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Legacy Effects of Human Land Use: Ecosystems as Time-Lagged Systems

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Abstract

Today, most ecosystems show some degree of human modification, ranging from subtle influences to complete remodeling and reshaping into anthropogenic ecosystems. In the first issue of the journal Ecosystems, the field of historical ecology, which focuses on the historical development of ecosystems, was prominently positioned with the papers of Foster and others (Ecosystems 1:96–119, 1998) and Fuller and others (Ecosystems 1:76–95, 1998). Starting from these two contributions, we (1) discuss how anthropogenic activities affect ecosystems and their development, (2) outline how land use can be assessed in ecosystem research, and we (3) discuss what the consequences of a historical perspective for our understanding of ecosystems are. We conclude by stating that whereas land-use intensity over time is an ecologically highly relevant parameter to grasp, the availability, quality, and characteristics of historical sources often restrict the analyses. In order to make optimal use of the sources and methods available and to strengthen this field of research and also increase its societal relevance, we suggest building interdisciplinary teams from a very early project phase on. Core task for these teams will be to jointly define research questions considering source availability, and including and merging modeling and experimental approaches in the study design. We propose that adopting a landscape perspective in historical ecology would provide a helpful framework and valuable background for such novel integrated analyses.

Key words: land use; historical ecology; legacy effects; anthropogenic disturbance; ecosystem processes; novel ecosystems; historical sources.

Introduction

The topic of land use and its legacy effects was very prominently positioned in the first issue of the journal Ecosystems with the papers of Foster and others (1998) and Fuller and others (1998), which were both very well received in their fields. Since then, there has been a great upsurge of work in ecology that recognizes the importance of information about the past to understand ecosystems and the often long lasting legacy effects that, for example, past land use can have. Although others had previously addressed land-use change effects, the papers of Foster and others (1998) and Fuller and others (1998) began to draw more attention to the idea of distinguishing persistent or long-term effects.

Human land use is one core component within historical ecology, which focuses on understanding the importance of past events to ecosystems, and

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the long-term legacies of these effects, or lags in ecosystem response. This topic has become increasingly recognized as an important approach within ecology (Szabó 2015). The roots of the historical ecology approach reach back into the eighteenth century and the term itself probably was used for the first time in 1940 (Szabó 2015). Further landmarks in historical ecology are the work of Rackham (for example, Rackham 1980) and Emily W. B. (Russell) Southgates's book ''People and the land—linking ecology and history'' (Russell 1997). A special section in Ecological Applications (Parsons and others 1999) was dedicated to the concept of historical variability. In this issue, Swetnam and others (1999) explicitly made a direct case for the need to understand past ecosystem drivers and their effects to manage for future environments. Whitney (1996) challenged the way natural scientists approached history and used historical records in his detailed and comprehensive study of historical ecology and ecosystem change in northeastern USA.

The general trend to put more weight on the temporal component and the human dimension in ecology is paralleled by developments in other disciplines, such as earth-system science (for example, Foley and others 2005), leading to the encompassing approach fostered by the Future Earth initiative, or more specifically in land change science, where for example, the call for ''socializing the pixel'' (Geoghegan and others 1998) has been taken up by many scholars. Also in landscape ecology, with its emphasis on broad scales and recognition of the human drivers, the societal and historical dimension increasingly became integrated over the last decade. A special issue of Landscape Ecology appeared on ''Why history matters in landscape ecology'' (Rhemtulla and Mladenoff 2007)—a title which soon after was adapted as ''Why history matters in ecology'' by Szabó (2010).

In this paper, we discuss specifically how humans interrelate with ecosystem development, what the resulting effects on ecosystems are, and what integrating the whole range of anthropogenic as well as natural disturbances means for our understanding of ecosystems in general. Thus, we want to

(a) discuss how anthropogenic activities affect ecosystems and their development,
(b) outline how land use can be assessed in ecosystem research, and
(c) discuss what a historical perspective means for our understanding of ecosystems.

By addressing land use and its effects, we focus largely on the time period in which humans play a role, but which operates within other ecosystem processes of change. We conclude with some thoughts about future trends in research in historical ecology.

Effects Of Land-Use History On Ecosystem Functions

The diverse ways and extent to which humans affect ecosystems is enormous and recently found its expression in the declaration of a new era, the Anthropocene (for example, Waters and others 2016). While historical ecology can address longer term questions and data sources, we focus in the following on the scale of relatively recent anthropogenic effects. There are different ways and terms of addressing such human impacts. In ecosystem research, the terms ''land use'' (for example, Foster and others 1998) or ''human activity'' (Fuller and others 1998) are used, or alternatively ''anthropogenic disturbance'' (Gimmi and others 2008), if the focus is more on the effects these activities have on ecosystems. Regardless of the terminology, it is important to consider at first the whole range of known impacts, before limiting a study to the ones that actually can be assessed. Human agency on the planet can have direct physical effects, such as land-cover change, for example, the conversion of forest or prairie to cultivated agriculture, or land-use change, without a change in land-cover class, for example, changing natural forest to intensive production forestry, or natural grassland to hay meadows. In actuality, land-cover change and land-use change define ends of a spectrum of intensity and detectability, but it still makes sense to distinguish them.

But ecosystems are not simply affected by the direct change. Humans also have indirect effects, such as modifying processes, including disturbance regimes, for example, reducing natural fire or native browsing by animal populations, changing river flooding regimes, or introducing exotic species. Indirect effects can also come about by modifying the physical environment, that is, site factors, such as changing climate (temperature, precipitation) or nitrogen deposition from the atmosphere to terrestrial or aquatic systems (Figure 1). In practice, data availability often determines which aspects can be addressed and which are either completely ignored or simply mentioned in the discussion section.

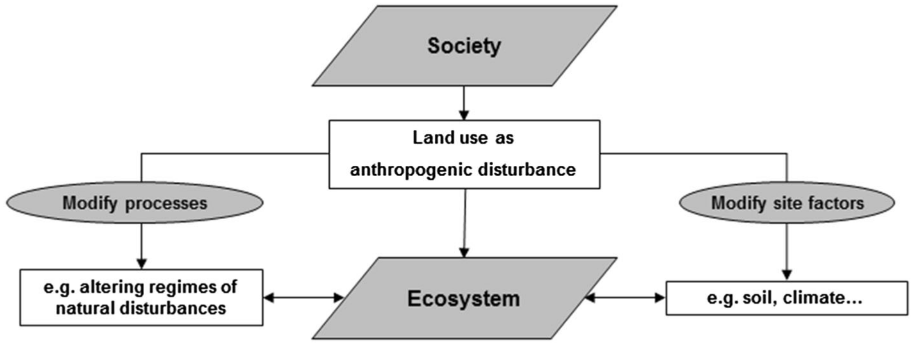

Figure 1. Conceptual graph depicting how society has an impact on ecosystems **A** directly by adding anthropogenic disturbances to the system, indirectly by **B** modifying processes, such as altering the regime of natural disturbances and **C** by modifying site factors (details in *text*).

The limitations or bias caused by not adequately considering the effects of land-use history in ecosystem research can be assessed by conceptualizing the diversity of land-use effects on ecosystem functions, a term which has different meanings (Jax 2005). In the following, we use the term to address the functioning of a complex system and the sum of the processes involved to sustain its state and trajectory.

Studies directed towards understanding land-use history and its effects on ecosystem function add a complexity beyond the quantification of human land-use and ecosystem change over time. As ecosystem state changes, alterations of processes and complex interactions and related changes over time have to be included (Jax 2005). Past land use may persist as memories or legacies for a very long time in ecosystems and may, for example, influence biodiversity and ecosystem productivity (Perring and others 2016). Also very subtle but long-term human impact may have long-term effects on soil and vegetation, and remain detectable centuries later (Freschet and others 2014). In the simplest equilibrium model, the intensity of impact in combination with the susceptibility of the ecosystem to this specific impact and/or its resilience to recover to the former state are decisive for the degree and durability of legacy effects (Figure 2), which ubiquity and importance has been discussed, for example, by Foster and others (2003) or specifically for biodiversity, where the concept translates into extinction debt and immigration credit, by Jackson and Sax (2010). These concepts imply that the ecosystem succession model is valid, and that it makes sense to use past states as a measure or baseline against which to measure change in a system. However, historical ecology recognizes that legacy effects on ecosystem pro-

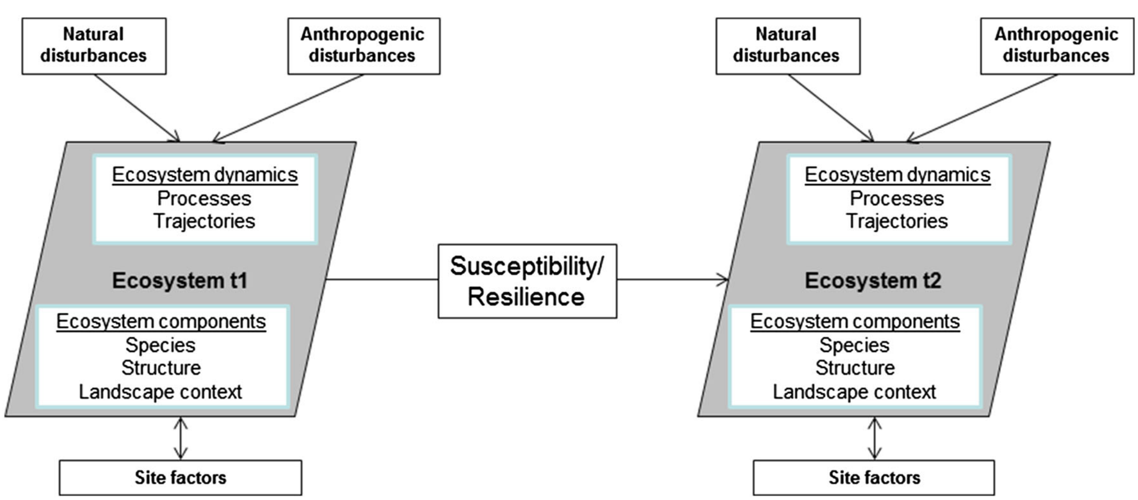

Figure 2. Ecosystem dynamics and components show different and specific susceptibilities and resiliencies to natural and anthropogenic disturbances.

cesses may be more complex, and the simplest recovery model may not often apply (Rhemtulla and Mladenoff 2007), though remaining a useful heuristic device. Legacy effects on ecosystem states imply changes in ecosystem process trajectories that may not aim toward recovery per se, but continuing novel states (Perring and others 2016). Importantly, this recognizes the value of simulation models as well as empirical approaches, and implicitly recognizes that due to legacy effects, the influence of past events will persist into the future.

Interpreting land-cover change and land-use change as opposite ends of a spectrum of intensity and detectability enables to structure the overview of how land use and its change influences ecosystem functions and the resulting legacy effects. Land-cover change can be interpreted as a consequence of land-use change surpassing certain thresholds. Land-cover changes have shown effects on structure, biodiversity, biomass, and therefore regional C dynamics (Casperson and others 2000; Rhemtulla and others 2009a, b; Smithwick and others 2007). Specifically, forests reverting from agriculture have been shown to have legacy effects on processes such as soil nutrient dynamics and biodiversity over decades (Fraterrigo and others 2005; Grossman and Mladenoff 2008), centuries (Compton and Boone 2000), and even millennia (Dupouey and others 2002). In many cases, site level studies have been used to generalize ecosystem function effects to broad scales, such as C dynamics (Drummond and Loveland 2010; Woodbury and others 2006). Land-use changes include more subtle changes that are not resulting in a change in land-cover class. Land-use changes therefore can be interpreted as a change in anthropogenic disturbance regime in an ecosystem.

Not only the intensity of an impact but also the ability of ecosystem functions to recover or to result in a new trajectory when the impact ends determine if a measurable legacy effect occurs. Within the forest research literature, there is ambiguity around the issue of disturbance intensity effects and recovery persistence (Nave and others 2010) and results are hard to generalize. Regarding ecosystem functions, higher biodiversity and C and nutrient retention, for example, are often assumed to result in greater ecosystem stability or resilience for recovery. However, ecotones, for example, are often high in biodiversity, but tend to be susceptible to human land-use impact. For example, Östlund and others (2015) modeled and reconstructed anthropogenic deforestation of a high-altitude ecotone forest almost a thousand years ago, which resulted in a permanent ecosystem state shift.

Assessing Land Use In Ecosystem Research

The two papers on land-use effects published in the first issue of Ecosystems illustrate what aspects of land use were being considered in ecological studies at that time. Both focus on a 5000 km^2 case study area in north central Massachusetts, in the northeastern USA. Foster and others (1998) follow a multi-proxy approach to assess ''changes in the intensity of land use and the extent of forest cover'' and their consequences for tree species composition over several centuries of intensive use following European colonization. Historical records on changes in human population density and distribution, as well as on the specific use of woodland, pasture, and cropland and the forces driving the changes therein, such as settlement expansion, industrialization, abandonment, and (sub-)urbanization, were considered, that is, direct anthropogenic disturbances and also both types of indirect effects (Figure 1) in the form of ''novel disturbance regimes,'' and ''permanent changes in the abiotic and biotic environment.'' Site factors modified include not only changes in soil water availability due to drainage but also changes in climate, atmospheric chemistry, and nutrient loadings. The decimation of native plants and animals and the introduction of disease and pathogens, which would not naturally occur in the region under study, triggered novel processes within the ecosystems.

Using a paleoecological approach, Fuller and others (1998) focus on aspects of land use visible in the palaeo-record, and a longer time scale (1000 years) than Foster and others (250 years). They used pollen data derived from lake sediment not only to detect changes in plant (largely tree) species composition but also estimated changes in proportion of the land covered by herbaceous vegetation. Charcoal abundance over time indicated changes in fire regime, and organic content of the sediment indicated changes in erosion. The date of European settlement was set at 250 years bp for all sites.

Both papers show a decline in climatic signal visible in regional forest composition, with novel disturbance factors due to European settlement being added to fire, wind, and Native American impacts. They illustrate that after massive clearing for agricultural use, forest area has re-expanded broadly over the last 150 years, though today's forest composition is far from the pre-European conditions, due to the novel disturbance regime, permanent changes in the physical factors, and ''perhaps insufficient time'' (Fuller and others 1998).

To widen the perspective, we look more closely at three more papers published in Ecosystems with the term ''land use'' in their titles. Latty and others (2004) study the effect of different disturbance histories on forest soil properties in the Adirondacks (USA) though actual land use is all forest, with different disturbances. Historical information on land-use histories is used to stratify the sampling along a gradient of different disturbance intensities, that is, from old-growth stands to partly or selectively logged stands and finally to stands which have been selectively logged and burned. Powers (2004) looks at the effect of three types of land-use transitions on soil properties, that is, the study is not restricted to forestland. Maps based on remote sensing data were generated to determine the spatio-temporal pattern in land cover. Interviews with landowners and managers were used to learn more about the specific land-use practice regarding crop-rotation, application of agrochemicals (fertilizing, herbicides, tillage, and so on). Gimeno and others (2012) finally evaluate how previous land use affects the successional pathways after agricultural abandonment in Central Spain. They provide a short overview on the land-use history of the region and inferred the specific land-use history from aerial photographs and differences in grass cover, morphology (that is, remains of terraces on former cropland), and soil features (rockiness).

From this brief overview of papers addressing land-use effects on ecosystems, two different approaches can be distinguished: (a) those using information on land use or land cover for stratification and (b) those focusing on land-use effects on a specific site.

The first group needs data on land use or land cover available over larger areas, such as historical maps or aerial photographs. As maps often do not show land use, but land cover, they can be used to stratify regarding former land cover (for example, pasture vs. cropland vs. continuous forest cover) within one current land-cover type (mostly forest), or alternatively along specific land cover (or sometimes land use) transitions (for example, Powers 2004). The core interest of this group of studies is to detect legacy effects of former land use, by performing classic ecological studies in the different strata, with a focus on ecosystem features which are suitable to show such legacy effects, such as soil properties, understory composition, or amount of dead wood in forest stands of different trajectories. To be able to detect legacy effects, the aspect under study has to be adequately represented in the sources used. But maps foremost show the dominant land-cover features—which are not necessarily the ecologically most relevant one. For example, certain types of old-growth lichens might well also be found in young secondary forests established on pastures, if single large trees were present on the former pasture land, for example, to provide shade and shelter for the animals. Conversely, continuously stocked forests might well have had a semi-open character, providing habitat for grassland species, which will be impossible to detect in most land-cover maps. In these cases, the sources do not allow the study of legacy effects adequately.

The second group, focusing on a specific site and its development, makes use of favorable source conditions and includes detailed information on specific anthropogenic disturbances, their intensities, and their changes over time. Foster and others (1998) set a mark regarding the diversity of information compiled and synthesized to tell a complex story of forest dynamics in Central Massachusetts (USA)—but being relevant far beyond its geographic boundaries (for an insightful discussion on the role and relevance of case studies see Flyvbjerg 2006). This approach allows the study of cascading effects of humans on ecosystems, such as modifications of fire regime, as in Zumbrunnen and others (2009), who made use of a 100-year-long series of systematic official reports of forest fires in an Alpine Valley in Switzerland, and Niklasson and Granström (2000) using large-scale dendrochronological analysis, or again Fuller and others (1998) using charcoal abundance. Land use itself can also be looked at more specifically such as by assessing agricultural yields, performing input–output analyses or calculating land-use intensity indices, for example, integrating information on the specific land-use practices (Bürgi and others 2015).

The two approaches are not exclusive, as for example in ''binary analyses,'' which are widespread in historical ecology, that is, studies on differences in species composition and soil chemistry in ancient vs. more recently established forests (based on historical maps). In other words, land-use effects are evaluated comparing sites with contrasting histories, where, depending also on the ecosystem-specific thresholds, legacy effects can occur or not. Cramer and others (2008) show how trajectories of plant community assembly on abandoned fields depend also on the intensity of agricultural land use. The potential of recovery to pre-agricultural conditions are higher with limited soil modification, but old fields might remain in a ''degraded'' state and invasive exotic species might have higher chances to colonize, after a period of high land-use intensity, as widespread in recent decades. Human forest clearing and agricultural use can result in both increase and decline in differing soil nutrients at the same time, with the result still being novel ''recovery'' following farm abandonment (Grossman and Mladenoff 2008). However, information on the type of management, that is, land-use intensity, is much more difficult and time-demanding to collect, as it is often not recorded on (land-cover) maps.

For both approaches, source availability from biological and/or historical archives is a limiting factor, largely, determining which aspects of land use can be addressed, for example, which effects of land-use history on ecosystem functions can be studied. Consequently, not all retrospective methods can be applied to all ecosystems. Pollen-analysis can only be used in areas where pollen have been preserved and the analysis of historical records relies on the extent and quality of historical documents and archives (compare Östlund and Zackrisson 2000). The lack of written records is particularly evident in regions where indigenous people have been living and where ecosystems often are considered to be pristine, or at least represent a state of less intensive human impact (Josefsson 2009; Rautio 2014). New interpretations of past human interactions with nature illustrate how people have been able to adapt to, and also to various degrees domesticate, very diverse ecosystems (Terell and others 2003).

A general challenge in historical ecology—and especially problematic when the aim is to quantify past land use and produce time series of ecosystem change—is that past uses might be unknown, or known, but not documented well, such as the knowledge on practices and sustainability of specific resources and plants by indigenous peoples most often has been passed on orally rather than being documented in historical records (Turner and others 2000). If time witnesses exist, oral traditions can be studied using interviews, as in the example of the practice of litter raking in European forests, which is an abandoned and often neglected practice with century-old tradition (Bürgi and Gimmi 2007). In a recent study, oral history interviews allowed collecting sufficient information on the related land-use intensity and its variability in time and space (Bürgi and others 2013) for assessing its long-term impact on soil carbon in a modeling study (Gimmi and others 2013). Such approaches can be tried for known, but undocumented practices. Besides, an unknown number of similarly relevant but unknown land-use practices might have existed, which cannot be accounted for, but their legacies influence ecosystems up to the present.

To summarize, we can state that information on land cover, land use, its intensity, and its change over time can be included in various ways in ecological studies. Whereas sometimes primarily used to stratify according to different trajectories of land cover or land use and to study legacy effects, more detailed analyses are also performed, revealing the complex interrelationship between societies and ecosystems and using a multitude of sources and approaches including, for example, oral history and archeological data and methods (Briggs and others 2006; Scharf 2014). In this way, detailed long-term and consecutive records of human impact on ecosystems can be produced (Rautio and others 2015). All these approaches are limited by source availability, and as a consequence, not necessarily the ecologically most relevant, but the best documented anthropogenic impacts on ecosystems are studied.

What Considering Legacy Effects Means For Our Understanding Of Ecosystems

In general, resilient and slowly adapting (and recovering) ecosystems experience more legacy effects, as it takes longer until they reflect the current disturbance regimes and stand factors—if such a state will ever be reached at all: novel trajectories and states at present and into the future may often result. Susceptible ecosystems change and adapt more quickly and it then depends on their resilience, if they show detectable legacy effects. Considering the whole range of natural and anthropogenic disturbances, their effects and interactions leads to a shift of focus and finally to an understanding of ecosystems as genuinely time-lagged, complex systems.

These considerations have consequences for restoration ecology, where historical ecology traditionally has been applied (Egan and Howell 2001). An early cornerstone in historical ecology research has been attempted to understand ''naturalness'' in contemporary ecosystems by using an historical perspective as a baseline for restoring ecosystems to a perceived more natural state. Whereas originally historical ecology has been used to determine conditions to which an ecosystem should be restored back to, a more dynamic understanding of the past led to the concept of historical range of variability (HRV) as applied to land management (for example, Morgan and others 1994; Keane and others 2009). This conceptual model includes that if the intensity of a disturbance or a change in a site factor surpasses a specific threshold, they move outside the HRV and consequently ecosystem functions change. The system may remain in the new stage even if the initial trigger is no longer there. The response may be a very long recovery or altogether switching to a new trajectory of change, therefore moving outside the HRV of the original system. Such thresholds exist on the level of (a) species (depending on species traits), (b) structures (availability of habitat elements, for example, stand structure in forests), or (c) processes (such as ecosystem net production) and (d) structures in the neighborhood of ecosystem (for example, the landscape context).

Recognizing some limitations of HRV in times of global change, the idea of ''novel ecosystems'' (Hobbs and others 2014) is increasingly discussed, as changes in climate or the arrival of new species make ecosystems move out of the range of historical analogues (Martinuzzi and others 2015). Also shifts in disturbance regimes that result in structurally, functionally, or compositionally novel ecosystems outside of observed characteristics for a time range of study are assumed to be novel or no-analogue conditions (Foster and others 1998; Williams and Jackson 2007). Such systems have exceeded thresholds of recovery (Scheffer and others 2001) resulting in new ecosystem trajectories (Allen and Breshears 1998). These changed outcomes have often been framed as products of cross-scale interactions with non-linear results (Peters and others 2007).

In a historical perspective, all ecosystems were novel ecosystems once, i.e., this concept is highly time scale dependent, requiring a definition of what thresholds have to be surpassed to justify the term ''novel.'' Along the same lines, we have to consider that in times of global (climate) change, reference conditions might no longer just have to be searched for in the past, but maybe in regions, where climatic conditions and species composition might be (or might have been) more similar to what can be found in the history of a given location (for example, Fulé 2008).

As outlined, acknowledging the inherently dynamic character of ecosystems puts limits on a too direct application of historical analogues (especially if thought to be stable) for restoration aims and it also limits how much novel insight the approach of ''novel ecosystems'' provides. Still, HRV time series might provide valuable information for management decisions if combined with simulated predictions, which are to a certain degree able to include selected stochastic factors such as future epidemic outbreaks or also regional climate dynamics, but miss effects of completely new factors, such as new invasive species (Keane and others 2009). Acknowledging the dynamic character of ecosystems foremost underlines that ''neither the definition of ecosystems nor of its reference state are trivial tasks'' (Jax 2005). The term ecosystem is a conceptual tool and its use is influenced by goals and norms coming from the individual researchers and their scientific and societal surroundings. For scientists working in historical ecology, defining their study system while explicitly considering ecological as well as historical boundaries and constraints (for example, source availability) should become a standard procedure—which eventually might raise further awareness among ecologists in general to consider that ecosystems do not define themselves.

Conclusions And Outlook

Our short overview on how humans, their activities, and resulting effects are considered in ecosystem research reveals a certain mismatch between current practice and ecological relevance. To overcome this, more weight should be given to the intensity of important human activities, considering the classical parameters used to assess disturbance events (range, extent, intensity), and the resulting legacy effects (see also Perringer and others 2016). Land-use intensity as a crucial parameter lately received more attention in neighboring fields such as land change science, where land use is no longer simply classified into, for example, pasture and cropland, but different levels of intensity of grazing or forestry are mapped and analyzed (Kuemmerle and others 2013; Erb and others 2013). At the same time, we have to be aware that often the availability, quality, and characteristics of historical sources determine what aspects of anthropogenic disturbances can be considered and on which scale.

How can historical ecology make optimal use of the sources available? Presently, the large base of historical ecology is formed by case studies at different spatial and temporal scales. Historical ecology would benefit from combining theoretical, experimental, and archival work, using interdisciplinary approaches, in which ecologists and historian/archeologist collaborate from an early project phase on. Jointly defining the ecosystem under study, based on a careful evaluation of the whole range of potential sources to be used in a given area, will serve as a good starting point for collaboration and mutual learning. Clearly, ecologists have a lot to learn from historians in terms of availability and critical interpretation of historical sources in their respective context. Correspondingly, historians have just a much to learn about ecosystem properties, dynamics and response to human intervention. A combination of all these approaches has proved fruitful to science in other fields of research (Loreau and others 2001). Multiple sources and approaches moreover allow some cross-validation of qualitative information, which increases the robustness and validity of results and insights.

There are several obstacles which must be overcome in order to facilitate interdisciplinarity: the general short duration of research projects, the inability (and sometimes unwillingness) to understand a different research discipline, its foundation and its language, and finally the problem of publishing broader studies in scientific journals. A first step in moving ahead might be more open meetings across scientific boundaries to explore possibilities for new collaborations and broader research programs.

As outlined, two different approaches in historical ecology can be roughly distinguished: (a) those using information on land use or land cover for stratification and (b) those focusing on land-use effects on a specific site. In ''binary analyses,'' the two approaches are combined. A pragmatic but rewarding step in the direction outlined above might be to develop the approach taken in binary analyses into a full-landscape perspective, that is, analyzing ecosystem dynamics in their spatio-temporal dynamics, as land use is always taking place in a spatial context with its own socio-economic and cultural constraints and rationalities. By doing so, historical ecology may become even more relevant, and provide knowledge and tools to address present-day societal issues such as protection of biodiversity (Lindbladh and others 2013) while also preserving the cultural heritage connected to historical land use (Mascia and others 2003). Such a context would prepare the ground for fruitful exchange with historians not only regarding sources but also interpreting the land-use practices in their historical context, and allowing to make good use of modeling (Gimmi and Bugmann 2013) and experimental approaches. We believe that historical ecology performed on the landscape level provides an excellent opportunity and a dynamic arena for bringing ''The two cultures''—the natural science and the humanities—as coined by Snow (1959), together, and providing not only novel perspectives on the history of ecosystems but also of societies and of socio-ecological interactions.

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