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Closing the gap between plant ecology and Quaternary palaeoecology

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Abstract

Ecology and Quaternary palaeoecology have largely developed as parallel disciplines. Although both pursue related questions, information exchange is often hampered by particularities of the palaeoecological data and a communicational gap has been perceived between the disciplines. Based on selected topics and developments mainly in Quaternary palaeoecology, we show that both disciplines have converged somewhat during recent years, while we still see untapped potential for closer interactions.

Macroecology is probably the discipline that most easily combines different time-scales and where co-operations between palaeoecologists, geneticists and vegetation modellers have been inspiring. Quantitative vegetation reconstructions provide robust estimates of tree composition and land cover at different spatial scales, suitable for testing hypotheses about long-term vegetation changes or as quantitative background data in studies on contemporary vegetation patterns. Palaeo-data also hold yet unexplored potential to study the drivers of long-term diversity and aspects of functional diversity may facilitate comparisons between continents and over glacial-interglacial cycles.

Introduction

As a subject, ecology is not associated with any defined timescale: it encompasses research spanning from the deep geological past to predictions of future developments (Rull 2010). Its practitioners, however, are separated into different disciplines (Jackson 2001), reflecting the different time scales: deep time – geological time scales of millions of years; Quaternary time – the most recent geological past and human history with time scales of decades to millennia; and real-time or ecological time extending from days to decades. Ecology and Quaternary palaeoecology (henceforth referred to as palaeoecology) emerged as parallel disciplines during the first two decades of the 20th century (West 1964). Often both disciplines were practised by the same researchers, as in the case of Franz Firbas (Beug

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1965), but over time the interactions between them have declined. This may partly be due to the fact that, in palaeoecology, higher plants cannot be studied directly and the remains indicating their past abundance are disproportionate to the abundance of their parent species. Taxonomic resolution, depositional effects and problems identifying the spatial scale represented by the remains further complicate the interpretation of palaeoecological results (Seppä & Bennett 2003; Rull 2010). As a consequence, palaeoecological data are not easily comprehended by ecologists and this creates a communicational gap between the disciplines. Palaeoecologists have addressed this perceived gap in several forum papers, advertising their field to ecologists and conservation biologists (e.g. Davis 1994; Froyd & Willis 2008; Rull 2010; Lindbladh et al. 2013).

The most useful palaeoecological data for plant ecologists are pollen data, as they represent changes in vegetation. Over the past decade, palaeoecologists have intensified studies of pollen vegetation relationships with the aim of correcting for inter-taxon differences in pollen production and dispersal. The resulting numerical models and user friendly software are now available to the larger scientific community (Gaillard et al. 2008). There are several databases holding pollen analytical and other palaeoecological data (Fyfe et al. 2009; Grimm et al. 2013) that have been utilized in continental scale analyses where palaeoecology matches the scale of macroecological studies. Palaeoecological publications also show an increased interest in changes in diversity and ecosystem function through time (Lacourse 2009; Fredh et al. 2013). The recent "top 50" palaeoecology priority question project (Seddon et al. 2014) showed that more than half of proposed questions were directed at ecological and conservation issues suggesting that the perceived disconnection between ecology and palaeoecology is disappearing. In the present paper, concentrating mainly on pollen analysis, we take a closer look at recent developments, exploring where ecology and palaeoecology have converged and propose areas for closer co-operation.

Continental scale analyses and macroecology

An individual pollen diagram from a large lake or bog represents an integration of past vegetation change over the entire region surrounding the site. A number of such diagrams spread out in space can describe subcontinental patterns in past vegetation change, such as shifts in biome boundaries (Williams et al. 2004). Much of the pollen data produced over recent decades are held in continental pollen databases that are maintained by the palaeoecological community and freely available to the public (Fyfe et al. 2009; Grimm et al. 2013). These databases provide an invaluable research tool for the analysis of continental-scale spatio-temporal vegetation patterns which often fall within the field of macroecology. An excellent example is the study of North American *Populus* covering the period from the Late Glacial to the present day, in which the results revealed that changes in the abundance of *Populus* were caused by the effects of climate change on its major competitors rather than the direct effects of climate on *Populus* itself (Peros et al. 2008).

A common use of palaeoecological data is in the reconstruction of past climate. Datasets of modern pollen collections are often analysed using ecological response models and ordinations to explore whether the climate parameter of interest determines the gradient in abundances of different pollen taxa (e.g. Seppä et al. 2004, Giesecke et al. 2008). Such

comparisons between taxa and climate parameters are conceptually similar to species distribution models (SDMs). While palaeo-studies use modern species climate relationships to reconstruct past climates, SDMs use species' responses to climate to predict species' distributions in the future under different climate scenarios (Dormann 2007). Climate simulations of the past in combination with the SDMs, have also been used to simulate species distributions in the Late Quaternary (e.g. Svenning et al. 2008). Although these provide interesting and thought-provoking academic exercises, without palaeoecological evidence the simulated past species distributions remain hypothetical, particularly because SDMs depend on climate simulations which generally fail to reproduce the spatial patterns in reconstructed climate variables (Brewer et al. 2007; Harrison et al. 2014). Comparing the SDM results with palaeo information on species distribution is, therefore, a test of the credibility of both species distribution models and climate simulations (Giesecke et al. 2007; Pearman et al. 2008; Harrison et al. 2014). These data model comparisons have, for example, highlighted the models' failure to reconstruct the early Holocene absence of some shade tolerant trees in parts of Europe (*Picea abies* and *Fagus sylvatica*). This shows that aspects of the species autecology and/or early Holocene climate are not sufficiently understood (Giesecke et al. 2007; Miller et al. 2008). Even in the 1950s, West (1964) expressed the wish that ecologists would tell palaeoecologists about "the factors which control the present distribution of species found in fossil". Fifty years later, that wish still stands and is echoed by vegetation modellers (e.g. Bykova et al. 2012). Although much has been learned about the ecophysiological reasons for the distribution limits of a number of plants, they are still largely unknown even for the dominant tree species. A welcome exception is the knowledge of the northern distribution of *Tilia*, where the low summer temperatures limit fertilization in northern England (Pigott & Huntley, 1980) and the short growing-season limits the maturation of seeds in more continental areas like Finland (Pigott 1981). This kind of knowledge would greatly benefit our understanding of past species distributions and climate variation and allow for more reliable future predictions.

Much of the debate on the impact of global warming on future plant distributions and diversity is connected to the question of how fast plants can track their climate envelope (Thuiller et al. 2005). Palaeoecology holds many insights to that question. At the same time, low plant abundances can often remain undetected using palaeoecological tools and the postglacial spread of species may, therefore, not be fully captured by pollen analyses alone. While macrofossil remains help to determine past species occurrences, spatial patterns of genetic markers in extant species provide a new understanding of these processes. The example of *Fagus* shows that its postglacial colonization of Europe was not a general westward spread from the Italian and Balkan refugia as assumed earlier (Comps et al. 2001), but commenced from multiple occurrences to both sides of the Alps without much contribution from the southern populations (Magri et al. 2006). The late expansion of *Picea* in southern Scandinavia also cannot be explained by migrational lags as was assumed earlier (Giesecke & Bennett 2004). Genetic information reveals ancestries across the southern Baltic (Tollefsrud et al. 2008) that could not be interpreted from pollen diagrams. Moreover, the detection of a *Picea* haplotype restricted to Scandinavia rejuvenated the discussion of an ice-age survival of spruce in Scandinavia (Parducci et al. 2012 vs. Birks et al. 2012). These new insights make it difficult to use apparent postglacial migration rates to parameterize the

models for future range shifts. Nevertheless, pollen and macrofossil records may still provide minimum rates (Feurdean et al. 2013) and more attention should be directed to the factors that limit or trigger population expansions (Giesecke et al. 2013).

Quantifying pollen analytical results in terms of vegetation change

A standard pollen diagram is only a semi-quantitative account of past vegetation change due to taxon-specific differences in pollen dispersal and deposition and the representation of results as percentages of identified terrestrial pollen. The combination of differences in pollen representation and the percentage calculation lead to non-linear correspondences between abundance changes of a particular taxon and its percentage representation, known as the Fagerlind effect (Prentice and Webb 1986). This problem can be circumvented when we can estimate the amount of pollen deposited per unit area and time (pollen accumulation rate: PAR). This representation of pollen analytical results has been increasingly used in recent years to analyse long-term changes in the population dynamics of trees (Seppä et al. 2009; Miller et al. 2009). The linear relationship between PARs and plant abundances (Matthias and Giesecke 2014) makes PARs especially useful for testing hypotheses about long-term effects of competition and facilitation that have rarely been studied in detail with the help of palaeoecological records (but see Jeffers et al. 2011).

It is not possible to obtain reliable PARs from all sediments that yield informative pollen percentage diagrams due to the complex sedimentation processes in lakes and wetlands (Davis et al. 1984). In such situations, the problems caused by differential pollen production and dispersal can be overcome by estimating the differences in pollen production and modelling pollen dispersal, taking account of the differences in pollen settling velocity (Prentice 1985; Sugita 1994). Using this principle, two vegetation reconstruction approaches have been developed and successfully verified. The Landscape Reconstruction Algorithm (LRA; Sugita 2007a,b) uses several pollen diagrams (from both large and small sites) to separate the regional and local pollen signal and to yield average plant abundances within areas around the lakes or bogs. The Multiple Scenario Approach (MSA; Bunting & Middleton 2009) tests the simulated pollen assemblages from plausible scenarios of past vegetation composition and knowledge of plant autecology against a single pollen diagram. We believe that both approaches hold great potential for providing robust estimates of tree composition and land cover in defined space, allowing for finer spatial grain in vegetation reconstructions and enabling more rigorous testing of the hypotheses about the importance of different drivers determining long-term vegetation dynamics. In this way, it is possible to evaluate the reaction times and extent of vegetation change in response to environmental change or human impact. For example, Caseldine & Fyfe (2006) used multiple scenarios to determine the magnitude of elm decline and forest clearance by early Neolithic farmers around 5500 years ago in a local (6 x 6 km) area in Ireland where almost 75% of the research area underwent a vegetation change during a 100-year period. Cui et al. (2013) used the LRA to evaluate long-term drivers of between-site differences in vegetation structure. They conclude that fire management and grazing are important factors increasing biodiversity in old pine woodlands in Sweden. The regional component of LRA has been successfully employed to differentiate between human and climate forcing in determining vegetation change during the last 5000 years across Estonia (Reitalu et al. 2013) and to

identify natural factors, such as soil characteristics or continentality, driving vegetation composition (Nielsen et al. 2012). These kinds of quantitative vegetation reconstructions can substitute or complement historical maps at local (Overballe-Petersen et al. 2013) and regional scales (Nielsen et al. 2012) and thus provide information on historical developments that have influenced the vegetation environment associations in the present-day landscape (Pärtel et al. 2007; Plue et al. 2008). We suggest that estimates of landscape openness and land-use from pollen-based vegetation reconstructions provide valuable quantitative background data to distinguish the importance of past processes and time-lags on present-day vegetation patterns – analyses that today are often limited by the availability of historical maps.

Diversity and ecosystem function

Palaeoecology permits an examination of the factors that influence changes in floristic diversity through time (e.g. Odgaard 1994; Birks & Birks 2008; Figueroa-Rangel et al. 2008; Giesecke et al. 2012). While ecology has developed a large number of measures for plant diversity, palaeoecology mainly uses a single diversity measure: palynological richness or the number of different pollen types encountered within a standardized pollen count (Birks & Line 1992). Recent efforts to explore which aspects of floristic diversity in the landscape are captured by palynological richness measures (Meltsov et al. 2011, 2013) show a strong positive relationship between palynological richness and the amount of unforested land in a forested landscape of Northern Europe. It is therefore no surprise that the gradual human-induced opening of northern European landscapes over the last 6000 years has increased palynological richness (Berglund et al. 2008, Giesecke et al. 2012). However, pollen diagrams also show that a rich herbaceous flora already occurred in ice-free areas of northern Europe during the Lateglacial and many of these species had to find “refugia” during the forest dominated phase of the Holocene (Bennett and Provan 2008).

While the above-described general trend of postglacial palynological diversity in northern Europe is visible in many carefully analysed pollen sequences spanning the full postglacial, detailed investigations focussing on past diversity changes are still rare. Among the exceptions are a test of the intermediate disturbance hypothesis by Odgaard (1994) and an investigation into detailed biological responses to rapid warming at the onset of the Holocene in western Norway (Birks and Birks 2008). Thus palaeoecology has so far little used its potential to yield insights into factors determining plant diversity.

During the past few decades, studies of contemporary plant diversity have concentrated on functional diversity, taking into account the functional and phenotypic differences between the species and providing better assessment of stochastic vs. deterministic processes in community assembly (e.g. Gerhold et al. 2013; Mason & de Bello 2013). In palaeoecological studies, plant functional types have been used to assign pollen samples to biomes and to characterize broad changes in vegetation in relation to climate over large spatial scales (Prentice et al. 1996; Fyfe et al. 2010). At the same time, combining palynological data with trait data from public databases like LEDA (Kleyer et al. 2008) and BioFlor (Kühn et al. 2004) allows for more detailed studies of the functional aspects of long-term vegetation change (Lacourse 2009). Community assembly in relation to climate

change during the Holocene and the last interglacial has been shown to be constrained by interspecific differences in traits. Low height, small seeds and ability to reproduce vegetatively were beneficial for survival close to the edge of the glacier, while low growth rate, large seeds and high shade tolerance were beneficial during the warmer, more stable climate periods (Bhagwat & Willis 2008; Lacourse 2009). Kuneš et al. (2011) used knowledge of species functional properties and ecological tolerances to show that the similarities in vegetation development during interglacial periods during the Quaternary can at least partly be explained by phosphorus availability. In each of the four studied Quaternary warm stages, arbuscular mycorrhizal species dominated in the beginning of the stage when P was readily available, whereas ectomycorrhizal species dominated close to the end of interglacial periods as P became depleted (Kuneš et al. 2011). The functional approach to late Quaternary palaeodiversity is promising as it allows more effective comparison between records from different regions and continents and even from different interglacial periods and helps to infer drivers behind vegetation change.

Conclusions

Quaternary palaeoecology has to certain degree converged with plant ecology. Macroecology represents the discipline that most easily combines different time-scales. Quantitative vegetation reconstructions provide robust estimates of vegetation composition and land-use that allow for testing hypotheses of vegetation change at different spatial and temporal scales and provide the historical background for studies of present-day vegetation patterns. Different measures of palaeo-diversity, especially the functional approach, have a great potential for exploring past changes in diversity and, together with quantitative vegetation reconstructions, enable studies exploring the roles of different drivers (e.g. land-use change, climate, soil development) on long-term vegetation dynamics and species interactions. Co-operations between palaeoecologists, geneticists and vegetation modellers have been inspiring; however, they are often limited to large cooperative efforts and networks and there is a danger that these co-operations cease once the projects are terminated. There is plenty of untapped potential for closer cooperation, including autecological studies of abundant species with a good palaeoecological record. We would like to encourage ecologists to make more use of the palaeoecological data readily available in large databases and/or to engage in joint projects. Designing new studies with practitioners from both communities may be another way forward. At the same time, palaeoecologists should make more use of ecological workshops and conferences such as IAVS symposia as a forum for communication.

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