Reply to Theuerkauf and Couwenberg (2020) comment on: "Pollen-based reconstruction of Holocene land-cover in mountain regions: evaluation of the Landscape Reconstruction Algorithm in the Vicdessos valley, Northern Pyrenees, France"

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Comments on Marquer et al. (2020) by Theuerkauf and Couwenberg (2020) revisit two issues important for pollen-based reconstruction of past vegetation with the Landscape Reconstruction Algorithm (LRA; Sugita 2007a, 2007b) and related models: the selection of pollen dispersal model and the appropriate use of pollen productivity estimates. We are aware of those issues, and our paper addresses those questions and advises for caution and necessary future steps to improve model-based reconstruction of vegetation in mountain environments and elsewhere. This reply restates briefly some of the important take-home messages from our study and presents our suggestion and proposal in response to Theuerkauf and Couwenberg's comments.

Two major modelling-schemes have been widely used since the 1950s to describe dispersal and deposition of pollen grains in the air: the Gaussian Plume models (GPMs) and the Lagrangian Stochastic models (LSMs). A modified version of GPMs (after Sutton, 1953) has been applied for the evaluation of pollen-vegetation relationships (e.g. Tauber, 1965; Gregory, 1973; Prentice, 1985, 1988; Sugita, 1993, 1994) and the estimation of relative pollen productivity (RPP). The GPM has also been implemented as a dispersal kernel in the REVEALS and LOVE models of the LRA (Sugita, 2007a, 2007b). Pros and cons of GPMs are discussed elsewhere (e.g. Pasquill and Smith, 1983; Prentice, 1985; Jackson and Lyford, 1999). Since the 1990s simulation approaches with LSMs have become available for a more advanced description of pollen and spore dispersal, considering realistic atmospheric airflows and wind fields (e.g. Wilson and Sawford, 1996; Aylor and Flesh, 2001).

Theuerkauf et al. (2013, 2015, 2016) and Mariani et al. (2016, 2017) have applied a LSM proposed by Kuparinen et al. (2007) for the evaluation of pollen-vegetation relationships, RPPs and REVEALS-based reconstructions of past vegetation in northern Germany and Tasmania, respectively. Theuerkauf et al. (2013) obtained RPPs for six tree taxa using an optimization method and Theuerkauf et al. (2015) for a set of open-land taxa based on the R-value model of Davis (1963). The LSM-based RPPs for some of these taxa differ from those previously obtained using the Extended R-value models with the GPM implemented for calculation of the distance-weighted plant abundance around study sites (Broström et al., 2008; Mazier et al., 2012). As expected, the selection of the dispersal model matters for both RPPs and LRA applications for vegetation reconstruction. Because of the limited number of LSM-based RPPs available in Europe and elsewhere, most of the LRA applications have so far used GPM-based RPPs (e.g. Mazier et al., 2012).

Theoretically, the choice of dispersal model needs to be consistent for both obtaining RPPs and in reconstructions of past vegetation using those RPPs. The simulation study in section 2 of Marquer et al. (2020) follows this general rule; the pollen assemblages simulated with the LSM are used for the REVEALS and LOVE applications that assume the LSM for pollen dispersal. Similarly, the pollen assemblages with the GPM are used for the LRA applications with the GPM implemented. This general rule is also clearly stated in our paper and discussed in section 5.2, including statements such as "*Ideally, when the LSM is used for the LRA, RPPs need to be obtained from other data sets by assuming the LSM as a pollen dispersal model for consistency.*". Results from a simple simulation exercise shown in Theuerkauf and Couwenberg (2020) are not surprising. We are puzzled by the concept of "true RPPs", however. The "true RPP" values differ from the estimates obtained in Theuerkauf et al. (2013, 2015, 2016). What are the "true RPPs"? Where do these values come from? In any case, further studies are necessary to evaluate the impacts on the LRA-based reconstruction of using different dispersal-models.

In practice, the number of plant taxa for which LSM-based RPPs are available is too limited to be used by Marquer et al. (2020). Additionally, the published LSM-based RPPs (Theuerkauf et al. 2013, 2015, 2016, 2020) are inconsistent. In Marquer et al. (2020), we therefore used the GPM-based RPPs from Mazier et al. (2012) that averages the RPP results from eight regions in Western Europe. The reasons behind the use of average values are given in Mazier et al. (2012). Using the GPM-based RPPs (Table 2 of Marquer et al. 2020), the GPM-based results of the REVEALS reconstruction in the Pyrenees tend to be closer to the surveyed land-cover data in the region than those using the LSM-based REVEALS model. For reconstructing the local-scale land-cover composition, the GPM-based and LSM-based LOVE results do not differ significantly from each other. Therefore, when a proper set of LSM-based RPPs becomes available, our current hypothesis is that the LSM-based LRA results should reveal closer to the surveyed vegetation data. This requires further studies from the pollen-based vegetation modelling community in the coming years.

The main research objective of Marquer et al. (2020) was to evaluate the extent to which the LRA-based estimates of the local vegetation within the relevant source area of pollen (RSAP) around small sites represent the observed vegetation composition above the tree line in the Pyrenees. The estimated RSAP is a ca. 2km radius-area at each site. In general, studies in mountain palynology select sites systematically at high altitudes (above the tree line) and thus violate the assumption of random selection of site locations in the region when only small-sized sites are available; the issue of site-selection is important for unbiased REVEALS-based reconstructions of the regional plant cover - a critical step for the LOVE-based estimates of the local vegetation composition. Wind fields in mountain ranges constitute another important factor that affects pollen transport in ways differing from that of flat landscapes. LSMs consider the complex nature of realistic airflows and wind fields in uneven terrains and surface roughness parameters affected by the canopy structure of the vegetation. We would therefore expect LSMs to be better suited for LRA applications in mountains. However, this is not the case of the Marquer et al. (2020) study. The current LSM implemented by Theuerkauf et al. (2013, 2015, 2016) assumes field conditions similar to those characteristic of Finnish pine forests (Kuparinen et al., 2007). Marquer et al. (2020) used computer programs for the LRA and POLLSCAPE that can select the LSM as a dispersal kernel (Sugita, unpublished). These programs use a lookup-table approach for the LSM calculation as in Theuerkauf et al. (2013, 2015, 2016); the LSM lookup-table implemented was provided by Theuerkauf and his colleagues. To extend the applicability of the LSM-based reconstruction of vegetation in different parts of Europe and elsewhere, other factors and conditions need to be considered in the LSM scheme, such as different types of vegetation canopies (e.g. broadleaved forests, parkland and meadows), different pollen-source heights (e.g. trees vs. herbs), and complex terrains (e.g. mountains vs. flat lands).

In conclusion, it is time for palynologists and palaeoecologists to develop new research initiatives and collaborations to produce new sets of RPPs based on LSMs, as suggested by Theuerkauf and Couwenberg (2020). Recent studies in China (Wan et al., 2020) are not conclusive about the extent to which the LSM-based RPPs improve over the GPM-based RPPs; this study used the Extended R-value (ERV) model (Prentice, 1988; Sugita, 1994) with the LSM and GPM options implemented (Sugita, unpublished) and a modern pollen-vegetation dataset collected in the region. Further comparative studies are also necessary in order to answer still open issues. For example, with the same GPM and LSM, are there systematic differences in outcomes between the ERV models and the optimization methods used in Theuerkauf et al. (2013, 2015) and Mariani et al. (2016))? What would be the spatial resolutions and scales (e.g. local/landscape vs. regional) most appropriate for obtaining the LSM- and GPM-based RPPs regardless of the analytical methods? Other approaches independent of dispersal-model selection would also provide additional information about RPPs of major taxa with direct and semi-direct measurements of the number of flowers, and thus pollen grains, produced per unit area (e.g. Wada et al., 2018).

In summary, we envisage some major objectives for new research initiatives, including: (1) compilation and reanalysis of the training datasets previously used for the GPM-based RPPs in many parts of the globe (e.g. the recent RPP synthesis for China, Li et al., 2018), (2) clarification and evaluation of the analytical tools and approaches that have been used and proposed for estimation of the RPPs, and (3) collaboration with atmospheric scientists to better understand the atmospheric dispersion of pollen and spores and to develop realistic and region-specific LSMs.

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