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Understanding long-term human ecodynamics through the lens of ecosystem collapse

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Abstract

Most research on long-term human ecodynamics examines changes in the size and structure of human populations, often in relation to climate change. Here we offer an alternative perspective that draws on recent progress in conservation science, examining the causes and consequences of ecosystem collapse. We identify human actions that can cause abrupt transformation of ecosystems, in relation to key mechanisms and underlying theory. Such ecosystem collapse can in turn affect human societies by altering flows of ecosystem benefits to people. In this way, human ecodynamics can be understood by separately analysing the dynamics of social and ecological sub-systems, which are reciprocally linked. Ecosystem collapse represents a perturbation of these sub-systems, and provides insights into the mechanisms underlying their respective dynamics. We illustrate this approach through four case studies, which examine the spread of agriculture during the Holocene. Four key knowledge gaps emerge through consideration of these case studies: the linkages between social and ecological sub-systems, and how these change over time; the presence of feedbacks between these sub-systems; the relationships between local- and regional-scale collapse; and the relationships with ecological recovery. Increased research on ecosystem collapse could help clarify the relative influence of environmental degradation on societal dynamics, while providing insights into resilience and sustainability. Given the outstanding societal importance of ecosystem collapse, such research could also strengthen the relevance of historical sciences to the contemporary world.

Keywords

biodiversity loss, environmental change, resilience, socio-ecological system, sustainability

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Introduction

Over the past two decades, a number of authors have suggested that investigations of human-environment interactions in the deep past might have potential value for addressing contemporary challenges associated with environmental change (Altschul et al., 2020; Burke et al., 2021; Costanza et al., 2005; Dearing et al., 2006; Degroot et al., 2021; Fordham et al., 2020; Guttmann-Bond, 2010; Hornborg and Crumley, 2006; Jackson et al., 2018; Ortman, 2019; Rick and Sandweiss, 2020; Scheffer, 2016; van der Leeuw and Redman, 2002; van der Leeuw et al., 2011). Potentially, such analyses could provide insights into the mechanisms underlying the dynamics of socio-ecological systems, and associated phenomena such as sustainability and resilience. For example, over the long term, socio-ecological systems are often characterised by irregular patterns of stability, change and transformation, the study of which can provide insights into resilience throughout the Holocene period (Burke et al., 2021). Examples of past societies where populations survived in the face of climatic pressures afford insights into resilience mechanisms (Degroot et al., 2021). Furthermore, studies focusing only on contemporary societies may fail to identify dynamical processes that can unfold over multiple generations, which may underlie current patterns of human migration (Altschul et al., 2020).

Despite such examples, progress in realising this potential has been limited to date (Ortman, 2019). Partly this reflects the many challenges facing research on long-term human ecodynamics, including variation in the quality, resolution and evenness of available data; a lack of balance and timing between social and environmental data; and the diversity of research approaches employed by different disciplines, which hinders interdisciplinary working (Costanza et al., 2007). Other problems that have been identified include a failure to analyse available data in ways that are relevant to the concerns of contemporary policy-makers (Altschul et al., 2020); a failure to explore the mechanisms underlying the patterns observed, coupled with a lack of broad theoretical frameworks and associated integrative approaches (Burke et al., 2021; Gremillion et al., 2014; Van der Leeuw et al., 2011); and a failure to consider spatio-temporal heterogeneity, both of human societies and of environmental change in the past (Degroot et al., 2021). Many of these challenges were also identified by Silva et al. (2022), who highlighted the potential value of computational modelling approaches in overcoming them. Modelling approaches can facilitate data integration and exploration across a

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range of scales, which can help address the spatial and temporal limitations of evidence derived from individual case studies (Kintigh et al., 2014). Nonetheless, the relevance of such research for addressing contemporary issues such as climate change still needs to be demonstrated.

Here we evaluate the potential value of understanding long-term human ecodynamics from the perspective of ecosystem collapse. This issue has recently been propelled to the top of the international policy agenda owing to a series of unprecedented environmental events, including the mass bleaching of the Great Barrier Reef, extensive fires in regions including California, southern Australia, Indonesia and the Amazon, and the sudden loss of ice habitat in polar regions (Newton, 2021a, 2021b; Newton et al., 2021; Vincent and Mueller, 2020). Evidence is increasing that extensive ecosystems of crucial importance to the functioning of the Earth system, such as the Amazon and Arctic tundra, are losing resilience and may be approaching large-scale collapse (Boulton et al., 2022; Chen et al., 2021; Lovejoy and Nobre, 2018). Ecosystem collapse represents a contemporary environmental issue of immense societal importance, given its potentially devastating impact on the provision of ecosystem benefits to people and the human livelihoods that depend on them; it could also significantly undermine efforts towards sustainable development (Newton, 2021a; Newton et al., 2021). This issue therefore provides a potentially informative test case, regarding the societal value of understanding long-term human ecodynamics.

In this paper, we first provide an overview of current knowledge regarding ecosystem collapse, and its potential implications for human society. We then explore the implications of ecosystem collapse for understanding the dynamics of coupled socio-ecological systems over long timescales, illustrated through a series of case studies drawn from the Holocene. On the basis of this analysis, we highlight a number of emerging issues and knowledge gaps that might usefully be addressed by future research.

Understanding ecosystem collapse

Scientific interest in ecosystem collapse has grown rapidly in recent years (Bergstrom et al., 2021; Canadell and Jackson, 2021; Newton, 2021a, 2021b; Sato and Lindenmayer, 2017). This reflects intensifying concerns about the current pace of environmental change and its ecological and societal impacts. Progress has been made in developing a scientific understanding of the phenomenon, and in operationalising the concept for environmental policy and management practice (Bland et al., 2019; Newton et al., 2021). These efforts have been given particular impetus by the development of the IUCN Red List of Ecosystems (RLE), which has developed an analytical framework for assessing the collapse risk of contemporary ecosystems (Keith et al., 2013, 2015). Following Newton et al. (2021), a collapsed ecosystem can be defined as a degraded ecosystem state that results from the abrupt decline and loss of biodiversity, ecosystem functions and/or services, where these losses are both substantial and persistent, such that they cannot fully recover unaided within decadal timescales.

A wide range of theoretical ideas are relevant to an understanding of ecosystem collapse, including disturbance theory, critical loads, succession theory, state-and-transition models and trophic cascades (Newton, 2021a, 2021b). Recent literature has particularly focused on a variety of approaches associated with dynamical systems theory, including bifurcation theory, catastrophe theory, theories of resilience and alternative stable states and linked phenomena such as tipping points, regime shifts and critical transitions (Andersen et al., 2009; Petraitis, 2013; Scheffer, 2009; Scheffer and Carpenter, 2003). While these ideas have spawned a substantial and informative literature, caution needs to be taken when applying them to field situations, as the different ecosystem states that can be observed in nature often do not correspond to those postulated by theory (Newton, 2021a, 2021b; Petraitis, 2013). Furthermore, key assumptions of dynamical systems theory are often not met in nature (e.g. Bruno et al., 2009; Dudgeon et al., 2010; Möllmann and Diekmann, 2012).

Table 1. Selected propositions relating to ecosystem collapse and recovery, derived from ecological theory and supported by empirical data. Adapted from Newton (2021a, 2021b). It should be noted that these propositions focus exclusively on ecological theory, and do not attempt to incorporate current understanding of social systems or human behaviour.

No.	Proposition
1	Any ecosystem can potentially collapse, if subjected to disturbance of an appropriate type and occurring at sufficient frequency, extent, intensity or duration, and especially if the disturbance is novel.
2	Ecosystem collapse is most often caused by extrinsic factors (i.e. disturbance), sometimes in combination with intrinsic factors (e.g. interactions between organisms).
3	Ecosystems subjected to multiple types of disturbance are more likely to collapse, especially if these disturbances interact.
4	Collapse is most commonly driven by chronic ('press') disturbances, although acute ('pulse') disturbances can also be influential.
5	Many ecosystems can exist in more than one state; transitions between these states can form part of natural dynamics. However, transitions that are normally transient can become persistent as a result of chronic disturbance or stabilising feedbacks.
6	A persistent ecosystem transition, or collapse, can arise when ecological recovery is impeded. This can occur if there are stabilising feedback processes that maintain an ecosystem in a degraded state, if there is chronic disturbance, or when the processes of ecological recovery fail. Understanding these reasons for lack of recovery is key to understanding collapse.
7	Collapse can be caused by breakdown of the stabilising feedback mechanisms maintaining an ecosystem state, or by feedbacks in the internal ecological processes of an ecosystem driving a system to a different state. As a result of these feedbacks, major ecological shifts can result from minor perturbations. Such shifts can occur when extrinsic factors reach a critical value.
8	Ecosystem collapse is more likely if disturbance events cause the loss of: (a) generalist species, (b) top predators and/or trophically unique species, (c) those at the base of food chains and especially (d) those that are highly connected to other species through ecological networks. Loss of such species can cause many secondary extinctions, which can lead to collapse of ecological networks.
9	Functional and structural change in an ecosystem undergoing collapse may be unrelated to loss of taxonomic diversity, but may be affected by loss of species with particular functional traits; species identity matters.
10	Ecosystem collapse can sometimes be positive by creating new opportunities, for example evolutionary diversification and radiation, or by increasing provision of benefits to people.
11	Ecosystem recovery is dependent on intrinsic factors, namely interactions of organisms between each other and with the physical environment. The rate or extent of recovery can be limited by intrinsic factors, and/or by extrinsic factors, such as the disturbance regime and the extent of ecosystem degradation.
12	Ecosystem recovery can take a long time, and always takes longer than collapse.

There is a need to consolidate these ideas into a general theory of ecosystem collapse, to provide a foundation for future research (Boitani et al., 2015). As a step towards this goal, Newton (2021a, 2021b) identified a series of propositions that are based on available theory, and are supported by empirical evidence (Table 1). Put simply, collapse of an ecosystem can result from an abrupt change in an anthropogenic pressure, from an interaction between different pressures, or from an abrupt change in the state of the ecosystem with a small change in a pressure (Andersen et al., 2009; Newton, 2021a; Ratajczak et al., 2018). The latter situation can occur when feedbacks between intrinsic ecological processes are triggered when a pressure reaches a critical threshold value; this is the key mechanism postulated by dynamical systems theory (Scheffer, 2009; Scheffer et al., 2015). A number of intrinsic processes can contribute to ecosystem collapse, such as secondary extinctions leading to extinction cascades and the disassembly of ecological networks (Bascompte and Stouffer, 2009; Brodie et al., 2014). However the most important cause of collapse in contemporary ecosystems is an abrupt change in anthropogenic pressures (Newton, 2021a), as occurs for example during land cover change, which is currently the principal cause of biodiversity loss at the global scale (IPBES, 2019).

Relationship to societal dynamics

Research on sustainability science, and on long-term human ecodynamics, has typically considered both human and environmental elements together, as components of integrated social-ecological systems (SES) (Berkes et al., 2003). An SES can be conceptualised as an ecosystem that is intricately linked with, and affected by, one or more social systems (Anderies et al., 2004). Although a number of different analytical frameworks have been developed for exploring SES dynamics, research progress in this area has been limited by semantic uncertainty (Colding and Barthel, 2019), and the SES concept has been criticised for neglecting the importance of cultural values, beliefs and worldviews in relation to use of natural resources (Sterling et al., 2017). Nonetheless, research on SES has been highly influential, particularly in relation to analysis of resilience and sustainability (Folke, 2006; Ostrom, 2009; Walker et al., 2004). Much of this research has been strongly informed by dynamical systems theory.

Cumming and Peterson (2018) reviewed research on collapse of SES, and its relationship to resilience, noting that the sustainability literature has focused much more on the latter than the former. In fact, collapse and resilience can be viewed as two sides of the same coin; collapse indicates that resilience has been lost, whereas resilient systems are less likely to collapse (Cumming and Peterson, 2018). These authors also noted that societal collapse has been defined in a number of ways in the literature, such as the rapid loss of social, political and/or political complexity, the failure of a political system, or a drastic decline in human population size. Collapse can also be viewed as one form of societal transformation that could alternatively lead to other outcomes, such as reorganisation or revitalisation (Faulseit, 2015; McAnany and Yoffee, 2010). The definition of SES collapse proposed by Cumming and Peterson (2018) shares many common features with the definition of ecosystem collapse presented here: it should lead to a substantial loss of system identity (i.e. key actors, system components or interactions); it should happen rapidly (i.e. $<$25 years, or a human generation); and its consequences should be persistent ($>$25 years). What constitutes a 'substantial' loss will again depend on context and the specific attributes of the system concerned.

Usefully, Cumming and Peterson (2018) also highlighted the importance of understanding the mechanisms responsible for SES collapse, noting that collapse can occur in many different ways as a result of a wide variety of different causes. Some key mechanisms relating to social systems were identified by these authors based on an evaluation of selected case studies; these are summarised here, together with mechanisms of ecosystem collapse (Table 2). Identification of these mechanisms provides a basis for rigorous comparison of different case studies to test alternative hypotheses about how, why and when collapse occurs. Such an approach could strengthen the theoretical foundations of

Table 2. Summary of hypothesised mechanisms that might lead to collapse of social-ecological systems (SES), focusing separately on (a) the social and (b) the ecological components of SES.

(a) Social component.

Specific mechanism	Summary of mechanism
Complexity threshold	Complexity creates problems that only more complexity can solve; diminishing marginal returns mean burden becomes too great for society to support, and collapse occurs.
Elite capture	Wealthy become parasitic on the poor. Resentment, revolution or technological change can cause collapse.
Overspecialisation and inability to adapt	Specialisation on a particular resource, sunk cost effects and/or a lack of diversity create other vulnerabilities that lead to collapse.
Scale mismatch	Scales of environmental variation and governance, or production and regulation, become misaligned. This can cause system dysfunction and collapse.
Upscaling	Obtaining resources remotely can detach people from environmental degradation, creating an overconsumption feedback and potential for collapse.
Speculation	Success leads to a decreasing investment in regulation; returns to speculation exceed those on investments in productive capacity. If expectations about future growth are threatened, abrupt collapse of speculation and general economic activity due to borrowing can occur.
Collapse by contagion	Perturbation or negative impact is transmitted through lateral connections.
Collapse by fragmentation	Loss of modularity and reliance on connections result in collapse if connections are broken.
External disruption	A force from outside the system destroys or undermines it.
Vulnerability threshold	Systems (or individual components) grow from less vulnerable sizes through more vulnerable sizes and may collapse during a vulnerable stage.
Leakage	Semi-permeable boundaries that are important for sustainability become permeable, leading to loss of key resources and/or influx of problem-causing agents.

(b) Ecological component.

Specific mechanism	Summary of mechanism
Disturbance increase	An abrupt increase in disturbance frequency, extent, intensity or duration, especially if the disturbance is chronic ('press') and is novel.
Multiple disturbance	An increase in multiple types of disturbance and/or interactions between them.
Species loss	Loss of species, especially: (a) generalist species, (b) top predators and/or trophically unique species, (c) those at the base of food chains, (d) those that are highly connected to other species through ecological networks, (e) those with particular functional traits.
Extinction cascade	Loss of species results in many secondary extinctions or an extinction cascade, leading to collapse of ecological networks.

(Continued)

Table 2. (Continued)

Specific mechanism	Summary of mechanism
Complexity loss	Loss of community complexity, such as a reduction in the number of trophic levels in a food web or a decline in food chain length
Loss of structure	Loss of ecosystem structure, biomass, heterogeneity, carrying capacity or condition
Loss of function	Loss of ecosystem function, e.g. decline in productivity or decomposition, disruption of nutrient and/or water cycles.
Loss of stabilising feedbacks	Breakdown of the stabilising feedback mechanisms maintaining an ecosystem state, causing a transition to a different state
Transition in ecosystem state	An increase in feedbacks in ecological processes drive the ecosystem to a different state; this can occur when extrinsic factors reach a critical value.
Loss of recovery capacity	Loss of key species, ecological processes or features limits the capacity of the ecosystem to recover following disturbance
Recovery impeded	Ecological recovery processes are impeded as a result of chronic disturbance and/or the occurrence of stabilising feedbacks that maintain an ecosystem in a degraded state

Note that these mechanisms are not mutually exclusive. Table (a) is adapted from Cumming and Peterson (2018), and Table (b) is adapted from Newton (2021a) and Newton et al. (2021).

sustainability science, and inform contemporary environmental analyses. However, a key challenge remains in terms of understanding the linkages between system structure, processes and change over time, across a range of scales (Cumming and Peterson, 2018).

The value of a long-term perspective

Historical sciences, such as archaeology and palaeoecology, could potentially make a significant contribution to an understanding of SES dynamics, by empirical testing of these hypothesised mechanisms and theoretical ideas using real-world case studies beyond those observable today. As suggested by Cumming and Peterson (2018), research into collapse can provide a useful corollary to analysis of resilience. In both cases, examination of system dynamics over long timescales can be of particular value in elucidating the relative importance of the different mechanisms underlying system dynamics (Silva et al., 2022).

We suggest that analyses of long-term human ecodynamics should differentiate between the social and ecological subsystems of SES, and consider them separately, while recognising that they are reciprocally linked to a greater or lesser degree (Figure 1). This reflects the fact that different mechanisms underlie the dynamics of the two subsystems (Table 2). In their review, Cumming and Peterson (2018) considered collapse of the entire SES as a single integrated system, yet the social and ecological components of the system can respond differently to an external perturbation such as climate change. Furthermore, many historic examples of ecosystem collapse are not associated with social collapse, and the converse is also true (Butzer, 2012, Middleton, 2012). Rather, many societal collapses can best be understood as the consequences of conflicts between and within different groups of people, which can be triggered or exacerbated by a wide range of factors, sometimes including those related to environmental change (Lawler, 2010). One of the most striking lessons from the archaeological record is just how resilient and adaptable people are when confronted with environmental change (McAnany and Yoffee, 2010; Middleton, 2012).

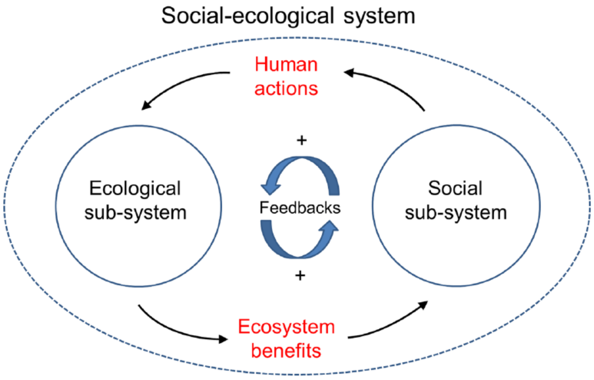

Figure 1. Structure of a social-ecological system, comprised of social and ecological sub-systems, with reciprocal links and possible feedbacks occurring between them. Human actions include harvesting wild species, ecosystem transformation (etc.), whereas ecosystem benefits (or services) include food, water, fuel (etc.) (for details, see text). Both social and ecological sub-systems are comprised of individuals, populations and communities, of humans and other species respectively. Intrinsic social and ecological processes independently influence the dynamics within each respective sub-system.
Source: Adapted from Wilcox et al. (2019) and Berkes et al. (2003).

Long-term studies of SES dynamics could also provide insights into how the two subsystems are linked together. This might be achieved by considering the different actions that humans undertake to support their livelihoods, which can include:

(i) harvesting, gathering or hunting wild species,
(ii) introducing and managing species (e.g. domesticated livestock or crop plants),
(iii) transforming or replacing an entire ecosystem (e.g. land cover change such as conversion of a natural forest to cropland, or urbanisation),
(iv) changing the disturbance regime (e.g. increasing fire frequency),
(v) extraction of abiotic resources (e.g. minerals, water).

Each of these actions can have a direct impact on ecosystems. Additional impacts can arise as indirect consequences of humans undertaking these actions, including production of waste and pollution; loss of abiotic resources (e.g. potable water or soil); disturbance to species (e.g. avoidance of people because of fear); and unintended introduction of species (e.g. disease organisms or vectors, commensal species such as rats). In return for undertaking these actions, humans receive a range of benefits (or services) from ecosystems to support their livelihoods, which can include provision of food, potable water, medicines, timber, fuel and fibre, as well as cultural, aesthetic and spiritual values. Long-term research could usefully identify how the flows of these benefits change over time, in relation to the dynamics of different livelihood actions and associated ecological impacts, to determine how these are interlinked.

Both the direct and indirect impacts of livelihood actions can contribute to ecosystem collapse via the mechanisms listed in Table 2b. Those actions leading to rapid conversion of an entire ecosystem, for example land cover change resulting from the spread of agriculture, are clearly associated with highest collapse risk. Late-Holocene examples such as New Zealand and

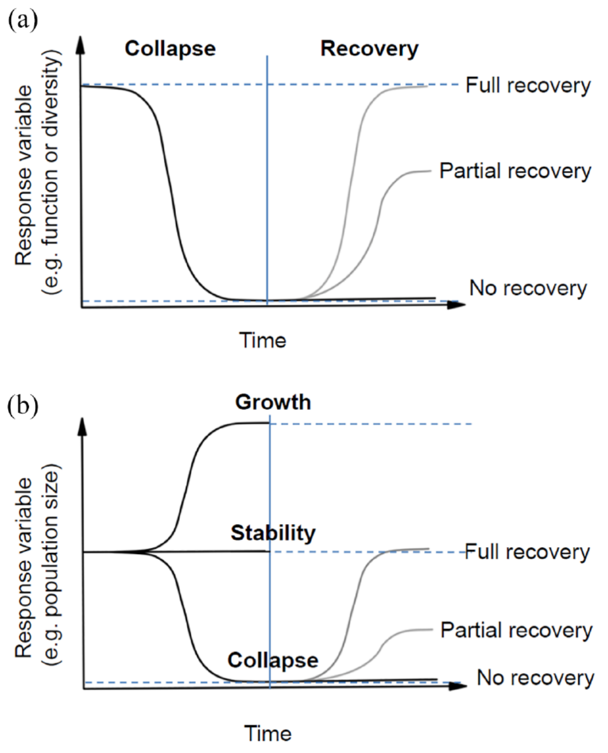

Figure 2. Dynamics of a social-ecological system undergoing ecosystem collapse, illustrating (a) the ecological sub-system and (b) the social sub-system. Note that these two sub-systems can demonstrate contrasting dynamics. In (a), after declining in condition as a result of a disturbance event, an ecosystem might undergo partial or complete recovery; if there is no recovery, and the ecosystem persists in a degraded state, it may be considered to have collapsed. Partly adapted from Newton (2021a, 2021b). In (b), human populations could remain unaffected by ecosystem collapse, or might increase in size or measures of human well-being as a result of increased exploitation of ecosystem benefits. Alternatively, the social sub-system could collapse, which might or might not be followed by subsequent recovery. Human populations that demonstrate growth, stability or recovery following ecosystem collapse might be considered to be resilient.

Madagascar illustrate how a change in the disturbance regime, especially an increase in fire frequency, can also result in rapid ecosystem transformation over extensive areas (Burney et al., 2004; McWethy et al., 2009; Newton, 2021a; Perry et al., 2012). Fire and livestock husbandry are particularly potent causes of ecosystem collapse, as they can lead to a shift in vegetation composition favouring plant species that are adapted to these forms of disturbance; this leads to a stabilising feedback mechanism that can cause the transformed ecosystem state to persist over long timescales (Newton, 2021a).

If an ecosystem collapses, it might be expected that the social subsystem will also collapse (Cumming and Peterson, 2018), owing to a decline in ecosystem benefit flows. However, the flows of some key benefits, especially food, can increase as a result of ecosystem collapse (Figure 2), for example when a forest ecosystem is replaced by cropland. This highlights the trade-off that exists between food production and provision of many other ecosystem benefits, which has been widely reported in the literature (Cordingley et al., 2015a, 2015b; Newton et al., 2012). Further trade-offs have been identified relating to increased water supply, following damming of rivers (Roy et al., 2018). Such trade-offs help explain the 'environmentalist paradox' that has been observed in the contemporary world: at the global scale, human well-being has increased in recent decades despite large global declines in most ecosystem services (Raudsepp-Hearne et al., 2010). This suggests that in the short term, human well-being is not closely coupled to provision of most ecosystem services apart from food, and that at the global scale, the benefits of increased food production currently outweigh the costs associated with declines in other ecosystem services, such as mitigation of flood risk or prevention of soil erosion (Newton, 2021a). Determining how this trade-off has been manifested at different locations throughout human history represents a key research challenge for studies of long-term human ecodynamics. In addition, human societies can respond to a decline in ecosystem benefit flows in a number of different ways, such as a change in livelihood strategy, technical innovation or a change in governance relating to resource use. The nature of these responses will also depend on local context and characteristics of human culture, which helps to account for the diversity of social responses to environmental degradation observed in the archaeological record (Butzer, 2012; McAnany and Yoffee, 2010; Middleton, 2012).

Social and ecological subsystems can also be linked by positive feedbacks, which can potentially drive the entire SES towards collapse. This can occur when a human action results in an increased benefit flow, which engenders more of that same action. This situation is best illustrated by the harvesting of wild species, which can lead to population collapse of the target species and subsequent transformation of the entire ecosystem. An example is provided by the current overexploitation of global marine fisheries, which is leading to widespread collapse (Pauly et al., 1998; Pauly and Zeller, 2016). Overexploitation has been a significant cause of species extinction throughout the Late-Holocene (Turvey and Fritz, 2011), and the same mechanism accounts for the 'boom and bust' extraction cycle described for many natural resources during the colonial era (Homma, 1992), which has left significant environmental legacies. Again, societies may respond to such feedbacks and associated resource collapse in a variety of different ways. Examples from earlier in the Holocene illustrate human population decline following overexploitation of faunal resources, such as in New Zealand (Brown and Crema, 2019) and South America (Goldberg et al., 2016). Alternative social responses might enable collapse of human populations to be avoided, despite the occurrence of such feedbacks, but identification of the mechanisms underlying this form of resilience remains a key knowledge gap.

Case studies

To examine the value of ecosystem collapse for understanding long-term human ecodynamics, we present a series of case studies drawn from the mid- to late-Holocene in different parts of the world. Each of these focuses on the spread of agriculture, which has been the principal cause of ecosystem collapse throughout the world during this period (Newton, 2021a).

Europe

From a theoretical point of view, the dispersal of early farming across Europe between the mid-9th mill calBP to the early 6th mill calBP (Lahtinen et al., 2017; Silva and Vander Linden, 2017) bears the hallmarks of a human-mediated process potentially leading to ecosystem collapse. This involved introduction of a range of species (e.g. cattle, pigs sheep, goats, various cereals, pulses and accompanying weeds: e.g. Coward et al., 2008; Manning et al., 2013), and accompanying environmentally aggressive practices (e.g. clearing of forest through fire or tree-cutting: Connor et al., 2019; Schauer et al., 2020). The archaeological literature yields numerous examples of early human impacts at a site level from the earliest stages of the Neolithic onwards. In Britain a trajectory of a decline and recovery in forest cover was observed, which closely mirrors the dynamics in suggested population size of the first farming communities (Woodbridge et al., 2014), suggesting close coupling of social and ecological components of the SES. However, at the regional or continental scales, extensive transformations in vegetation cover only occur from the late 5th mill. calBP onwards. Several studies have suggested an increasing role of land use change in this process, although climate factors remained the primary driver (Marquer et al., 2017; Roberts et al., 2018, 2019). It is only during the last 1000–1500 years that a decline in forest cover has become more dramatic, eventually leading to the modern situation (Mottl et al., 2021).

This marked time-delay between the introduction of early farming and the effective reduction in forest cover at the regional scale raises several issues. How do we account for this apparent temporal discrepancy? Several of the propositions listed in Table 1 provide an incipient framework to re-considering the ecological component of this SES. Early farming in Europe arguably falls under several of the criteria outlined in Propositions 1 and 2, in the sense that it corresponds to extrinsic factors (i.e. introduced species), leading to disturbance occurring at sufficient frequency over a long duration. However, factors relating to its extent and intensity remain difficult to assess. As for Proposition 3, early farming is associated with multiple potential disturbance factors (e.g. clearing of forests, fire regimes, grassland opening and livestock husbandry), though the nature of their interactions remains unclear, as do their respective impacts on local ecosystems.

This relative lack of knowledge also extends to feedback processes (Propositions 6 and 7). The characterisation of such feedbacks relies upon in-depth understanding of causality in human-environment interactions, an issue often overlooked in environmental archaeology (Carleton and Collard, 2020). Similarly, the impacts of early farming on individual species and their role in ecosystems (Propositions 8 and 9) remain poorly understood. This last point is of particular importance for understanding the long-term interplay between farming and ecosystem dynamics. Another key issue is the twin problem of spatial and temporal scale. Although farming was undoubtedly practised since the turn of the 6th and 5th mill. calBP across most of Europe, its exact spatial extent and structure, and thus its possible impact upon ecosystem loss and fragmentation, remains largely unexplored. The same issue applies to temporal trajectories, and underlines the difficulties associated with identifying thresholds and tipping points in SES dynamics. Understanding the relationships between ecosystem collapse and recovery (Proposition 11) at a range of scales also emerges as a key issue in this case study. If early farmers spread through Europe as a travelling wave-front, as Silva and Vander Linden (2017) have suggested, then ecosystem collapse at a local scale may have stimulated onward human migration, allowing local-scale ecosystem recovery. Patterns of demographic collapse that have been observed in Neolithic Europe may therefore reflect contrasting rates of human population increase and ecosystem recovery (Downey et al., 2016).

Southern Brazil

The highlands of southern Brazil provide an illustrative case where local- and/or regional-scale ecosystem collapse appears not to have been detrimental to humans. Unlike the European Neolithic, where agricultural expansion involved the introduction of a coherent ‘package’ of human-borne crops, cultivars arrived piecemeal to Brazil over several centuries. Consequently, a demographic transition analogous to the Neolithic across Eurasia does not appear to have taken place until well into the Late-Holocene (De Souza and Riris, 2021; Fausto and Neves, 2018). Late-Holocene pollen records from this period generally indicate a contraction of Campos grasslands, while forests across the region expanded significantly. In certain locales, this pattern manifests extremely rapidly. For example, near São Francisco de Paula in the Brazilian state of Rio Grande do Sul, the percentage of recorded tree pollen in the Rincão das Cabritas core (Jeske-Pieruschka and Behling, 2012) increased from 36% to 80% in less than two centuries (~3000–2800 cal BP) and maintained values above 90% for the 1500 years before European Conquest. Archaeology demonstrates that over this interval, human pressures (cultivation practices, population size, anthropogenic fire) also intensified (Behling et al., 2004; De Souza and Riris, 2021; Iriarte and Behling, 2007; Robinson et al., 2018, etc.), in large part owing to the expansion of the southern proto-Jê archaeological culture across southern Brazil (Iriarte et al., 2016, 2017). Moist highland forests in this region are characterised by *Araucaria angustifolia*, a cultural and ecological keystone tree species that Jê groups exploited intensively for their nutritious starchy seeds in both pre- and post-Conquest times.

The mechanisms responsible for the widespread and often rapid expansion of *Araucaria* forests in the southern Brazilian highlands are a topic of active debate, typically focusing on the relative importance of anthropic versus climatic drivers of change (Bitencourt and Krauspenhar, 2006; Iriarte and Behling, 2007; Robinson et al., 2018; Souza, 2021). Both played a role. For example, the Itapeva core yields 39,509–69 cal yr BP (Behling et al., 2007) reveals ⩽7% arboreal pollen around the Last Glacial Maximum, increasing to >20% by the deglacial period, coincident with the earliest human records in south-eastern Brazil. Additional increases in forest pollen >50% coincide approximately with the onset of the relatively warm and wet conditions of the Late-Holocene (~4200 cal BP). The exceptional speed of the shift from grassland to forest in the ~1500 years before European Conquest was likely driven by changing land use patterns (Lauterjung et al., 2018; Robinson et al., 2018; Souza, 2021). At the same time, southern proto-Jê groups in the highlands likely achieved unprecedented population densities and political complexity, coeval with the recorded expansions of *Araucaria* forests (De Souza, 2016a, 2016b; Iriarte et al., 2017), in which forests and the people whose livelihoods they supported likely formed a socio-ecological feedback loop (Bitencourt and Krauspenhar, 2006; Iriarte and Behling, 2007).

The outcomes of interacting climatic, social and ecological dynamics appear to have been beneficial to Indigenous groups in southern Brazil, as indicated by a florescent Late-Holocene material record. This appears to have been coincident with the collapse of an ecosystem (dominant grasslands) into an alternative state (forest mosaics) following the introduction of novel disturbances (changed climate conditions and human-mediated tree recruitment). The patterns observed in the archaeological and environmental record over the last two millennia correspond relatively well to the criteria of Propositions 1 and 3 (Table 1) – a loss of identity and extent owing to the emergence of novel, interacting disturbances. In this sense, increasing population densities qualify as a growing pressure over time (Proposition 4). Furthermore, it has been suggested that in the absence of humans, on millennial timescales forest-grassland dynamics exist in a shifting, non-equilibrium state (Costa et al., 2018; Souza, 2021). Bearing this in mind, anthropogenic tree recruitment and maintenance of established forest cover (a plausible proxy for which may be persistent >50% arboreal pollen in sediment cores) could correlate with the entrenchment of an ecosystem state that would otherwise be transient (Proposition 5). Excepting the last 500 years of deforestation and grazing (Hamilton et al., 2021), the capacity of grasslands to attain extents observed during the LGM may be limited by anthropogenic Late-Holocene disturbance regimes (Proposition 11). Despite the increasing precipitation over this period, charcoal influx in cores (as a proxy for burning) heightens considerably during the late pre-Columbian period (Jeske-Pieruschka et al., 2013). This may indicate that relatively minor yet chronic disturbances (fires), selectively applied to Campos by humans, were sufficient to promote local-scale ecosystem collapses (Proposition 6) that led to transformation into the forest ecosystems favoured by the southern proto-Jê.

These suggested mechanisms of SES dynamics are speculative and require some reshaping of typical archaeological expectations. In particular, the mechanisms of grassland replacement need further investigation in order to better understand the unprecedented speed of this process in the Late-Holocene. What combination of factors offers the most parsimonious fit to the striking pace of Late-Holocene *Araucaria* forest expansion? Anthropic fire activity in grasslands is evident from an early date in southern Brazil, but at what point (if any) does the frequency, intensity and purpose of firesetting change? A key research need is to contrast the flow of ecosystem services provided by grasslands *vis a vis* highland forests, in the context of the gradual adoption of cultivated food, enabling any trade-offs in benefit flows to be identified.

South-west Asia

The earliest evidence of the origins of agriculture currently comes from Southwest Asia, from which the European agricultural package subsequently spread (Bellwood, 2005). Recent perspectives emphasise Neolithisation as a process, rather than a single event, comprising a constellation of different socio-ecological developments, all of which were part of long-term trends in human-environment relationships (Asouti and Fuller, 2013; Bogaard et al., 2021; Fuller et al., 2018; Zeder, 2011). The transition to a sedentary, farming way of life was relatively slow, and happened during a time of relative climatic stability. From around 14,600 cal BP, small settlements with semi-subterranean circular structures located close to water sources began to grow into increasingly larger and more settled communities, representing the emergence of complex sedentary village societies increasingly reliant on cultivated resources. However, it is not until the Pre Pottery Neolithic B (PPNB; 10,500–8700 cal BP) that true farming was fully embedded into lifeways. At this time we find reliable evidence for both domesticated plants and animals as well as for large and complex settlements comprised of rectilinear buildings. Some 'mega-sites' covered up to 10 ha and potentially housed communities of 3000 people or more (Borrell et al., 2015; Kuijt, 2000). The location of sites varied greatly: while many are found in the Mediterranean Zone, others were located in more arid regions such as the southern Sinai. This change in settlement type was accompanied by a profound socio-economic and cultural transformation evidenced by an increase in ritual and symbolic behaviour and associated material culture (Borrell et al., 2015).

By around 8700 cal BP, many larger sites, including the 'mega-sites', were abandoned and others shrank in size. While cultivation of domesticated plants continued, local populations in the Levant increasingly switched to pastoral lifeways (Goring-Morris and Belfer-Cohen, 2010; Rosen, 2011), with agriculture per se becoming more focused in more easterly regions. The causes of this so-called 'PPNB collapse' have been extensively discussed and include climatic deterioration; environmental degradation; settlement/economic reorganisation; invasions; epidemics (particularly from newly evolved zoonotic diseases); and social breakdown (Banning, 2001; Goring-Morris and Belfer-Cohen, 1997; Henry et al., 2017).

Climate deterioration proponents point to regional climate variation impacting the abundance of summer grazing and the increased erosion of agricultural land. Such changes may have been associated with the global 8.2k event thought to have led to a rapid drying of the Eastern Mediterranean, leading to terrestrial ecosystem change that would have had a direct impact on early farmers (Weninger et al., 2009, 2006). However, more recent studies adopting more stringent data-auditing procedures for the relevant radiocarbon dates, suggest that the 8.2k event is not chronologically correlated with the PPNB collapse and is thus unlikely to be a direct cause (Flohr et al., 2016).

Doubt has also been cast on the environmental degradation theory. Originally it was suggested that over-exploitation of resources led to soil erosion and a decrease in soil fertility. In particular, research has focused on over-grazing (the 'peak goat' hypothesis; Köhler-Rollefson, 1988, though cf Rosen, 2011) and on the possibility of massive deforestation, particularly driven by a social/cultural imperative to burn considerable quantities of lime to manufacture lime plaster for house-proud Neolithic village societies (Köhler-Rollefson, 1988). However, more recent work based on the modelling of ethnographic data from agricultural societies suggests that Neolithic subsistence practices are unlikely to have been intensive enough to cause a level of degradation sufficient to cause large-scale ecosystem collapse (Campbell, 2010).

Evidence for the increasing significance of zoonotic and density-dependent diseases in early villages makes these plausible factors in a decline (e.g. Buzic and Giuffra, 2020; Goring-Morris and Belfer-Cohen, 2010), although direct 'smoking gun' evidence is as yet lacking. Recent attention has also focused on the potential for social breakdown, but there is some debate over the likely causes of such an occurrence. In some formulations, increasing social stress associated with larger and more permanently co-habiting communities (Coward and Dunbar, 2014) could not be compensated for, despite attempts to maintain social cohesion. In some locations, this might have been exacerbated by external climatically forced and/or human-induced environmental stress (Kuijt, 2000; Simmons, 2011; Verhoeven, 2002).

A major issue for understanding the socio-ecological processes at play in these early village communities is that some fundamental questions about the livelihood strategies that were practised remain unanswered. Previous approaches have characterised PPNB villages as founded on complementary but highly segregated practices of crop farming and herding of ovicaprines, of regimes structured principally around cultivation of alluvial flood-plains, or of more integrated sets of practices in which ovicaprine husbandry cross-fertilised (literally) intensive and extensive cultivation (see Bogaard and Isaakidou, 2010). Likewise, while some researchers focusing on the social and cultural elements of these groups have identified both incipient hierarchisation and early urbanisation (Price and Bar-Yosef, 2010), others emphasise a collective, sharing ethos not dissimilar to that documented among many historical forager societies (see e.g. Bogaard and Isaakidou, 2010). It thus remains unclear to what extent analogues from historical and contemporary small-scale farming communities can be applied to these potentially unique and non-analogue early Neolithic lifeways.

This case study illustrates a situation where societal collapse was apparently not driven by ecosystem degradation or collapse, at least in isolation. Rather, early village societies were characterised by non-linear dynamics that included phases of rapid growth, including an increase in settlement size and regional networks in the PPNB, but also phases of at least partial societal 'collapse' or system re-organisation. These dynamics were influenced by a complex constellation of socio-ecological factors, although the relative importance and interactions of these factors remain poorly understood. The relative impact of ecosystem collapse on societal dynamics is difficult to elucidate, but it is clear that human actions associated with the onset of farming could have influenced the collapse mechanisms listed in Table 2b. For example, Asouti et al. (2015) summarises evidence for the widespread use of fire as a vegetation management tool during the early Holocene in the southern Levant, together with the routine management of *Pistacia* woodlands as a source of fuel and food. In addition, in the PPNB there is evidence for the widespread conversion of semi-arid grassland ecosystems into intensively grazed rangelands dominated by legumes, as a result of increased grazing and browsing pressures (Asouti et al., 2015). These observations indicate major changes in the prevailing disturbance regime, including the introduction of novel chronic disturbances (Propositions 1, 2, 3 and 4, Table 1). How such ecosystem transformations affected human societies remains unclear, although the impacts could have been highly significant owing to associated processes such as increased soil erosion and declining crop yields. These provide a potential mechanism for recursive and dynamic feedbacks to occur between the social and ecological components of the system, which have the capacity to cause drastic and persistent change in both components, as demonstrated by Ullah (2013) using modelling approaches.

Guanzhong Basin, China

The Loess Plateau of northern China today experiences the most intense soil erosion in the world and suffers from decreasing water tables and subsequent water supply shortages (Qiang-guo, 2001). However, written records attest that this region, which was the cradle of Chinese culture, once had a good coverage of grasses and trees, flourishing agriculture and a semi-humid climate with deep loess soils (Elvin, 2004). Historical writings reveal the intensive deforestation that this region withstood in pre-industrial China, primarily resulting from firewood collection, charcoal making, construction and land reclamation for farming (Fang and Xie, 1994). Such intensive vegetation destruction may extend further back in time to prehistory (Rosen et al., 2015; Zhuang and Kidder, 2014) owing to the Loess Plateau having been home to the domestication of millet, as well as comprising an economic and political centre during the Bronze Age (Liu and Chen, 2012).

The Guanzhong basin of Shaanxi province, located in the southern end of the Loess Plateau, was home to an early centre of millet farming that was introduced to the region around 6500 cal BP (Stevens et al., 2016). Guanzhong continued to be a core agricultural region throughout the Neolithic (c. 9000–4000 cal BP) and Bronze Age (c. 4000–3200 cal BP) from whence it grew into a significant political centre and home of the capital of the Shang, Western Zhou, Qin, Han and Tang dynasties. As such, it is often considered to be the heartland of Chinese civilisation. The historical records indicate that the basin underwent significant agricultural development, with plots of land being granted to men of rank in the Qin and Han dynasties, who were meant to work them (Barbieri-Low and Yates, 2015). Also, the massive Zheng Guo canal and dam were built by the Qin polity to irrigate an area of about 1800 square kilometres in the northern part of the basin (Will, 1998).

Figure 3 summarises relevant archaeological, palaeoecological and climatic time series data to examine the issue of ecosystem collapse in the prehistory and early history of Guanzhong basin. Both proxies of forest cover, measured here as percentage of tree pollen in the record (panel A, Figure 3), show a sustained decrease in values in the latter half of the Holocene. However, they do not agree in terms of its onset nor its intensity. At the largest scale, namely the whole of the Loess Plateau, data from Ren (2007) show that forest cover peaked around 6000 cal BP then declined substantially over the subsequent four millennia. In contrast, recent pollen-based land-cover modelling (Li et al., 2020) based on data from Tianchi lake, immediately to the east of Guanzhong basin, shows very little change in forest cover until about 2000 cal BP, after which there was a similarly sustained decline. The speleothem $\delta^{18}O$ from Jiuxian Cave in the Qinling mountain range immediately south of Guanzhong basin (panel B) attests to decreasing precipitation in the second half of the Holocene as expected by the weakening of the East Asian Summer Monsoon (EASM). Macro-charcoal (panel C), a proxy for local fire events, indicates some activity around 7000 cal BP, but much more substantial activity from 3200 cal BP, especially from the Qin dynasty onwards. Micro-charcoal (panel C), a proxy for regional fire events, shows low activity throughout the mid Holocene, with a sustained increase, with secular variations, from 4200 cal BP, culminating during the Han dynasty. Archaeological site counts (panel D), a commonly used demographic proxy (French et al., 2021), show increases in human activity from 7000 cal BP onwards, likely sustained by millet farming. However, the most substantial demographic boom occurred during the Western Zhou period, when Guanzhong basin became the centre of the Chinese world, and precisely when the earliest historical records attest to politically decreed deforestation (Elvin, 2004; Fang and Xie, 1994).

The earlier onset of deforestation afforded by the pollen data for the whole of North China (Ren, 2007) temporally tracks the weakening of the EASM as evidenced by the speleothem record. This may be indicative of a pan-regional trend that was more directly affected by climate change than by human activities. On the other hand, the more localised pollen data from Li et al. (2020) shows a significant decline only from the Qin dynasty onwards, contemporaneous with significant fire activity, and coincident with historical evidence that indicates more extensive ecosystem change in this period (Lander, 2021). This point therefore suggests major changes in the prevailing disturbance regime, providing support for Propositions 1, 2, 3 and 4 (Table 1). It is likely that prior to the Qin, farming in the Guanzhong Basin was on a relatively small scale, with families producing only enough to sustain themselves; this did not lead to significant regional ecosystem collapse. However the Qin dynasty brought about significant political and economic changes, involving the taxation of farming families to feed the people and animals who laboured on the empire's ambitious construction projects (Lander, 2021).

The results of this case study highlight challenges in analysing ecosystem collapse in the deep past, owing to limitations in the temporal and spatial resolution of the available data. For example, low spatial resolution of the forest cover proxies makes it difficult to identify episodes of ecosystem collapse that were quickly followed by recovery (Proposition 6). This may have happened after early dynastic collapses, which were routinely followed by periods without centralised political control. This example also highlights the difficulty of establishing causal relationships in prehistory. A further challenge relates to identifying the linkages between proxies of changes in ecosystem extent and condition, such as forest cover, and measures of ecosystem function such as protection from erosion (Proposition 9). Research in different areas of China has suggested that major increases in soil erosion may have been caused by both widespread deforestation and the intensification of agriculture in the middle and late Neolithic (e.g. Rosen et al., 2015; Zhuang and Kidder, 2014). However, further research is required to determine the extent to which land use change was responsible for the changes in soil erosion observed, and its subsequent impacts on human communities.

Emerging issues

These case studies demonstrate the potential value of viewing long-term changes in human ecodynamics through the lens of ecosystem collapse. In each case, ecosystem collapse occurred at least at the local scale as a result of agricultural expansion. Support for propositions drawn from ecological theory illustrates the potential value of these ideas for understanding the processes involved. However, these case studies also demonstrate contrasting demographic responses to ecosystem collapse. While initial human population increases were observed in all case studies, concomitant with an increase in food supply, three of the four cases (Europe, south-west Asia and China) provide evidence of subsequent population declines occurring at least at local scales.

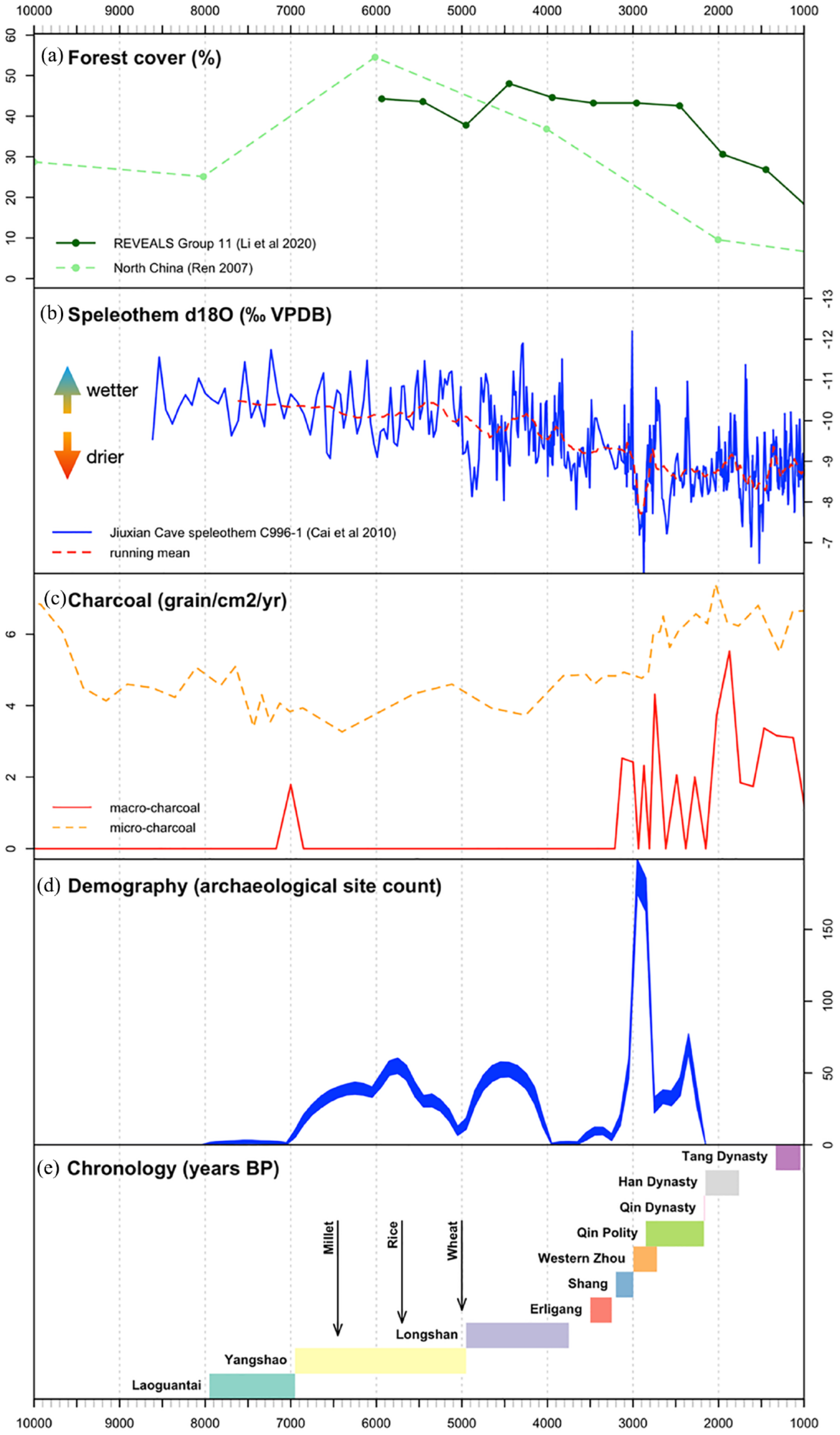

Figure 3. Comparison of palaeoecological (panels a and c), palaeoclimatic (panel b), and archaeological (panels d and e) time series data related to Guanzhong Basin in Shaanxi province of China. Charcoal data (panel c) from Tan et al. (2015). Archaeological site counts (panel d) obtained from data from Hosner et al. (2016) using the aoristic random duration method of Palmisano et al. (2017). All other data sources are indicated in the figure. The vertical arrows in panel E indicate the timing of the introduction of cereals into Guanzhong Basin.

Based on contemporary observations, we suggest that transformations of ecosystems to increase food production in the deep past will have resulted in abrupt declines in the provision of other ecosystem benefits, such as soil formation and quality, nutrient cycling, fresh water, climate regulation, flood protection, wild foods, raw materials, fuel, wild medicines, etc. The potential impacts of these declines on human populations have been little explored, but provide a possible mechanism for some of the demographic changes observed.

On the basis of these case studies, we identify a series of key emerging issues that could usefully provide a focus for future research:

- *Linkage*. Evidence from these case studies demonstrates that ecosystem collapse is often not associated with immediate societal collapse, a finding that is consistent with the broader archaeological literature (Carleton and Collard, 2020). This raises the question of how the social and ecological sub-systems of SES are actually linked, for example through the impact of human actions on provision of multiple ecosystem benefits. Understanding these linkages is crucial for differentiating between external factors that might have influenced the dynamics of the system, such as climate change, from those processes that are intrinsic to the system. This focus of analysis can also help to determine causality in human-environment interactions, which has previously been identified as a research priority (Carleton and Collard, 2020).
- *Feedbacks*. Identifying the feedbacks that can occur between the social and environmental components of SES is of key importance for understanding the mechanisms underlying system dynamics, especially in cases of abrupt change. However, these feedbacks are not well documented or understood, despite their importance for identifying sustainable livelihood strategies for both pre-historic and contemporary societies. We know from contemporary SES that identifying feedbacks, and establishing their contribution to system dynamics, is often difficult (Watson et al., 2021). Obtaining this understanding for SES in the deep past is even more challenging owing to limitations in palaeo datasets, including their temporal and spatial resolution (Carleton and Collard, 2020). Exploration of integrated computational models together with time-series data offer a potential way forward (Silva et al., 2022).
- *Scaling*. In contemporary ecosystems, collapse principally occurs at the local scale (Bergstrom et al., 2021), and the same is likely to have been true in the past. However, ecosystem collapse can also occur at the regional scale. How multiple local-scale collapses may influence the risk of ecosystem collapse at the regional scale remains a key unknown (Newton, 2021b). This is illustrated by the case studies presented above from both Europe and China, which highlight an apparent disconnect between local- and regional-scale collapse; this merits further attention. Analysis of some contemporary ecosystems has identified feedback mechanisms that can result in non-linear responses and potential thresholds or tipping points occurring at larger scales; the same may have been true in the past (Boulton et al., 2022; Newton, 2021a). Scaling effects are also highly relevant to the social element of SES. How causal relationships vary across spatio-temporal scales has been identified as one of the main epistemological challenges relating to research on human-environment interactions (Carleton and Collard, 2020).
- *Recovery*. Both the social and ecological sub-systems of SES can demonstrate recovery after perturbation. A wide variety of ecological recovery mechanisms have been identified, which differ in terms of the spatial and temporal scales over which they operate (Suding and Gross, 2006). Similarly human societies may adapt to environmental change by altering their subsistence practices, moving to different locations, developing new technology, or changing the way they use their landscapes (Carleton and Collard, 2020). The relationships between ecological and social recovery mechanisms and their impacts on flows of ecosystem benefits have been little explored, but are fundamental to understanding properties of SES dynamics such as resilience and sustainability.

Conclusion

Most previous research on long-term human ecodynamics has focused primarily on examining the human component of SES, such as the potential causes of societal collapse or transformation. Here we offer an alternative perspective that examines the impacts of human societies on ecosystems, then considers how these impacts might in turn affect societies by altering flows of ecosystem benefits to people. This perspective draws on recent progress in conservation science, which makes use of a body of theory that has been developed for understanding risks to ecosystems arising from human activities (Newton, 2021a). While recognising that environmental degradation can often be a gradual process, it is now well established that ecosystems can also undergo abrupt change, which can have profound implications for human societies. We suggest that such ecosystem collapse provides a useful lens through which to examine long-term ecodynamics, as it represents a form of perturbation of an SES. How both the social and ecological components of an SES respond to such a perturbation provides insights into how the two sub-systems are linked together, and the mechanisms underlying their respective dynamics.

Most of the world's terrestrial ecosystems have been profoundly altered by human activities that have occurred during the Holocene, especially the use of fire and the development and spread of agriculture (Boivin et al., 2016; Ellis et al., 2021; Mottl et al., 2021; Stephens et al., 2019). Many of these impacts have left enduring legacies that continue to influence contemporary ecosystems (Mottl et al., 2021). As noted by Boivin et al. (2016), millennia of anthropogenic transformations have also created novel ecosystems throughout the world, incorporating domesticates and non-native species. What is less widely appreciated is that such transformations can occur rapidly, especially at the local scale. When persistent, these abrupt transformations – including the creation of novel ecosystems – can be considered as examples of ecosystem collapse (Newton, 2021a). Such collapse will lead to changes in provision of multiple ecosystem benefits to people, with potential impacts on livelihoods.

A range of different frameworks have previously been developed to examine SES dynamics. While some of these consider the social and ecological sub-systems together as an integrated whole (e.g. Cumming and Peterson, 2018), we suggest that the two subsystems should be considered analytically as distinct but reciprocally linked. This reflects the fact that different mechanisms underlie the dynamics of the two sub-systems; they can also display very different trajectories following perturbation. Other frameworks (e.g. see Schlüter et al., 2019) fail to differentiate those human actions that contribute to ecosystem degradation and ultimately collapse, and fail to link these actions to the underlying mechanisms that can lead to ecosystem collapse, as we suggest here. Application of our suggested framework could strengthen understanding of coupled environmental and societal dynamics and associated emergent phenomena such as resilience and sustainability. However, we also recognise that ecosystem collapse is only one of a complex array of interacting factors that can influence societal dynamics, as illustrated by the case studies presented here.

Given its outstanding societal importance, an increased research focus on ecosystem collapse within the historical sciences could help strengthen their relevance to the contemporary world. In particular, future research needs to develop a better understanding of the relationships between climate, ecosystems and humans (Mottl et al., 2021) to ensure the future resilience and sustainability of SES. Research has identified many abrupt changes in ecosystems that occurred during the Holocene, which were often attributable to hydroclimate variability and associated changes in disturbance regimes (Crausbay et al., 2017; Shuman et al., 2019; Williams et al., 2011). Understanding the mechanisms underlying such abrupt responses of ecosystems to past climate change could help inform development of contemporary climate-adaptation strategies (Williams et al., 2011). By incorporating these mechanisms, the analytical framework presented here could support the development of dynamic models that are required to strengthen forecasts of potential climate change impacts on ecosystems and the humans that depend on them (Jackson et al., 2009; Williams et al., 2021). An improved understanding of ecosystem collapse would also support a shift towards managing rates of change in SES, rather than maintenance of historical states. Such a shift is urgently needed, to reduce mismatches among rates of change occurring between climate, ecosystems and societal responses (Williams et al., 2021).

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