for *Nuxia*-type (for both REVEALS and LOVE plant cover) (Figure S2). SEs are also quite large for Moraceae and *Prunus africana/Rubus pinnatus* (for LOVE plant cover) in the Early Holocene (Figures S2 and S3). All other taxa exhibit small SEs over most of the Holocene. There are generally few values not different from zero (i.e. $SD \geq$ REVEALS/LOVE estimate) and they occur mainly for very low values of plant cover, except for *Podocarpus* (RPP 0.06) that has also very large SEs for high LOVE plant cover over most of the Holocene (Figure S2).

12.3.2.1 Mountain woodlands: Mbi and Bambili (Figure 5; Figures S2–S5)

The pollen sum of the 11 taxa used in the LRA reconstructions represent 61–81% (mean 69.4%) (Mbi) and 59–76% (mean 65.5%) (Bambili) of the total pollen sum of terrestrial plant taxa (SOM-12.2.1, Table S3A). The REVEALS and LOVE reconstructions are strongly influenced by the RPP used for *Podocarpus*. The low RPP (0.06) results in a very strong dominance of *Podocarpus* 9.5–0.5 ka BP in the regional vegetation (Mbi) and 10.5–2 ka BP locally around

Figure 5. REVEALS-based regional and LOVE-based local plant cover using the pollen records from Mbi and Bambili, respectively, and three alternative RPPs for *Podocarpus* (0.06, 2.62, and 6.38). Plant cover in percentage of an area of $100 \text{ km} \times 100 \text{ km}$ for Mbi, and of minimum 2 km radius for Bambili. Upper panel: pollen percentages for Mbi and Bambili, REVEALS (Mbi)- and LOVE (Bambili)-based plant cover using 0.06 for *Podocarpus*; Lower panel: REVEALS (Mbi)- and LOVE (Bambili)-based plant cover using RPP 2.62 (left) and 6.38 (right) for *Podocarpus*. The colours relate to those in Figures 1, 2 and 3; the five shades of red correspond to carmine red and three shades of green to the two shades of green together in Figures 1 and 2.

Bambili. The other nine tree taxa have a reduced abundance compared to their pollen %, except Moraceae. Regional woodland cover (Mbi) is larger than total tree pollen %, and local woodland cover at Bambili is 100% 12–3 ka BP while percentages of total tree pollen increase from *c.* 50% (12 ka BP) to 97–98% (8–4.5 ka BP) to decrease back to *c.* 55% at 3 ka BP.

When higher RPPs (2.62 and 6.38) are used for *Podocarpus*, regional openland (Poaceae) around Mbi represents > 50% of the total vegetation cover over the entire Holocene, while pollen % exceed 50% only 12–11 ka BP, 5–4.5 ka BP, and 1 ka BP to present. In contrast, local vegetation cover at Bambili is 100% wooded 11–3.5 ka BP, and the decrease of woodland from 3 ka BP is much larger and more abrupt than the decrease in total tree pollen %. Woodland cover drops from 100% to 29% (RPP 2.62) or 22% (RPP 6.38) between 3.5 and 3 ka BP, whereas pollen % decrease from 98% to 55% between 4.5 and 3 ka BP. While *Podocarpus* maintains pollen % > 10% at Bambili 7–4.5 ka BP, its reconstructed local cover around the site is < 10% and not different from zero 6–5.5 ka BP (Figure S2). The major effect of using RPP 2.62 rather than 6.38 on the reconstruction of regional vegetation is a larger cover (*c.* double) of *Podocarpus* throughout the Holocene at the expense of Poaceae, while the cover of other trees does not change significantly. The largest differences in composition of tree taxa between pollen %

and regional plant cover (Mbi) is mainly a larger cover of Combretaceae/Melastomataceae in relation to *Alchornea*, *Macaranga*, and *Celtis*. In terms of the local tree composition around Bambili, the major difference between pollen percentage and plant cover is a larger cover of *Schefflera* at the expense of *Podocarpus* 10.5–3.5 ka BP, and a larger cover of Moraceae and *Macaranga* at the expense of *Alchornea* and *Celtis* (except for the last 50 years). In recent time, the cover of Combretaceae/Melastomataceae is larger than earlier and *Schefflera* dominates the tree cover.

12.3.2.2 The Sudanian and Guineo-Congolian wooded grasslands: Tilla and Mbalang

The pollen sum of the 11 taxa used in the LRA reconstructions represent 68.1–95.8% (mean 82.7%) (Tilla) and 48.7–94% (mean 72.2%) (Mbalang) of the total pollen sum of terrestrial plant taxa (SOM-12.2.1, Table S1A) (Figure 6). The REVEALS reconstructions of regional plant cover around Tilla are characterized by a very large cover of openland (Poaceae) throughout the Holocene whatever RPP is used. Moreover, the cover of Poaceae is larger than their pollen %.

Figure 6. REVEALS-based regional and LOVE-based local plant cover using the pollen records from Tilla and Mbalang, respectively, and three alternative RPPs for *Podocarpus* (0.06, 2.62, and 6.38). Plant cover in percentage of an area of 100 km × 100 km for Tilla, and an area of minimum 2 km radius for Mbalang. Upper panel: pollen percentages for Tilla and Mbalang, REVEALS (Tilla)- and LOVE (Mbalang)-based plant cover using 0.06 for *Podocarpus*; Lower panel: REVEALS (Tilla)- and LOVE (Mbalang)-based plant cover using RPP 2.62 (left) and 6.38 (right) for *Podocarpus*. The colours relate to those in Figures 1 and 2; the five shades of red correspond to carmine red and three shades of green to the two shades of green together in Figures 1 and 2.

There is no significant difference between the three reconstructions except a slightly larger cover of *Podocarpus* when RPP 0.06 is used. The total cover of trees is smaller than tree pollen %, and Combretaceae/Melastomataceae are dominant over the other tree taxa, which is not the case in pollen %.

The LOVE reconstructions for Mbalang exhibit a total cover of tree of 100% with RPP 0.06 for *Podocarpus* over the period 6–3 ka BP, and of 40–60% with RPPs 2.62 and 6.38. With RPP 0.06, *Podocarpus* is dominant, while all other trees have a cover smaller or much smaller than their pollen percentage, except *Prunus africana*/*Rubus pinnatus* and Moraceae that have a higher, respectively slightly higher cover than their pollen %. With RPPs 2.62 and 6.38, Poaceae has a cover slightly smaller than its pollen %, especially 6–3 ka BP. *Prunus africana*/*Rubus pinnatus* has a larger cover than its pollen % over the entire period 6–0 ka BP, as well as Moraceae and *Macaranga* 6–3 ka BP, and Combretaceae/ Melastomataceae 4.5–3 ka BP. *Podocarpus*, Combretaceae/ Melastomataceae, *Celtis* and *Alchornea* have a smaller cover than their pollen %. LOVE plant cover and pollen of *Syzygium* and *Schefflera* are similar in proportions. *Podocarpus* has a larger cover in the reconstruction with RPP 2.62 than in the one with RPP 6.38. The decrease in total trees at 3 ka BP is sharp in both cover and pollen %, but the decrease in cover (48 to 9%) is larger than in pollen % (30 to 7%).

12.4 DISCUSSION

12.4.1 Relative Pollen Productivity (RPP)

12.4.1.1 Effects of violation of model assumptions and other factors

The effects on RPPs of deviations from the ERV model assumptions and other factors have been discussed earlier in syntheses of RPP values in Europe (Broström *et al.* 2008; Mazier *et al.* 2012), temperate China (Li *et al.* 2017) and the Northern hemisphere (Wieczorek and Herzschuh 2020). The number of factors affecting RPPs and/or causing between-study variability in RPP values for a taxon are numerous. They span from between-study region differences in climate, land use, vegetation type/structure and plant species (including their pollination strategies), between-study variation in methods used to collect the pollen-vegetation dataset (including methods in field and laboratory, and data handling), to differences between models and/or model implementation (including dissimilarities in parameter setting, parameter values, and calculation procedures). Because of the relatively low number of RPP values (response variables) compared to the number of factors (explanatory variables), statistical quantification of the effect of these factors on RPP estimates has never been attempted so far. In this pilot study, the major factors that need to be considered with care are the violation of the ERV model's assumptions in terms of stationarity of the vegetation in the study area, random distribution of sites, mode of dispersal and deposition of pollen, and taphonomy and preservation of pollen in soil samples.

Vegetation dispersion and mean plant composition over distance (Figure 3A) indicate that vegetation is not stationary in the study region, and site distribution did not follow a true random scheme, but a stratified random one. Both factors may explain the shape of the log L curves obtained from the ERV runs (example in Figure 3A) (e.g. Broström *et al.* 2005; Li *et al.* 2017). Moreover, the difference in vegetation data collection within and beyond 100 m (also seen in the difference in mean plant composition within and beyond 100 m, Figure 3A) may also cause the 'overshoot' of log L values at short distances (< 100 m) before the curve decreases and/or plans out. The shape of the log L curve implies that the definition of the RSAP is uncertain. Based on the empirical and simulation study of Broström *et al.* (2005) on the effect of non-random site distribution on likelihood function scores and the identification of the RSAP, we assume that the large RSAP, i.e. the distance at which all curves of RPP with distance stabilize (1500 m), is most realistic.

Eight of the twelve plant taxa involved in the analysis are entomophilous, of which three have been described as partly anemophilous (Table 1A). The assumption of the ERV model that all pollen is transported by wind is therefore violated. However, these taxa are common in lake sediments and peat deposits of tropical Africa, which suggests that part of the pollen produced is transported by wind. Therefore, an estimate of the relationship between vegetation and pollen transported to palaeoecological archives such as lakes and bogs remains useful. Nevertheless, such estimate will not be comparable with true pollen productivity in the plant stamina, but can be used as a measure of the proportion of pollen transported and deposited in soils, moss pollsters, lakes and bogs. The use of soil samples instead of moss pollsters in regions where mosses are uncommon and/or poor in pollen (e.g. Wan *et al.* 2020) may also imply biases of the pollen assemblages compared to mosses/lake sediment/peat. Gajewski *et al.* (2002) analysed a database of all surface pollen data available in Africa and concluded that percentages of the three most abundant pollen taxa did not show any bias among sampling methods. However many studies have indicated biases of pollen assemblages in soil samples compared to, e.g. pollen traps due to poor preservation conditions (e.g. Zhang *et al.* 2015). We therefore assume that the most common pollen types in soils are those that are well preserved due to their species/taxon-specific wall structure, and that their amount corresponds to the pollen transported and deposited in the soil. To our knowledge, little is known on the number of years of pollen deposition in soil samples (e.g. Havinga 1984). Thus, we assume that they represent some years of pollen deposition. One of the basic assumptions of pollen analysis as a tool to reconstruct past vegetation change is that pollen productivity is a constant, although pollen-trap studies have shown that inter-annual variation occurs in the absence of changes in plant cover (e.g. Abraham *et al.* 2021; Gosling *et al.* 2005; Haselhorst *et al.* 2013; Julier *et al.* 2019). These known variations are considered as ‘noise’ in terms of the pollen productivity measure needed to interpret sedimentary pollen records (e.g. Fang *et al.* 2020). Individual pollen assemblages from lake sediments or peat used? to be from multiple years-samples, and each quantitative reconstruction of plant cover using the LRA (REVEALS and LOVE) seldom represents less than 100 years, and generally covers 100 to 500 years (e.g. Cui *et al.* 2014; Trondman *et al.* 2015).

Fall Speed of Pollen (FSP) is an important parameter in pollen-vegetation modelling. Between-study differences in FSP for a given taxon will influence the RPP results (e.g. Bunting *et al.* 2004). However, there is little difference in the estimated FSPs of pollen taxa between this study and other studies in the tropics and subtropics, except for *Podocarpus* (0.0175 m/s in this study; 0.074 in Hill *et al.*, this volume). Fall speed for Poaceae varies between studies from 0.0133 m/s in tropical China (Wan *et al.* 2020) to 0.050 m/s in South Africa (Hill *et al.*, this volume). However, the FSP estimate from the study in Namibia (0.031 m/s, Tabares *et al.* 2021) is close to the FSP we are using (0.035 m/s; Broström *et al.* 2004).

12.4.1.2 Comparison with RPPs from other studies in the tropics

RPP values are available from other studies in the tropics for six taxa included in our study (number of values in brackets, our study excluded): Combretaceae/Melastomataceae (1), Cyperaceae (2), *Macaranga* (1), *Moraceae* (3), *Podocarpus* (1) and Rosaceae (3; for comparison with the RPP of *Prunus africana*/*Rubus pinnatus*) (Table 1B). RPPs for each of these taxa are surprisingly similar given that studies are from geographically very different regions and often use different methods. The comparison confirms RPPs smaller than that of Poaceae for Combretaceae/Melastomataceae, Cyperaceae, and Rosaceae, and RPPs larger than that of Poaceae for *Macaranga*. However, *Moraceae* exhibit contradicting results with RPPs that are either larger (one value in tropical China) or smaller (two values) than the RPP of Poaceae. Similarly, *Podocarpus* has a much smaller RPP than Poaceae in our study, but much larger RPP than Poaceae in South Africa (see Hill *et al.*, this volume). Earlier studies have also reported that both *Moraceae* and *Podocarpus* can exhibit high and low pollen quantities in surface samples within only a few

meters (e.g. Gosling *et al.* 2005; Maley *et al.* 1990; Vincens 1984; Wan *et al.* 2020). Moreover, results indicated that *Podocarpus* pollen % in surface soils were often high within the forest (up to 40% in Vincens (1984) or 60% in Maley *et al.* (1990)), and decreased abruptly over the forest edge (to *c.* 10%) and beyond, to < 5% already 10 m from the edge (Maley *et al.* 1990) or to *c.* 5% and 1% 10 km and 50 km from the edge, respectively (Vincens 1984). Lézine (unpublished) also reported that *Podocarpus* pollen percentage in soil samples within the *Podocarpus* forests of Cameroon can vary between very low and high values within a few meters. The very low RPP of *Podocarpus* obtained in our study is probably due in part to the low proportions of the taxon in the studied forests (*c.* 8–23%, max. 29%, in distance-weighted plant abundance within 100 m of the studied sites) with corresponding pollen percentages of 0.2–2.5%, maximum 8% for 29% plant cover. Such ‘fuzzy’ pollen-vegetation relationships need to be further investigated. New, carefully designed RPP studies are necessary before we can conclude on this issue and the relevance of quantitative reconstruction for this type of taxa. Moreover, the pollen-vegetation relationship of *Podocarpus* can be biased by long-distance pollen transport, as reported in earlier studies (e.g. Maley *et al.* 1990; Vincens 1984; Wan *et al.* 2020).

Earlier studies of modern and fossil pollen spectra and related vegetation provide some hints on whether the RPP we obtained for the remaining six taxa roughly agree with those results in terms of representation of vegetation by pollen. Pollen of several entomophilous tropical taxa have been found in large numbers, e.g. *Alchornea* (Elenga *et al.* 2000; Reynaud-Farrera 1995; Vincens *et al.* 1997, 2000; Watrin *et al.* 2007), and *Celtis* and *Syzygium* (e.g. Verlhac *et al.* 2018; Watrin *et al.* 2007). Lézine *et al.* (2013) suggested that *Schefflera* might be overrepresented in the pollen record from Bambili due to high pollen productivity and long-distance transport. Our results suggest that these four taxa all have RPPs larger (*Schefflera*, *Syzygium*) or much larger (*Alchornea*, *Celtis*) than Poaceae (Table 1A).

12.4.2 LRA reconstructions of Holocene plant cover at regional and local spatial scales

Although the 11 pollen taxa used in the LRA reconstructions generally represent > 60–70% of the total pollen sum of terrestrial pollen types in the four pollen records (Table S3A), it is essential to keep in mind that we are missing in many cases a third of the pollen record. Major taxa for which we would need RPP estimates to achieve more complete reconstructions of the plant cover are: *Aerva*-type, *Antidesma*-type, *A. venosum*, *Ficus*, *Gnidia*, *Justicia*, *Maesa*, and *Rapanea* (mountain woodlands), and *Cussonia*, *Hymenocardia*, *Ixora*, *Olea*, *Tetrorchidium*, and *Uapaca* (wooded grasslands). One RPP value (19.19 relative to Poaceae) is available for *Justicia* (Navya 2020). Based on a large database of surface pollen samples in Africa, Gajewski *et al.* (2002) concluded that *Olea* pollen (*O. capensis*-type) represent the presence and abundance of the plant correctly. *Uapaca* was found to be either over-represented or under-represented by pollen (Julier *et al.* 2019). The information we have so far on the pollen-vegetation relationships of the taxa mentioned above is still too poor to anticipate the effect they would have on the LRA reconstructions. They could influence (in terms of plant cover) the timing, rate and magnitude of change in the woodland/openland relationship, and the taxa composition in woodlands over time.

We consider that the LRA reconstructions using the lowest RPP (0.06) for *Podocarpus* are unrealistic. The low RPP results in an extreme dominance of *Podocarpus* over all other tree taxa, and over Poaceae for most of the Holocene (see also discussion on RPPs above). We therefore focus on the reconstructions performed with the alternative RPPs 2.62 and 6.38, i.e. pollen productivities higher than that of Poaceae. These RPP values are also in a comparable range of values as common entomophilous tree taxa in African pollen records such as *Alchornea*, *Celtis*, *Schefflera*, and *Syzygium*.

12.4.2.1 Mountain woodlands: Mbi and Bambili

The assumed minimum size of the landscape represented by REVEALS estimates of plant cover is 100 km × 100 km (see Methods), which corresponds to an area around the site Mbi covering today montane and submontane vegetation (*c.* 55%), Guineo-Congolian rain and semi-deciduous forests (*c.* 20%), and secondary forests and grassland (25%), i.e. vegetation types from altitudes between *c.* 1000 and 3000 m asl. (Figures 1 and 2).

The REVEALS reconstructions suggest a clear dominance of grasses in the regional vegetation over the entire Holocene. The composition of trees is significantly different in plant cover compared to the pollen percentages, with a generally smaller cover than pollen percentage of *Schefflera*, *Podocarpus* (high altitude taxa) and *Alchornea* (low altitude taxon), and larger cover than pollen percentage of Moraceae and Combretaceae/Melastomataceae (mid-altitude taxa) and Poaceae (mainly mid- and low altitude) (see Figure 2 for the altitudinal distribution of taxa). Thus, the REVEALS reconstruction suggests that the regional landscape was much more open than suggested by the pollen percentages, and the high altitude and low altitude trees less abundant in relation to mid altitude trees. However, the REVEALS reconstruction does not alter the overall history and timing of changes in woodland abundance documented by the pollen percentages.

The LOVE reconstructions represent plant cover over a 2 km-radius area (assumed RSAP, Methods and SOM-12.1.4) around the lake of Bambili, which includes essentially afro-alpine grasslands and montane forests. The reconstructions suggest that the vegetation at Bambili was 100% forested 11–3.5 ka BP with a stronger dominance of the high altitude taxa (including Moraceae; *Ficus* in Figure 2) over the low altitude taxa than pollen percentages indicate. The sudden decreases in cover of *Podocarpus* at 7 ka and 3 ka BP are more pronounced than the declines in percentages, and the general collapse of the mountain forest more rapid. The landscape openness (cover of Poaceae) 3–0.5 ka BP is significantly larger than suggested by the pollen percentages.

12.4.2.2 The Sudanian and Guineo-Congolian wooded grasslands: Tilla and Mbalang

The REVEALS reconstructions of Tilla represent the regional plant cover in the Sudanian dry forests with grasslands and shrublands at low altitudes (Figures 1 and 2) and confirm that tree cover was very small all through the Holocene in contrast to Sahel's more tree-rich vegetation over early and Mid-Holocene (Salzmann *et al.* 2002). However, Combretaceae/Melastomataceae might have been more abundant in relation to *Alchornea*, *Celtis*, and *Macaranga* than pollen percentages suggest.

The assumed RSAP of Lake Mbalang (2 km) lies within the Sudano-Guinean wooded grasslands. The LOVE reconstruction suggests a 10–15% higher cover of tree taxa in the vegetation compared to the pollen percentages 6–3 ka BP and confirms a local presence of *Podocarpus* and *Prunus africana/Rubus pinnatus*. However, the larger abundance of trees compared to pollen percentages might be a bias due to the pollen record from Tilla representing only the very open regional vegetation North of Mbalang and not the areas West and South of the lake that might have been more wooded. Therefore, the LRA might have substracted too large amounts of Poaceae (background pollen inferred from the REVEALS-based regional vegetation of Tilla). If this is the case, pollen percentage of Poaceae might be closer to the actual vegetation openness at Mbalang than its LOVE-estimated cover indicates. A pollen record from a large lake closer to Mbalang would be more appropriate for a LOVE reconstruction.

12.5 CONCLUSIONS

The results from this first attempt at estimating RPP for major taxa of the Holocene vegetation of Cameroon confirm the insights gained earlier from traditional studies of the relationship between

pollen and vegetation. *Alchornea*, *Celtis*, *Macaranga*, *Schefflera*, and *Syzygium* have been found to be overrepresented by pollen (Elenga *et al.* 2000; Lézine *et al.* 2013; Reynaud-Farrera 1995; Verlhac *et al.* 2018; Vincens *et al.* 1997, 2000; Watrin *et al.* 2007) and are also the taxa for which the estimated RPP are larger than that of Poaceae. Of the taxa for which RPP values are available from other studies, Combretaceae, Cyperaceae, *Macaranga* and *Prunus africana*/*Rubus pinnatus* exhibit relatively small between-study differences in RPPs. Existing RPP values for both Moraceae and *Podocarpus* are either lower or higher than that of Poaceae, which corroborates earlier observations on the representation of these taxa in modern pollen samples compared to the plant abundance in the vegetation (e.g. Gosling *et al.* 2005; Maley *et al.* 1990; Vincens 1984; Wan *et al.* 2020).

The major uncertainties of our RPP study are due to the strong effect of non-stationary vegetation in the study region on the calculation of RPPs using the maximum likelihood approach. It implies that the RSAP of the pollen samples (here surface soil) is difficult to identify, and therefore the best RPP values are uncertain. Nevertheless, whatever RSAP we would choose (either a few hundred meters or 3 kilometres), ranking of the RPP values would remain the same and, therefore, the correction of the pollen percentages identical. However, the relative cover/abundance of taxa would probably be influenced. In regions where it might be difficult to find large enough areas of stationary vegetation to estimate RPP of forest taxa in particular, one might test the robustness of the obtained RPPs using other models and calculation approaches that might be less sensitive to non-stationary vegetation (Fang *et al.* 2020; Tabares *et al.* 2021). In future work, the use of combined satellite and drone data might help to decrease the amount of field work and increase the consistency of vegetation datasets over large areas around each pollen sample site. The latter would probably improve the performance of models for estimation of RPPs.

The LRA reconstructions in this study provide a first tentative quantification of changes in the Afromontane woodlands and wooded grasslands of Cameroon over the Holocene. The results suggest that the regional landscape in the mountain region was more open than pollen percentages suggest, and that the collapse of the high altitude forests around Bambili at 3 ka BP was faster and of larger magnitude than indicated by the pollen record. The latter will need to be confirmed by further studies involving a larger number of major taxa characteristic of the Holocene vegetation history of Cameroon. The reconstructions also suggest that the woodlands' taxa composition, at both regional and local scales, is different once the pollen percentages are corrected using the RPP dataset and RPPs 2.62 or 6.38 for *Podocarpus*. The LRA reconstruction for Mbalang confirms the local occurrence of mountain woodland around the lake in Mid-Holocene. The correction of the pollen percentages indicate a larger cover of *Prunus africana*/*Rubus pinnatus* and Moraceae than their pollen percentages. *Podocarpus* and Moraceae are the most problematic taxa to model with the RPPs currently available. The reconstructions using high RPPs for *Podocarpus* are the most probable so far. It is not possible, based on this study, to assess the reliability of the available RPPs for Moraceae.

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