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# Ecology and Palaeoecology: Two Approaches, One Objective

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**Abstract:** Despite what their names might suggest, ecology and palaeoecology have progressed historically as well separated disciplines. This unfortunate disjunction is analyzed here from a theoretical point of view. Among the factors that have facilitated the separation are: 1) the past-present dissociation characteristic of the human mind, 2) the diversity of fields of provenance of palaeoecologists, 3) the contrasting nature of the evidence and associated methodological differences, and 4) misunderstandings caused by the use of prefix *palaeo-*. The principle of uniformitarianism emphasizes that past, present and future are not discrete units but a time continuum through which species and communities flow, change and evolve; and that ecology and palaeoecology are only different approaches with a common objective, which is the ecological understanding of the biosphere. Therefore, a terminological clarification is needed. Ecology in a broad sense, includes inferences about the past (palaeoecology), present studies (neoecology or contemporary ecology) and future projections (predictive ecology). Palaeoecology is thus a means by which ecology studies the past using proxies. Other disciplines beginning with the prefix *palaeo-* (notably palaeoclimatology and palaeoenvironmental reconstruction) are not necessarily ecological. It is recommended that ecologists and palaeoecologists develop joint projects, and that palaeoecologists increase their participation in ecological journals, books and meetings. These collaborations will demonstrate that a palaeoecologist is not simply a palaeoscientist whose data may be of interest for ecology but is primarily an ecologist working on another time scale, with different methods.

**Keywords:** Palaeoecology, neoecology, long-term ecology, evolution, succession, uniformitarianism, ecological theory.

## INTRODUCTION

It is commonly stated that the present condition of the biosphere is the result of the combined action of ecological and historical factors, and that the relative importance of each of these agents in shaping present-day world can be evaluated (Qian *et al*. 2007, Emerson & Gillespie 2008, Alvarez *et al*. 2009). However, the distinction between history and ecology is not always clear, and may create confusion. Ecology refers, in this context, to present-day ecological factors that reflect the extant species' niches, whereas history accounts for longer term processes linked to ecological succession, range shifts and evolution. A relevant question is where the boundary between concepts has to be placed or, in other words, where past (history) ends and the present (ecology) begins. The ecological time frame might be defined as the time interval in which the extant species live under the same ecological conditions we know today. This has been called ecological time or real time, and has been defined as ranging from weeks to decades or, occasionally, centuries (Jackson 2001). It has been recognized that such time frame is often insufficient to fully resolve the ecological dynamics associated with succession, stability, biotic responses, biodiveristy patterns, and so forth, underscoring the need for a historical or longer term view (Gorham *et al*. 2001, Jackson & Erwin 2006). Palaeoecology, defined as "the ecology of the past" (Birks & Birks, 1980), is the discipline charged to provide this longer temporal scope. In spite of this, ecology and palaeoecology have been traditionally kept as separate fields, and palaeoecological results have traditionally had little impact on ecological thinking (McGlone 1996).

This paper presents a conceptual approach to the subject, aimed to show that palaeoecology is part of ecological study and thus that ecology already includes history. The nature of palaeoecological study and its differences from the ecological approach are analyzed, in order to find possible causes for the ecology-palaeoecology segregation. The paper is addressed primarily to ecologists and palaeoecology beginners. It is not an attempt to explain the contribution of palaeoecology to ecological study, a matter that has been satisfactorily addressed elsewhere (West 1964, Rull 1990, Delcourt & Delcourt 1991, Schoonmaker & Foster 1991, Davis 1994, Huntley 1996, Gorham *et al*. 2001, Bush 2003, Seppä & Bennett 2003, Jackson & Erwin 2006, Williams & Jackson 2007, Willis *et al*. 2007, Froyd & Willis 2008, MacDonald *et al*. 2008) but an attempt to convince modern ecologists that both palaeoecology and ecology, despite methodological differences, aim for a better understanding of the biosphere patterns and processes (Rull 1990), and there is an urgent need for collaboration to attain this objective.

## PAST, PRESENT, AND PSYCHOLOGICAL SYNDROMES

According to Hanski (2008), humans are only able to perceive a short length of time due to our limited sensual and

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cognitive capacities as a result of biological evolution. A manifestation of this is our logarithmic perception of time that make past phenomena appear relatively closer the more distant in time they are, until the point that all of them are grouped into a single category called "the past". Intuitively, present is what is currently happening and past is what we keep in museums. So, present is moving (alive) and past is static (dead). On the other hand, we perceive the present as a snapshot of events linked in time, whereas when we are in a museum, we see groups of objects that may represent discrete time units or intervals. In other words, the present is continuous, while the past appears fragmentary. Hence, present events can generally be analyzed with much higher resolution than can past events. In summary, from an intuitive point of view, we could call the "living syndrome" the combination of alive, dynamic, continuous and accurate attributes and "museum syndrome" the mixture of dead, static, fragmentary and rough properties. In the context of the present discussion, the analogy is clear: the ecological subjects, the extant species, have the living syndrome, while the palaeoecological subjects, the fossils, suffer from the museum syndrome. We should not forget, however, that past was once present and was alive, dynamic, continuous and accurate. Is the evidence of the past, and not the past itself, that displays the museum syndrome. Therefore, to properly know and interpret the past, we should first understand the nature of this evidence.

## METHODOLOGY MATTERS

The difference between ecology and palaeoecology is not only a matter of timing, but also of methodology (Birks & Birks 1980). Ecology deals with living beings, while palaeoecology uses fossils (the concept of fossils used here is broad and includes the subfossils or incompletely fossilized remains especially abundant in Quaternary sediments and rocks). A key goal of palaeoecological study is to reconstruct past species and communities from fossil evidence. The process is so laborious and specialized that it has been turned into a separate discipline by itself: the palaeontology. In ecology, this reconstruction is unnecessary, as species, populations and communities can be directly identified, observed and measured. Moreover, the background of scholars working in each area also makes a difference. Palaeoecologists come from varied fields such as biology, geology, geography, climatology, environmental sciences, anthropology, and many others. It is especially noteworthy the amount of geologists working on palaeoecology, likely due to the fact that fossils are found on rocks and sediments. The varied origin of palaeoecologists is a positive feature that has enriched past reconstructions, but it has also produced some terminological confusion and has contributed to the lack of synergy between ecology and palaeoecology.

On the one hand, many ecologists are reluctant to consider palaeoecological results in their research because they believe that such static, fragmentary and rough evidence cannot advance their research. On the other hand, many palaeoecologists accept the nature of palaeoecological data and feel comfortable just doing reconstructions for their particular "museums". Others simply have no ecological interest. These ways of thinking maintained a prolonged disengagement between ecology and palaeoecology, which is now just starting to disappear. Recent technological developments have notably improved the quality of palaeoecological data, attracting the attention of many ecologists. In addition, the vast amount of useful information provided by palaeoecology during the last years in relation to ongoing global change has stimulated both scientists and funding agencies to develop more studies on the past. In this way, the confidence of ecologists in palaeoecological results, and the commitment of palaeoecologists to ecological tasks, have notably increased, and now there is a promising framework for collaboration (Flessa & Jackson 2005). The important role that palaeoecology plays in the last Intergovernmental Pannel for Climatic Change report (Solomon *et al*. 2007) is especially noteworthy. This emphasis is, in part, attributable to the ability of palaeoecology to provide insights into the important ecological questions, but also to the development of high-resolution techniques yielding more continuous and accurate time series approaching the resolution of present-day ecological data (Hunter 1998, Jones *et al*. 2009, Hughes & Ammann 2009).

## THE PALAEO POWER

The prefix *palaeo-* (or *paleo-*) has a major impact on ecological and biological study. Indeed, it has a tremendous homogenizing power. Disciplines as diverse as zoology, botany, geography, ecology or climatology go straight to the same drawer when preceded by *palaeo-*. Researchers working on such palaeosciences are implicitly considered part of a homogeneous community dealing with the past and linking such disparate topics as the evolution of bird's wings, the origin of Angiosperms, the average temperature of the last interglacial, or the Paleocene distribution of tropical mangroves. There is no need to explain that wings, flowers, temperature or spatial arrangement are studied by experts belonging to different fields of knowledge such as zoology, botany, climatology or biogeography; but when the evidence is found in rocks/sediments, all of them become geologists working on different geological subdisciplines with some biological meaning. The prefix *palaeo-* is intrinsically associated with methodological issues such as rocks and fossils or, in other words, museum stuff. As a result, ecology and palaeoecology have traditionally been maintained as separate disciplines with their own and well differentiated language, journals, societies, methodologies and world-views (Jackson 2001).

Another consequence of the homogenizing power of the prefix *palaeo-* is that palaeoecology is frequently confused with other palaeodisciplines, notably with palaeoclimatology and, in general, the study of paleoenvironments. Palaeoscientists have earned their share of blame for this, as reconstructions of past environments using biological proxies are commonly labeled palaeoecology. Palaeoecology is not palaeoenvironmental reconstruction (Rull 1990). When fossils are used as palaeoenvironmental proxies, ecological knowledge is used to reconstruct the physical environment; therefore, ecology is part of the method but the objective is climatic, not ecological. As a simile, if we use the presence of polar bears to locate the North Pole, we are not studying bears, but using them as geographic proxies. Thus, multi-proxy paleoclimatic reconstructions based on an array of different biological indicators, though they need

palaeoecological expertise for confident interpretations, are not palaeoecological (nor palaeolimnological) surveys in essence. A palaeoecological survey, by definition, should have an ecological objective. Of course, climate is part of the ecosystem, and palaeoclimatic reconstructions are needed for an adequate ecological reconstruction, but to consider that palaeoclimatologists are palaeoecologists is equivalent to accepting that meteorologists are ecologists.

## UNIFORMITARIANISM, THE KEY

Geology is a discipline in which the concept of time and the influence of past events in the shaping of the modern Earth are implicit. Any geologist is aware of this, and interprets present-day landscapes as the result of the continued action in the present of events like those in the past. It is thus not surprising that one of the most fundamental palaeoecological tenets, Hutton's principle of uniformitarianism, emerged from the field of geology. Despite the existence of several expressions of this principle, the most common is that "the present is the key to the past" (Tomkeieff 1962). This means that natural processes operating in the past are the same as those that can be observed operating in the present, though rates can vary. Geological and ecological processes, however, differ in several ways (Mayr 2004). An important one is evolution. The geological actors have been essentially the same through time, while the biological elements in play have undergone evolutionary changes. This implies that the more distant the past, the less confident we are about the ecological requirements of organisms. In the case of extinct species, the features of their niches may be even totally unknown. However, it is beyond all doubt that these organisms had ecological niches, lived in populations, were part of a community, interacted with the physical environment, and established a variety of biotic relationships, just like extant species do. Even in the ancient and simple stromatolites, there is a typical trophic organization into primary producers and consumers/decomposers. Therefore, it is reasonable to accept that ecological principles have been operating in a similar way in a geological time frame (ecological uniformitarianism).

In a museum, we can adopt a purely aesthetic attitude or we can view their objects as remains of a society or a community with their present in the past, trying to figure out how their lives would have been. In this case, we straightforwardly apply the principle of uniformitarianism, and the barrier between present and past (or history) vanishes. Then we realize that we live in a time continuum, in which there is no reason to assume that we are the end point. This is the essence of palaeoecological approach. The ideal tool for a palaeoecologist would be a time machine, in order to fully appreciate the past as an alive dynamic, continuous and accurate world. Palaeoecologists do not particularly like fossils by themselves (as palaeontologists do) but as the only available biological evidence for the past. When we use the genealogy to understand our own origin as individuals, we perceive ourselves and our ancestors as part of the same story. This cultural continuum is a good simile for the ecology *vs.* history (or palaeoecology) issue. There is only one single biosphere and, as a consequence, one single ecology. There is no separate biosphere of the past and another of the present (nor of the future). To concede such difference would be analogous to accepting Cuvier's theory of recurrent catastrophes and creation acts (Rudwick 1997). Today, we are aware of the continuity of the biosphere in time, which is maintained by the process of biological evolution.

## THE ECOLOGY OF THE FUTURE

The famous statement of Heraclitus of Ephesus: "everything flows, nothing stands still" is particularly appropriate in the present context. In evolutionary terms, the clock was set at the beginning of the universe and since then it has been permanently running, with the time arrow pointing to the future (Rull 2009). In this frame, the present can be seen as a floating point with a permanent movement along the time line, which displacement continuously transforms the future into past. Therefore, past is constantly growing. In ecological terms, the present is not a non-dimensional point but a short segment of the timeline -the ecological time- which is nothing but a short piece of past. In the last decades, however, the increasing interest in the future of ecosystems, especially in relation to predicted global environmental changes, has provided a wider temporal scope for ecology. The present ecosystems are considered to have a future and their study has become part of the ecological study in a natural way. The future of ecosystems is considered an ecological matter and is studied by ecologists, under the assumption that the species of the future will respond to environmental changes as extant species do: "the present is the key for the future". The main -though not the only- tool is modelling, which involves complex and sophisticated technologies and processes resulting in the need for close collaboration with specialists from other disciplines such as mathematics, physics and engineering. In this way, the field of ecology has extended in time, and ecologists have adopted the future as part of their temporal domain. No any different name has been coined for the study of the ecology of the future, which is implicitly considered part of ecology. Hence, paleoecology remains the study of the past, while ecology has become the study of the present and the future.

## WHAT IS PALAEOECOLOGY?

There are many definitions of palaeoecology. The shortest one is etymological: "Palaeoecology is the ecology of the past" (Birks & Birks 1980). Others are much more exhaustive but often incomplete, as they consider only the relationship between organisms and the (physical) environment, thus forgetting biotic interactions. Some other definitions are purely descriptive, as they refer solely to the reconstruction of past organisms and communities. An explicit and more complete definition would be: "the reconstruction and study of past ecosystems, including the relations between organisms and their environments" (Roberts 1998). However, this statement fails to note that not only past ecosystems, but also the past of present ones are palaeoecological subject matter. A key point in the palaeoecological study is the use of "proxies" or inditect environmental indicators and this should be reflected in the definition. Furthermore, the definition should incorporate the

already discussed idea of continuum between past and present ecosystems. Therefore, a possible definition of palaeoecology that contains all these requirements would be: "the branch of ecology that studies (the) past (of) ecological systems and their trends in time using fossils and other proxies".

Regarding terminology, while ecologists feel comfortable with the name of their discipline, a number of palaeoecologists do not. For this reason, some have coined the term neoecology, to refer to the ecological study of living ecosystems. Other names for the same concept are actuoecology and modern ecology. In this frame, ecology is implicitly considered a higher level discipline embracing both neoecology and palaeoecology. To be consistent, the ecology of the future should be also differentiated and named. Expressions such as predictive ecology or ecological forecasting seem appropriate. Another proposal is to name long-term ecology the study of ecological processes exceeding the temporal domain usually considered in traditional ecology, or ecological time. For practical purposes, long-term ecological records have been considered those embracing more than 50 years (Willis *et al*. 2007). Thus ecology emerges as the only term needed to account for the study of ecological systems, no matter the time scale considered, and the use of prefixes such as *palaeo*-, or *neo*- are only needed for methodological reasons.

## SYNTHESIS AND SOME REMARKS

The lack of synergy between ecology and palaeoecology has its roots in several scientific and non-scientific factors. On the one hand, the psychological dissociation between past and present has been transmitted to biological sciences, determining the undervaluation of palaeoecology to explain present ecological patterns and processes. On the other hand, methodological differences have created a chasm between these two sciences and their respective practitioners. Furthermore, the homogenizing power of the prefix *palaeo*- has created some confusion, leading to the misunderstanding of the real meaning and objectives of palaeoecology. However, the principle of uniformitarianism reminds us that past, present and future are not discrete units but a time continuum through which species and ecosystems flow, change and evolve; and that ecology and palaeoecology are only different approaches with a common objective: the ecological understanding of the biosphere.

Ecology is considered here the study of ecological systems in a broad sense, which includes past inferences, present studies and future projections. Palaeoecology is the arm by which ecology studies the past, using proxies. Other disciplines beginning by *palaeo*- are not necessarily ecological. Under this scope, two common ecological statements become redundant. The first is that the present biosphere has been shaped by the combined action of "ecological and historical factors", which should be replaced by "past and present ecological and evolutionary factors". Therefore, it is desirable to avoid use of the term "historical" to refer to the past in an ecological context -as, for example, in historical ecology- because it can create confusion with the same term applied to social sciences. This is especially manifested in palaeoecological studies covering recent centuries, where historic (as opposed to prehistoric) documentary data are commonly used as ecological proxies.

The second redundancy is that "palaeoecology can contribute to ecological knowledge". Instead, it should be said that "part of ecological knowledge is based on past evidence". Just as examples, some relevant questions that need past evidence to be answered are: what are the origins of the present biodiversity and geographical patterns? How and when did present ecosystems emerge? What has been the role of dispersal and migration? Did present communities remain constant in composition through time? When did extant species emerge? Did they appear synchronously? Did environmental factors remain constant through the species' existence? How did the species react to environmental changes? Did the species change their ecological requirements with time? How did intra-genetic variability affect the ecological performance of species? Are ecological communities stable through time and space? Did communities respond to eventual environmental changes as a whole or individually? What are the expected responses of species to future environmental changes? What were the characteristics of ecological systems before human disturbance? Any ecologist would recognize these as relevant ecological topics.

## PROPOSALS FOR THE NEAR FUTURE

Davis (1994) predicted the intensification of the synergy between ecology and palaeoecology, and suggested some ways to contribute to it, from a palaeoecological perspective. The main recommendations were the development of hypotheses to be tested using palaeorecords, rather than simply descriptive sediment studies, and the refinement of quantitative methodologies to increase the objectivity of interpretations. At present, these objectives are close to being achieved (Seppä & Bennett 2003, MacDonald *et al.* 2008), and a further step is needed in the same direction, this time involving modern ecologists. The development of joint projects, especially within the frame of global change issues, is currently on track (Flessa & Jackson 2005, Willis *et al*. 2008) and should be continuously encouraged. In addition, palaeoecology possesses a fundamental value for ecological theory, especially in processes involving medium to long time periods (Rull 1990), and this should be exploited. Palaeoecologists should take every opportunity to propose joint activities, and to emphasize that we are not palaeoscientists who produce interesting data for ecology but ecologists working on another time scale with different methods. We should also be able to increase the presence of palaeoecology in ecological journals and books and to intensify our participation in general ecological meetings. The recognition that is currently taking palaeoecology into global change issues could be a good excuse. Furthermore, the potential role of phylogenetic studies as a bridge between ecology and palaeoecology should be also considered. The usefulnes of phylogenetic biology for community ecology is gaining support, especially in aspects such as the niche-based *vs.* neutral processes in community assembly, the influence of evolution on community interactions and successional processes, or the responses of communities to global change (Cavender-Bares *et al*., 2009).

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