

Ecological palaeoecology: a missing link between ecology and evolution

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Abstract

ECOLOGICAL PALAEOECOLOGY: A MISSING LINK BETWEEN ECOLOGY AND EVOLUTION.— Palaeoecology is more than a palaeoenvironmental discipline; it is a science that is well-suited for supplying the empirical evidence necessary to test ecological hypotheses and contributes to our understanding of the interface of ecology and evolution. A critical time frame in palaeoecology is the often-overlooked *Q-time* dimension (centuries to millennia), which tends to be the most appropriate time dimension to examine ecology-evolution interactions. This paper discusses these topics from a conceptual perspective and provides examples of the contributions of palaeoecology to the study of ecology-evolution interactions. It also admonishes researchers about the threats of overlooking palaeoecology. Specifically, this paper argues that the neglect of palaeoecology may result in the loss of empirical support for ecology and its interactions with evolution as DNA-based phylogenetic and phylogeographic studies become more and more prevalent. The main concepts discussed are the time continuum, the notion of ecological palaeoecology and the empirical nature of palaeoecology in the face of more hypothetical approaches. More practically speaking, several examples are provided that highlight the utility of ecological palaeoecology for understanding a variety of processes, including ecological succession, community-environment equilibria, community assembly, biotic responses to environmental change, speciation and extinction, and biodiversity conservation. The ecology-evolution interface is analysed using two processes in which these disciplines interact intensively: ecological succession and long-range migration. This work concludes that both ecological palaeoecology (including ancient DNA records) and DNA-based phylogenetics and phylogeography are needed to better understand the biosphere ecologically and the processes occurring at the ecology-evolution interface.

Key words: ecology-evolution interface; genomics; palaeoecology; phylogenetics; phylogeography; *Q-time*; Quaternary.

Resumen

PALEOECOLOGÍA ECOLÓGICA: UN ESLABÓN PERDIDO ENTRE ECOLOGÍA Y EVOLUCIÓN.— La paleoecología es más que una disciplina ambiental, ya que proporciona las evidencias empíricas necesarias para verificar hipótesis ecológicas y contribuye a una mejor comprensión de la interfase ecología-evolución. El ámbito temporal de la paleoecología es la dimensión denominada *Q-time* (siglos a milenios), que parece ser la más adecuada para examinar las interacciones ecología-evolución. Este artículo discute el problema desde una perspectiva conceptual y proporciona ejemplos de la contribución de la paleoecología al estudio de dichas interacciones, además de advertir de las posibles consecuencias de ignorar esta disciplina. En concreto, se propone que una infravaloración de la paleoecología podría llevar a la pérdida de soporte empírico para la ecología y sus interacciones con la evolución. Los principales conceptos discutidos son el continuum temporal, la noción de paleoecología ecológica y la naturaleza empírica de la paleoecología, frente a enfoques más hipotéticos como las filogenias moleculares. En un sentido más práctico, se muestran ejemplos que enfatizan la utilidad de la paleoecología ecológica para la comprensión de procesos como la sucesión ecológica, el equilibrio comunidad-ambiente, el ensamblaje de comunidades, las respuestas bióticas a los cambios ambientales, eventos de especiación y extinción, o la conservación de la biodiversidad. La interfase ecología-evolución se analiza mediante dos procesos en los que estas disciplinas interactúan intensamente: La sucesión ecológica y la migración a

gran escala. Se concluye que tanto la paleoecología ecológica (incluyendo los registros de ADN fósil) como la filogenia y filogeografía de ADN son necesarias para un mejor conocimiento ecológico de la biosfera y de los procesos que tienen lugar en la interfase ecología-evolución.

Palabras clave: Cuaternario; filogenia; filogeografía; genómica; interfase ecología-evolución; paleoecología; *Q-time*.

INTRODUCTION

An increasing number of ecologists are aware of the need to consider the past to properly understand the temporal nature of ecological patterns and processes. Deep time is the most common temporal dimension used. Deep time accounts for evolutionary phenomena that take place over millions of years, and the preferred empirical tool for studying events in deep time is DNA-based phylogenetics (Cavender-Bares *et al.*, 2009, 2012; Fritz *et al.*, 2013). Recently, some palaeoecologists have called for increased study of a commonly neglected temporal dimension—Q-time, which takes place from centuries to tens of millennia (Jackson, 2001)—for a more thorough understanding of ecology (Willis *et al.*, 2010; Mitchell, 2011; Rull, 2012a). Examples of ecological processes typically occurring at the Q-time scale are manifold: range expansion and contraction, migration, extinction, community assembly and disassembly, changes in community composition, ecological succession, human impact on ecosystems and climate-human synergies, and others. Evolution interacts with these ecological processes, and ecology, in turn, influences subsequent evolution. A detailed understanding of Q-time processes and their environmental drivers is required not only to study population and community dynamics but also to unravel the ecological conditions under which actual species evolve, that is, the ecological causes of evolution (MacColl, 2011). This makes the Q-time dimension well suited for linking ecological and evolutionary time frames.

For present-day ecological features, the Quaternary period makes the largest contribution to the Q-time dimension because it is during this period when extant ecosystems and their communities have been shaped. Because of the general lack of interest in palaeoecology by the ecological community, Birks *et al.*

(2010) considered the Quaternary as a “missing dimension” that is in sore need of study to understand multiple aspects of modern-day ecology, conservation and science in general. Some ecologists appear to be accepting this fact and have started to include the Quaternary in their research plans; however, molecular phylogenetics based on extant species and its geographical expression (phylogeography) is still a favourite empirical approach (Feder *et al.*, 2013; Het *et al.*, 2013; Marske *et al.*, 2013; Petren, 2013). Palaeoecology is often overlooked and ignored, a situation that has only become more severe in the last few decades due to the rapid growth and the increasing impact of genomic research. This attitude jeopardises palaeoecology as an active discipline of research, long before its utility will have been fully appreciated by ecologists and evolutionary biologists.

This paper demonstrates the utility of Q-time palaeoecology for general ecology and also discusses why and how this discipline is well suited to bridge the gap between ecology and evolution. The discussion is subdivided into three main parts: (1) conceptual insights, (2) selected palaeoecological contributions and (3) the ecology–evolution interface. The first section introduces some concepts (i.e. the time continuum, ecological palaeoecology and evidence vs. inference) that are considered fundamental for understanding the intrinsic nature of palaeoecological study and its suitability as an ecological discipline. The second part briefly discloses some relevant examples of the contribution of palaeoecology to unravel keystone ecological processes at the Q-time dimension, namely, succession and climax, community–environment equilibrium, biotic responses to environmental change, community assembly, speciation, extinction and biodiversity conservation. The third section focuses on processes, such as long-range migration and ecological succession, where both ecology and evolution interact.

CONCEPTUAL INSIGHTS

The time continuum

The “time continuum” (Rull, 2010) may be considered a basic concept in ecological palaeoecology, as it provides a straightforward link between past and present and between ecology and evolution. The concept is a logical consequence of the principle of uniformitarianism (Tomkeieff, 1962) and emphasises that past, present and future are not discrete units but are part of a continuum through which species and communities flow, interact, and evolve (Rull, 2010). There is no such thing as a biosphere of the past and a biosphere of the present; there is a single biosphere where evolution has occurred continuously since the origin of life on earth. Indeed, none of the mass extinctions documented so far has totally eradicated all of earth’s life. It has been estimated that the largest extinction occurred approximately 250 million years ago (the Permian event), which resulted in the extinction of approximately 96% of species (Barnosky *et al.*, 2011). However, the survivors and their evolutionary descendants were able to fully re-colonise the planet, thereby promoting the continuity of the biosphere (albeit in a different state than if the extinction had not occurred). It follows then that there is no ecology of the past (palaeoecology) and an ecology of the present (neoecology) but rather a single ecology (general ecology) that includes both. Historically, ecology and palaeoecology have been separated for primarily psychological and methodological reasons, not because there any differences between them per se (Birks & Birks, 1980; Rull, 2010).

The time continuum cannot be viewed as an idle linear process; on the contrary, the concept of a time continuum can be highly complex spatially and temporally. An example of such complexity may be found in the relationships between population dynamics, succession, evolution and biogeography. According to the Darwinian principles formulated by the Modern Synthesis, evolution takes place in a gradual fashion at the population level and evolutionary change is guided by natural selection, which affects individual gene mutations (Kutschera & Nikas, 2004). In contrast, proponents of the theory of punctuated equilibria contend that evolution occurs through the alternation of rapid species selection events, involving larger chromosome sections,

and stationary phases of genetic constancy known as stasis (Gould & Eldredge, 1977). Whatever the case, evolution occurs within a species context with populations as the main actors. On the other hand, ecological succession is a community-level process acting on a complex of species with different autoecological traits such as age of origin, evolutionary state and niche features. In addition to various autoecological traits, ecological succession is affected by regional-scale environmental features and internal biotic interactions. Therefore, the present biosphere, as a whole, may be viewed as a complex and temporary array of communities at different successional stages (Margalef, 1986), composed of populations of species at diverse ages of origin and evolutionary states, continuously interacting among themselves and with a constantly changing environment. Therefore, the time continuum concept involves diverse subjects such as populations, species and communities, different time scales such as the short-term, the Q-time and the deep-time, as well as their corresponding interactions and overlap (Jackson, 2001). Spatial heterogeneity, climatic variability and continental drift continuously change geography and the atmosphere in a way that adds further complexity. In such a complex space-time framework, any past or present short-term ecological study merely represents a snapshot influenced heavily by transient observer’s particularities.

Ecological palaeoecology

There are several reasons for ecologist’s lack of interest in palaeoecology. Foremost among them is the bias of palaeoecologists towards past climatic and environmental reconstructions. This view may be correct in many cases. However, a number of palaeoecologists that focus on the study of ecology argue that neoecology and palaeoecology, despite their methodological differences, have a common objective that is the ecological understanding of the biosphere (Rull, 2010). This has led to the emergence of so-called “ecological palaeoecology” in which, rather than merely unravelling past climatic and environmental trends, the main aims are to reconstruct ecosystem dynamics, to understand their environmental drivers and underlying mechanisms, and to provide empirical data for testing ecological hypotheses (Birks, 2013; Rull *et al.*, 2013). Under this view, palaeoecology is considered an ecological subdiscipline and defined

as “the ecology of the past” (Birks and Birks 1980) or “the branch of ecology that studies (the) past (of) ecological systems and their trends in time using fossils and other proxies” (Rull, 2010). A number of recent reviews discuss the potential significance of ecological palaeoecology not only for general ecology but also for conservation biology (Birks, 1993, 2008, 2013; Huntley, 1996; Jackson, 2001; Willis *et al.*, 2007, 2010; Vegas-Vilarrúbia *et al.*, 2011; Rull, 2010, 2012a). A common conclusion of these papers is that, without palaeoecological evidence, it is virtually impossible to acquire a full understanding of the origin and development of extant ecosystems, as neither evolution nor neoecology can provide the necessary empirical basis. Unfortunately, neoecologists do not take advantage of sources of palaeoecological evidence because model-data integration in neoecology and palaeoecology is still in its infancy, despite the abundance of data already available and well organised in global and regional data bases (Mitchell, 2011; Peng *et al.*, 2011).

Evidence and inference

The empirical nature of palaeoecological study needs to be highlighted, as physical evidence is the primary source of scientific knowledge. Neoecology often addresses Q-time processes using inductive inference, extrapolations from short-term observations, and modelling. Palaeoecology, on the other hand, is able to provide the necessary empirical evidence to test existing hypotheses, generate new hypotheses, calibrate and validate models, and improve model assumptions (Rull, 2012b). Regarding DNA molecular phylogenies based on extant species, it should be noted that they are largely dependent on sampling completeness, age calibration and methodological features related to the building of cladograms and phylogenetic trees (Rutschmann, 2006; Ricklefs, 2007; Wheat & Walberg, 2013). As a consequence, the resulting phylogenies are in constant adjustment and cannot be regarded as primary evidence but, rather, as transient hypothetical models to be tested with future observations. Treating these hypotheses as if they were empirical observations, a practice that is not infrequent, may lead to confusion and should be avoided (Parenti & Ebach, 2013).

The message is by no means that molecular phylogenetics is useless to address ecological problems

involving the Q-time dimension but that the results of these studies should be contrasted with the existing empirical evidence (Cruzan & Templeton, 2000). The establishment of stable interdisciplinary synergies appears to be the best option. This way, the unavailability of required palaeoecological evidence would be viewed as an opportunity for developing collaborative projects, rather than a reason to neglect palaeoecology. Molecular phylogenetics can rectify inaccuracies stemming from the incompleteness and fragmentary nature of the palaeoecological record in both time and space, whereas palaeoecology may provide sound and constraining evidence for aspects such as chronology, community composition and dynamics, and environmental drivers of ecological change, among others.

DNA could also be a part of palaeoecological evidence. Indeed, the recovery of ancient DNA preserved in Quaternary sediments, either included within biological structures or in a free state, is beginning to be used in palaeoecology, and initial results are encouraging (Pääbo *et al.*, 2004; Anderson-Carpenter *et al.*, 2011; Hofreiter *et al.*, 2012).

SELECTED PALAEOECOLOGICAL CONTRIBUTIONS

Palaeoecological studies have been especially useful for advancing ecological knowledge. However, this fact has been rarely acknowledged in the general ecological literature, and the message has not spread widely within the ecological community. As a result, most ecologists are unaware or forget that some well-accepted ecological concepts and insights emerged from, or with the contribution of, palaeoecology. The following are some remarkable examples—see Rull (2012b) for a more thorough review.

Succession and climax

The earlier view of the so-called spatial chronosequences as representatives of successional stages and their space-for-time substitution to recreate ecological succession has been determined to be unlikely given palaeoecological records. Indeed, successional trends reconstructed from sedimentary evidence usually failed to reproduce the formerly assumed stages derived from the observation of present spatial patterns

(Johnson & Miyanishi, 2008). Another old paradigm deeply questioned by palaeoecology is the deterministic concept of communities as “superorganisms” with predictable successional trends and stages ending with an eventual “climax”, in which the final community is in perfect equilibrium with its climate (Clements, 1916). Indeed, such equilibrium states have not been observed in palaeoecological records, where continual change is the norm. Past records have shown that succession is largely stochastic and contingent and hence an unpredictable process under the influence of changing environmental drivers and human activities.

Community–environment equilibrium

Palaeoecology has documented how communities are permanently responding to external environmental pressures according to their own biotic features and the nature and intensity of external drivers (Delcourt & Delcourt, 1991). The dismissal of the “climax” concept resulted in a reconsideration of community–environment relationships. For example, it was proposed that high community diversity may be maintained by continuously changing environmental conditions, which minimises extinction and hinders one or few species from becoming dominant (Hutchinson, 1961). This proposal was known as the “continuous disequilibrium” hypothesis and was further confirmed by palaeoecological observations, in combination with the “dynamic equilibrium” hypothesis, in which periods of relatively constant environmental conditions and community composition are also observed (Delcourt & Delcourt, 1983).

Biotic responses to environmental change

Another contribution of ecological palaeoecology to general ecology is the corroboration that individual species, rather than their communities, are the units of response to environmental shifts, which leads to changes in community composition over time. The hypothesis of species-specific (individualistic) responses was also suggested by earlier ecologists working on vegetation dynamics (Gleason, 1926) and who were opposed to the “superorganism” concept. A couple of decades after its proposition, the individualistic hypothesis was considered a more general feature leading to the spatial continuum concept,

according to which communities are ephemeral species assemblages arranged in loose and continuous spatial patterns (Whittaker, 1951). However, sound and consistent empirical support for the individualistic view did not arrive until the late 1900s with the first palaeoecological reconstructions of postglacial colonisation of Europe and North America by vegetation after the Last Glacial Maximum (LGM, which occurred *ca.* 21,000 years ago) (Davis, 1981; Huntley & Birks, 1983). This allowed the spatial continuum concept to be extended to time and was further supported by similar studies on a variety of organisms, thus becoming a more general ecological rule (Delcourt & Delcourt, 1991). As a result, communities are now viewed as transient species assemblages, whose composition varies over time depending on the multitude of interactions between the particular autoecological features of each individual species, and the nature and magnitude of environmental changes at several spatial and temporal scales.

Community assembly

Palaeoecological records and molecular phylogenetic analyses have shown that a community may be considered a complex assemblage of species of diverse evolutionary ages and places of origin, whose entry into the community occurred at different times under the action of different environmental drivers (Rull, 2012a). This framework is rarely considered in current ecological models of community assembly, especially in those that use neutral models as premises. Neutral models assume that species within a community are functionally equivalent and their particular niche features are not relevant for community assembly (Hubbell, 2001). As mentioned above, Quaternary records of community change have shown that niche features at the species level have been essential for determining community assembly and disassembly over time under the action of environmental agents (Davis, 1981), which supports the efficacy of idiosyncratic approaches to the study of community assembly (Chase & Leibold, 2003).

Speciation and extinction

Diversification is a balance between speciation and extinction, two processes that are greatly influenced

by environmental change (Erwin, 2009). During the Quaternary, both speciation and extinction have been active and have contributed to shaping extant biodiversity patterns. The relevance of Quaternary speciation has been often underrated in comparison with major evolutionary changes that have occurred at the deep-time scale. However, a significant number of extant species are of Quaternary origin and their emergence seems to have been favoured by climatic changes, especially the Pleistocene glacial–interglacial cycles (Rull, 2008, 2011*a*, *b*). So far, molecular phylogenetics has been more effective than palaeoecology in documenting and dating speciation events, but extinction records still rely mostly on palaeoecological evidence (Quental & Marshall, 2010; Slater *et al.*, 2012). For example, the relatively recent (*ca.* 50,000 to 10,000 years ago) extinction of large vertebrates across the world (Koch & Barnosky, 2006) has significantly affected biogeographical patterns and ecological processes at a global level. In contrast, only a single worldwide Quaternary extinction has been documented so far among plants (Jackson & Weng, 1999). In this case, rather than favouring extinction, Quaternary climatic changes have resulted mostly in spatial reorganisations and changes in community composition (Willis & Bhagwat, 2009). At a more local and regional scale, plant extinctions have occurred at higher rates, but they have not been as relevant as in the case of animals (Postigo-Mijarra *et al.*, 2010).

Biodiversity conservation

The reinforcement of the individualistic species' response model can be important for addressing potential biotic responses to ongoing and future global change. Indeed, it has been predicted that, by the end of this century, the occurrence of novel climates may result in the assembly of novel and unexpected communities with no modern analogues, which complicates the development of efficient conservation programs (Williams & Jackson, 2007; Williams *et al.*, 2007). Palaeoecology is able, and eager, to provide empirical evidence on past environmental changes and their corresponding biotic responses to help guide future conservation practices. For example, a consequence of the individualistic response model might be that emphasis should be placed on conservation at the species, rather than the community, level (Vegas-Vilarrúbia *et al.*, 2011).

Additionally, the asymmetry in the number of plant and animal extinctions during the Quaternary, especially the almost absent plant extinction events at a global level, has been considered a call for caution in reference to current extinction projections as a response to future climate change, including the widespread belief of the so-called sixth extinction (Willis & Bhagwat, 2009).

BRIDGING THE GAP

In practice, but not conceptually, speciation might be viewed as a frontier between ecology and evolution. Indeed, ecologists are usually familiar with actual species and their populations and often with micro-evolutionary phenomena occurring below the species level. On the other hand, evolutionists deal primarily with macroevolutionary processes occurring above the species level. However, the real boundary between ecology and evolution is not as sharp as this pragmatic discrepancy would suggest because ecological and evolutionary phenomena interact in ways that often make their study inseparable. Ecology addresses physical and biotic factors, as well as environmental drivers, while evolutionary biology addresses topics such as genetic variability, reproductive isolation and natural selection. To properly understand the biological dynamics of this diffuse ecology–evolution interaction, both palaeoecology and molecular phylogenetics, preferably at a population level, are needed (Rull, 2012*a*; Marske *et al.*, 2013). Long-term processes are the best source for studying the ecology–evolution interface because ecological and evolutionary mechanisms are more likely to interact the longer the study period. Examples of long-term ecological processes are succession and long-range migration, which, in turn, may facilitate a variety of evolutionary phenomena, including allopatric speciation and adaptive radiation (He *et al.*, 2013; Petren *et al.*, 2013). A significant amount of phylogenetic and phylogeographic studies on these subjects are already available, but many of them lack the appropriate ecological context due to the absence of corresponding palaeoecological data (Parenti & Ebach, 2013).

Long-range migration

An example of fruitful synergies between palaeoecology and phylogeography at the Q-time dimension is

the postglacial re-colonisation of Europe by present-day biota, a process that has been more or less accurately described for a variety of plant and animal species, notably dominant forest trees (Hewitt, 1999). First, palaeoecological records identified the southern refugia to which the studied species were confined during the LGM, when northern ice sheets reached central Europe and most of the continent was covered by cold and dry steppes (Huntley & Birks, 1983). These studies also reconstructed migration pathways between the LGM and the present by analysing several characteristic time slices and comparing them with present-day geographical patterns. Some important ecological caveats derived from these observations were that (1) migration patterns differed among species and populations depending on their place of origin, response lags, topography and microclimatic features, (2) the composition of temperate and boreal forests has not been constant through time, and (3) the estimated migration rates for each species notably exceeded present-day observations. Similar studies and conclusions are available for North America during the same time period (Davis, 1981). The evolutionary consequences of these palaeoecological trends were derived from DNA phylogeography, which showed that LGM refugial populations differed genetically depending on their geographic location and that further expansions of these populations were derived from the formation of hybrid populations at zones of secondary contact. Also noteworthy was the realisation that genetic diversity declined from south to north (Hewitt, 1999). This general pattern was disrupted by the occurrence of small spots of higher genetic diversity in the north that were interpreted as additional LGM refugia called “cryptic refugia” or “microrefugia”, a term that had been previously introduced after palaeoecological observations (Rull, 2009). These microevolutionary trends, occurring during the last glacial cycle, could be viewed as incipient speciation processes that might have proceeded to completion if the Quaternary glacial–interglacial cycles were to continue (Hewitt, 2000).

Succession

Ecological succession has also been considered a key process for analysing the ecology–evolution interface. Indeed, succession is in progress everywhere and is not only a critical process in community structuring but is also the ecological context where evolution

takes place (Hutchinson, 1965; Margalef, 1997). To my knowledge, no studies similar to those described above for long-range migration exist for successional processes thus far. Therefore, proposals in this context still remain as hypotheses that originated from theoretical ecology and should be tested with relevant empirical data. Some of these hypotheses were erected from a deterministic concept of succession based on short-term observations, which dominated the ecological thinking for a long time (Margalef, 1968; Odum, 1969). It is expected that the current view of ecological succession as a contingent and unpredictable process, to which palaeoecology has greatly contributed, may lead to different expectations. For example, under the classical expectation, significant evolutionary change is not expected to occur within the framework of one single successional process, which occurs at a time scale of centuries, at most. However, under the dynamic equilibrium (or continuous disequilibrium) framework, succession is expected to extend over millennia without reaching a climactic stable state. In addition, a given species or some of its populations may be part of different successional processes in both space and time, which may result in progressive genetic differentiation, eventually leading to speciation. This is expected to occur, for example, in the context of a metacommunity (space) or in a species that is migrating or expanding its range (time). In both cases, different communities that experience different successional states are being studied. Again, palaeoecological records provide the ecological context and the relevant environmental drivers, whereas DNA molecular phylogenetics and phylogeography supply the genetic details at a taxonomic resolution inaccessible to palaeoecological records. The discovery of palaeogenetic evidence—that is, ancient DNA preserved in sedimentary records—would be an additional input providing both the ecological context and the genetic resolution necessary for evolutionary inference.

CONCLUSIONS AND FUTURE PROSPECTS

Ecological palaeoecology is a discipline well suited for unravelling ecological and evolutionary processes occurring in the Q-time dimension using empirical evidence, rather than inductive inference and modelling based on short-term ecological surveys.

When dealing with extant communities and ecosystems, the more appropriate Q-time framework for ecological palaeoecology is the Quaternary, whose study has already provided abundant sources of evidence for testing general ecological hypotheses and made major contributions to the study of ecology. A key concept in ecological palaeoecology is the time continuum, which provides the link between ecology and evolution, as well as the link between different time scales and their corresponding patterns and processes. In addition, the time continuum framework allows ecology to be understood more generally by embracing both neoecology and palaeoecology. Genomics and DNA molecular phylogenetics may well contribute to ecological knowledge at the Q-time scale, but this discipline still relies on a number of methodological assumptions that make it more similar to a modelling discipline than to an empirical one. Interdisciplinary synergies between palaeoecology and molecular phylogenetics may help circumvent some of the weaknesses of both disciplines and may be the best approach for addressing deficiencies in our understanding of the role of the Q-time dimension in the ecology–evolution interface. In this sense, long-range migration and ecological succession are proposed as suitable target processes for studying phenomena occurring at the ecology–evolution interface. For these synergies to be established, palaeoecology needs to be accepted by the ecological and evolutionary communities and viewed as a necessary discipline, as palaeoecology has long been undervalued while the study of molecular phylogenetics has grown rapidly over the last few decades. Continued neglect of palaeoecological research could result in a major loss of empirical data that would have been an invaluable source of information to ecologists. Going forward, neoecology, palaeoecology and molecular phylogenetics need to be studied together for the sake of ecology and evolution, as well as the study of their interactions.

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REFERENCES

- Anderson-Carpenter, L., McLachlan, J. S., Jackson, S. T., Kuch, M., Lumibao, C. Y. & Poinar, H. N. 2011. Ancient DNA from lake sediments: Bridging the gap between paleoecology and genetics. *BMC Evolutionary Biology* 11: 30. <http://dx.doi.org/10.1186/1471-2148-11-30>
- Barnosky, A. D., Matzke, N., Tomiya, S. *et al.* 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51–57.
- Birks, H. J. B. 1993. Quaternary paleoecology and vegetation science—current contributions and possible future developments. *Review of Palaeobotany and Palynology* 79: 153–177.
- Birks, H. J. B. 2008. Paleoecology. In: Jorgensen, S. E. & Fath, B. (Eds.), *Encyclopedia of Ecology*. Elsevier, Amsterdam: 2623–2634.
- Birks, H. J. B. 2013. Ecological palaeoecology and conservation biology: controversies, challenges, and compromises. *International Journal of Biodiversity Science, Ecosystem Services & Management* 8: 292–304.
- Birks, H. J. B. & Birks, H. H. 1980. *Quaternary palaeoecology*. E. Arnold, London.
- Birks, H. J. B., Heiri, O., Seppä, H. & Bjune, A. 2010. Strengths and weaknesses of quantitative climate reconstructions based on Late-Quaternary biological proxies. *The Open Ecology Journal* 3: 68–110.
- Cavender-Bares, J., Ackerly, D. D. & Kozak, K. H. 2012. Integrating ecology and phylogenetics: the footprint of history in modern-day communities. *Ecology* 93: S1–S3.
- Cavender-Bares, J., Kozach, K. H., Fine, P. V. A. & Kembel, S. W. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693–715.
- Chase, J. M. & Leibold, M. A. 2003. *Ecological niches, linking classical and contemporary approaches*. University of Chicago Press, Chicago.
- Clements, F. E. 1916. *Plant succession, an analysis of the development of vegetation*. Carnegie Institute, Washington.
- Cruzan, M. B. & Templeton, A. R. 2000. Paleoecology and coalescence: phylogeographic analysis of hypotheses from the fossil record. *Trends in Ecology & Evolution* 15: 491–496.
- Davis, M. B. 1981. Quaternary history and the stability of forest communities. In: West, D. C., Shugart, H. H. & Botkin D. B. (Eds.), *Forest Succession: concepts and applications*. Springer, New York: 132–153.
- Delcourt, H. R. & Delcourt, P. A. 1991. *Quaternary ecology: a paleoecological perspective*. Chapman and Hall, London.
- Delcourt, P. A. & Delcourt, H. R. 1983. Late-Quaternary vegetational dynamics and community stability reconsidered. *Quaternary Research* 19: 265–271.
- Erwin, D. H. 2009. Climate as a driver of evolutionary change. *Current Biology* 19: R575–R583.
- Ferder, J. L., Flaxman, S. M., Egan, S. P., Comeault, A. A. & Nosil, P. 2013. Geographic mode of speciation and genomic divergence. *Annual Review of Ecology, Evolution, and Systematics* 44: 73–97.
- Fritz, S. A., Schnitzler, J., Eronen, J. T., Hof, C., Böning-Gaese, K., Graham, C. H. 2013. Diversity in space and time: wanted dead and alive. *Trends in Ecology & Evolution* 28: 509–516.
- Gleason, H. A. 1926. The individualistic concept of plant association. *Bulletin of the Torrey Botanical Club* 53: 7–26.
- Gould, S. J. & Eldredge, N. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* 3: 115–151.

- He, Q., Edwards, D. L. & Knowles, L. L. 2013. Integrative testing of how environments from the past to the present shape genetic structure across landscapes. *Evolution* 67: 3386–3402.
- Hewitt, G. M. 1999. Post-glacial colonization of European biota. *Biological Journal of the Linnean Society* 68: 87–112.
- Hewitt, G. M. 2000. The genetic legacy of Quaternary ice ages. *Nature* 405: 907–913.
- Hofreiter, M., Collins, M. & Stewart, J. R. 2012. Ancient biomolecules in Quaternary palaeoecology. *Quaternary Science Reviews* 33: 1–13.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.
- Huntley, B. 1996. Quaternary palaeoecology and ecology. *Quaternary Science Reviews* 15: 591–606.
- Huntley, B. & Birks, H. J. B. 1983. *An Atlas of Past and Present Pollen Maps for Europe: 0–13,000 years Ago*. Cambridge University Press, Cambridge.
- Hutchinson, G. E. 1961. The paradox of the plankton. *The American Naturalist* 95: 137–145.
- Hutchinson, G. E. 1965. *The ecological theater and the evolutionary play*. Yale University Press, New Haven.
- Jackson, S. T. 2001. Integrating ecological dynamics across timescales, realtime, Q-time and deep time. *Palaios* 16: 1–2.
- Jackson, S. T. & Weng, C. 1999. Late Quaternary extinction of a tree species in eastern North America. *Proceedings of the National Academy of Sciences of the United States of America* 96: 13847–13852.
- Johnson, E. A. & Miyanishi, K. 2008. Testing the assumptions of chronosequences in succession. *Ecology Letters* 11: 419–431.
- Koch, P. L. & Barnosky, A. D. 2006. Late Quaternary extinctions: state of the debate. *Annual Review of Ecology, Evolution, and Systematics* 37: 215–250.
- Kutschera, U. & Niklas, K. J. 2004. The modern theory of biological evolution: an expanded synthesis. *Naturwissenschaften* 91: 255–276.
- MacColl, A. D. C. 2011. The ecological causes of evolution. *Trends in Ecology & Evolution* 26: 514–522.
- Margalef, R. 1968. *Perspectives in ecological theory*. University of Chicago Press, Chicago.
- Margalef, R. 1986. Sucesión y evolución: su proyección biogeográfica. *Paleontologia i Evolució* 20:7–26.
- Margalef, R. 1997. *Our biosphere*. Ecology Institute, Oldendorf/Luhe.
- Marske, K. A., Rahbeck, C. & Nogués-Bravo, D. 2013. Phylogeography: spanning the ecological-evolutionary gap. *Ecography* 36: 1169–1181.
- Mitchell, F. J. B. 2011. Exploring vegetation in the fourth dimension. *Trends in Ecology & Evolution* 26: 45–52.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* 164: 262–270.
- Pääbo, S., Poinar, H., Serre, D. *et al.* 2004. Genetic analyses from ancient DNA. *Annual Review of Genetics* 38: 645–679.
- Parenti, L. R. & Ebach, M. C. 2013. Evidence and hypothesis in biogeography. *Journal of Biogeography* 40: 813–820.
- Peng, C., Guiot, J., Wu, H., Jiang, H. & Luo, Y. 2011. Integrating model data in ecology and palaeoecology: advances towards a model-data fusion approach. *Ecology Letters* 14: 522–536.
- Petren, K. 2013. The evolution of landscape genetics. *Evolution* 67: 3383–3385.
- Postigo-Mijarra, J. M., Morla, C., Barrón, E., Morales-Molino, C. & García, S. 2010. Patterns of extinction and persistence of Arctotertiary flora in Iberia during the Quaternary. *Review of Palaeobotany and Palynology* 162: 416–426.
- Ricklefs, R. E. 2007. Estimating diversification rates from phylogenetic information. *Trends in Ecology & Evolution* 22: 601–610.
- Quental, T. B. & Marshall, C. R. 2010. Diversity dynamics, molecular phylogenies need the fossil record. *Trends in Ecology & Evolution* 25: 434–441.
- Rull, V. 2008. Speciation timing and neotropical biodiversity: the Tertiary-Quaternary debate in the light of molecular phylogenetic evidence. *Molecular Ecology* 17: 2722–2729.
- Rull, V. 2009. Microrefugia. *Journal of Biogeography* 36: 481–484.
- Rull, V. 2010. Ecology and palaeoecology: two approaches, one objective. *The Open Ecology Journal* 3: 1–5.
- Rull, V. 2011a. Origins of biodiversity. *Science* 331: 398–299.
- Rull, V. 2011b. Neotropical biodiversity: timing and potential drivers. *Trends in Ecology & Evolution* 26: 508–513.
- Rull, V. 2012a. Community ecology: diversity and dynamics over time. *Community Ecology* 13: 102–116.
- Rull, V. 2012b. Past natural history and ecological biodiversity modeling. *Systematics and Biodiversity* 10: 261–265.
- Rull, V., Montoya, E., Nogué, S., Vegas-Vilarrúbia, T. & Safont, E. 2013. Long-term records of vegetation dynamics as a basis for ecological hypothesis testing in the neotropical Gran Sabana region. *Perspectives in Plant Ecology, Evolution and Systematics* 15: 338–359.
- Rutschmann, F. 2006. Molecular dating of phylogenetic trees: a brief review of current methods that estimate divergence times. *Diversity and Distributions* 12: 35–48.
- Slater, G. J., Harmon, L. J. & Alfaro, M. E. 2012. Integrating fossils with molecular phylogenies improves inference of trait evolution. *Evolution* 12: 3931–3944.
- Tomkeieff, S. I. 1962. Unconformity—an historical study. *Proceedings of the Geologists' Association* 73: 383–417.
- Vegas-Vilarrúbia, T., Rull, V., Montoya, E. & Safont, E. 2011. Quaternary palaeoecology and nature conservation with an emphasis on global warming and fire, with examples from the Neotropics. *Quaternary Science Reviews* 30: 2361–2388.
- Wheat, C. W. & Wahlberg, N. 2013. Critiquing blind dating: the dangers of over-confident date estimates in comparative genomics. *Trends in Ecology & Evolution* 28: 636–642.
- Whittaker, R. H. 1951. A criticism of the plant association and climatic climax concepts. *Northwest Science* 25: 17–31.
- Williams, J. W. & Jackson, S. T. 2007. Novel climates, no-analogue communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5: 475–482.
- Williams, J. W., Jackson, S. T. & Kutzbach, J. E. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America* 104: 5738–5742.
- Willis, K. J., Araújo, M. B., Bennett, K. D., Figueroa-Rangel, B., Froyd, C. A., Myers, N. 2007. How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362: 175–186.
- Willis, K. J., Bailey, R. M., Bhagwat, S. & Birks, H. J. B. 2010. Biodiversity baselines, thresh-olds and resilience: testing predictions and assumptions using palaeoecological data. *Trends in Ecology & Evolution* 25: 583–591.
- Willis, K. J. & Bhagwat, S. 2009. Biodiversity and climate change. *Science* 326: 806–807.