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Temporal and sociocultural effects of human colonisation on native biodiversity: filtering and rates of adaptation

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Modern human societies have negatively impacted native species richness and their adaptive capacity on every continent, in clearly contrasting ways. We propose a general model to explain how the sequence, duration and type of colonising society alter native species richness patterns through changes in evolutionary pressures. These changes cause different 'filtering effects' on native species, while simultaneously altering the capacity of surviving species to adapt to further anthropogenic pressures. This framework may better explain the observed native species extinction rates and extirpation legacies following human colonisation events, as well as better predict future patterns of human impact on biodiversity.

Keywords: extinction/extirpation, evolutionary history, human colonisation, native biodiversity, sociocultural niche construction

Colonisation of habitats by modern human societies have radically changed local and regional native species richness and the ecological and evolutionary processes of ecosystems (Koch and Barnosky 2006, Barnosky 2008, Ellis 2015, Malhi et al. 2016). As a hypothesis to explain these changes, we propose that the rates and types of changes in native species richness following modern human colonisation are mediated by the temporal dynamics and types of the coloniser's societies. Specifically, rates of extinction and extirpation following modern human colonisation can be understood as

Synthesis

Human societies have contributed to species extinctions, extirpations, and population declines that have altered ecosystem functioning locally and regionally. Tackling the many management challenges associated with these ecological changes requires a better understanding and incorporation of human history. Our framework links the temporal and sociocultural aspects of human inhabitation events with observed shifts in current biodiversity patterns and their broader ecological consequences. This approach helps to advance both theoretical and applied ecology and evolutionary science, with broad implications for conservation practice in an increasingly human world.

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analogous to habitat filtering processes (Cornwell et al. 2006, Kraft et al. 2015). In this framework, time elapsed since colonisation, the number of times colonised by a different society type and its sociocultural regime at the time of colonisation all play significant roles in shaping the ecological and evolutionary responses to sociocultural filtering processes.

Previous studies have shown a divergence in life history traits through nest predation constraints between regions colonised by humans at different times (Martin and Colbert 1996). Rates of change (e.g. alterations of reproductive strategies) may be more rapid in sites more recently colonised by humans (Cartwright et al. 2014). We propose that these patterns result from two processes; 1) anthropogenic filtering, whereby extinctions of non-adaptive species occur rapidly following colonisation, and 2) adaptation processes occur within species that survive the habitat changes following colonisation. We suggest that these processes can be applied together with well-established biogeographic principles, such as latitude, altitude, habitat size and degree of isolation (McArthur 1972, Helmus et al. 2014), to predict current and future patterns of native species richness and life-history traits, especially with regard to the capacity of species to adapt to changing environments and climate. By incorporating the temporal and sociocultural aspects of human colonisation alongside the classic dimensions of biogeography, it may be possible to develop a more comprehensive framework for understanding biodiversity patterns in an increasingly anthropogenic biosphere. Indeed, previous studies using chronometric resolution have highlighted that large-sized fauna extinction were more related to anthropogenic causes than to a climatic role in Australia (Rule et al. 2012), Patagonia (Villavicencio et al. 2016) and in New Zealand (Holdaway et al. 2001, Trewick and Gibb 2010).

Changes in human societies

In this study, we consider the differing effects of human colonisation on species richness by three major types of human societies: hunter–gatherer, agrarian and industrial, each with profoundly different levels of societal complexity, subsistence regimes, resource use, ecological and material inheritances, and ecosystem engineering practices (Ellis 2015, Table 1). Admittedly archaeological, historical and ethnographic evidence has highlighted a strong correlation between these societies complexities and the land productivity, the resource management, the human population size and its density and the amount of nonhuman energy used per capita (Ellis et al. 2018, Freeman et al. 2020). Hunter–gatherer societies, while still present today represent the earliest forms of human societies (Ellis 2015). These societies generally depend on mobile to moderately sedentary social foraging strategies for subsistence (i.e. on primary and secondary productivity), which maximise the use of seasonally available local or regional food resources Typical patterns of resource exploitations are first by harvesting pressure (i.e. unsustainable hunting and overharvesting) on the most desirable large-sized fauna, then by broadening hunting (Stiner et al. 1999) and foraging strategies across taxa (niche broadening) as well as on flora with the used of wood for fuel or other parts of the plant for their antibacterial, antifungal, anti-inflammatory, antimicrobial or feeding properties (Esteban et al. 2020) and then later by the intentional use of fire to maintain more productive early-successional ecosystems (Hamilton et al. 2007, Ellis 2015, Ellis et al. 2016, Table 1). The practice of this society has acted as a first anthropogenic and unatural force transforming ecological pattern and process across the biosphere through the harvesting and the predation, and then by the burning practices (Braje and Erlandson 2013, Sullivan et al. 2017, Burger and Fristoe 2018), that drove to first natural failure in the ecosystems functioning. These societies have shown the first taxonomic turnover on biodiversity through the direct effect of harvesting pressures (causing translocation, extinction, extirpation, range shifts and, through landscape modification and the use of fire, both intentionally and unintentionally) (Grayson 2001, Barnosky et al. 2004, Koch and Barnosky 2006, Boivin et al. 2016). For example in some region of Chile (Villavicencio et al. 2016) or in Madagascar (Burns et al. 2016), the arrival of hunter–gatherer communities have led to strong decline megafauna and some case sone species extinction due to overhunting (Andersmann et al. 2020) and the burning of human society. These societies generally mediated species introductions, through the intentional introduction of human commensals, species used as hunting aids (e.g. dogs), and the unintentional establishment of species (e.g. rats, mice; Table 1, Weissbrod et al. 2017). This first translocation of species might also have had an important impact on behavioural ecology and evolutionary biology of endemic taxa, like in insular system (e.g. in New Zealand avifauna, Whitwell et al. 2012). More than, the subsistence and habitat-modifying behaviours of this society, depending on the presence or absence of transition with pre-hominins societies, have mediated varying effects on the natural ecosystem as well as their contribution role in biodiversity extinction. The presence of pre-hominins societies and the dietary change observed in some of them via the consumption of animal material, through the combination of hunting and passive or active scavenging, has already started pre-anthropogenic filtering by extirpating some wildlife, due to pre-hominins diet pressure, as observed by Werdelin and Lewis (2013) on eastern Africa carnivore guilds. The pre-hominins–environment interactions through their harvesting strategies could have already mediated ecological changes (Werdelin and Lewis 2013), which would explain the divergent impact on cascading effect on local ecosystem function from hunter–gatherer society in the different ecosystem (e.g. New Zealand versus North America versus Europe), leading to different starting point for modern human-environment filtering.

A transition from hunter–gatherer to early agrarian societies produces even greater alterations of native biodiversity (Table 1). Indeed, the cumulative cultural evolution observed into the hunter–gatherer societies through innovations has allowed pushing back some constraints that previously limited

Table 1. Human sociocultural systems classified by primary subsistence regime, in order of historical emergence (based on Nolan and Lenski 2010 and Ellis 2015) in relation to anthropogenic transformation and their impact on local ecosystems and biodiversity ([a] Kuneš et al. 2008, [b] Grayson 2001, [c] Huston 2005, [d] Smith 2011, [e] Cartwright et al. 2014, [f] Croci et al. 2008, [g] Stockwell et al. 2003, [h] Sullivan et al. 2017).

					Impact on native species				
					Flora		Fauna		
Sociocultural system	Subsistence regime	Technological innovation	Ecological impact	Introduced species	Observed	Potential traits selected by humans	Observed	Potential traits selected by humans	General impact native ecosystems
Hunter–gatherer	Hunting foraging	Land clearing using fire, social hunting, food processing and cooking, projectiles, ceramics	Extensive use of ecosystem resources, resource depression, diet breadth strategy	Dispersion of commensal species (e.g. rat, dog) and consumed species (e.g. seed), consumed species translocation (e.g. kumara).	Reduced abundance of harvested native plants for consumption in located area, decline of megafauna-adapted plant [h]	Light, nitrogen, nutrient rich soil demanding taxa, body size reduction [a, h]	A decline of the large predator to reduce human carnivore conflict	Body size reduction, earlier sexual maturity, reduced antler size [b, h]	Human predation pressure at the local scale, an abundance of higher return prey (i.e. larger) reduced first. The abundance of lower return prey (i.e. smaller) reduced as a secondary effect. Exotic species impact native species via predation pressure on native flora and fauna, or via the dispersion of novel diseases. The decline of megaherbivore due to predation and the use of burning technic drive the shift in vegetation and habitat structure.
Agrarian	Continuous subsistence agriculture, handicrafts	Plough, animal tractions	Strong use of high net primary productivity area for food production, landscape modification to increase prey abundance (clam garden, fish-weirs, diversion dams), released of nutriment in soil.	Dispersion of annual crops, translocation of domesticated species (i.e. herbivores), transplantation of perennial fruit, nut-bearing and root crops species.	Early successional stage plant communities increase, higher ratio of production to respiration, loss of perennial plants, slower growing species decline. Reduction of woody biomass and shift to earlier successional sequence vegetation communities.	Smaller sized, annually reproducing species and higher ratio of production to respiration favoured [c]. Fallow-cycle vegetation community lost of germination dormancy, increase of seed size [d].	Native grazers favoured, reduction in population size of large vertebrates and species diversity.	Grazing herbivores [c], selection of early life reproduction [e].	Mosaic vegetation landscape, native vegetation converted to annual crops, domesticated herbivores substituted for native ones. Dispersion of rare and/or endemic species to marginal habitats (low productive area). Increased animal diversity (species richness) due to translocation.

(Continued)

Table 1. Continued.

Sociocultural system	Subsistence regime	Technological innovation	Ecological impact	Introduced species	Impact on native species				General impact native ecosystems
					Flora		Fauna		
					Observed	Potential traits selected by humans	Observed	Potential traits selected by humans	
Industrial	Commercial, agriculture, manufacturing.	Fossil energy, synthetics, rapid bulk transport, telecommunication.	Intensification in land use (reduced energy availability, high human population density in settlements), colonisation of new land near high NPP (net primary production) land (lakes , rivers, aridity, wetness area) marginal lands due to their transportation requirements, resource extraction increases, urban/ industrial growth, drainage of wet area, flood control.	Introduction of exotic predators, translocation of exotic species to enrich the diversity of the region (i.e. acclimatisation society).	Decline of vegetation with slow growth, invasion by exotic species	Fast growth species, speed of germination, tolerance to metal [g].	Extinction of native vertebrates due to introduction of exotic predator species, decline of native predator and herbivore species remaining in marginal habitats.	Sedentary, omnivorous, long life expectancy, importance parental care [f], pesticide resistance [g].	Switch of biodiversity composition with appearance of introduced species replacing native species but increase of richness.

the geographic and population expansions of these societies and now favoured the emergence of the agrarian society (Ellis et al. 2018). These culturally inherited and socially learned technologies, practices and more productive strategies, led to an increase of human density on the order of 100 times higher than the most abundant period of hunter–gatherer society (Ellis et al. 2018, Freeman et al. 2020). With a change to Agrarian societies came a change in their associated impacts, through their intensive agricultural practices that systematically denuded vegetation from landscapes (e.g. grazing by livestock; Briggs et al. 2006, Mensing et al. 2018) to increase the productivity of specific resources (e.g. horticultural and agricultural practices; Lightfoot et al. 2013, Mensing et al. 2018). Agrarian practices ranged from temporary shifting cultivation that, resembled burning by hunter–gatherers, to the continuous use of land by annual cultivation and the use of irrigation, causing permanent habitat loss and fragmentation (Ellis 2015, Boivin et al. 2016, Mensing et al. 2018). Further impacts of agrarian societies include the introduction of domesticates, diseases, ruderals and feral species (Table 1), as well as additional pressures from larger, denser and more rapidly growing human populations (Grayson 2001, Koch and Barnosky 2006, Ellis 2015, Boivin et al. 2016). The permanent settlements associated with these societies, has also shifted the hunting pressure to a more localized area, while also increasing the rate of exotic species introductions (e.g. weeds; Boivin et al. 2016, Table 1), ultimately leading to a loss of biodiversity at the local scale. Thus, the change in patterns of hunting pressure has caused a widening set of pressure on local biodiversity such as on the carnivore community to avoid human–carnivore conflict (i.e. competition on wild prey, predation on domestic livestock...; Galetti et al. 2018) or by the selection and protection of 'noble game' species (e.g. deer, wild boar in Europe; Ashby 2002) for recreational hunting (Crees et al. 2019). This new human sociocultural niche construction through its different inheritance (e.g. cultural, material, ecological…) and its increasing population density has helped the cultural evolution of the human species to outpace the rate of biological evolution, putting humans as the major ecosystems engineer of the transformation causing the terrestrial biosphere (Ellis 2015, Mensing et al. 2018) and significant impacts on global biodiversity (Sullivan et al. 2017). This new societal evolution represents the second anthropogenic force to transform ecological patterns and processes across the biosphere, through the intensification and the sophistication of ecosystem engineering. This has occurred via domestication and agriculture practices, by shaping new trajectories of environmental change and new ecological disturbances, and so by exerting new evolutionary pressures for biodiversity. These new transformations of ecological patterns and process, through the reduction and fragmentation of natural habitats and the development of a new anthropogenic habitat 'cropland', has caused a substantial reduction of native biodiversity, which were often replaced by a fewer number of domesticated species.

Most recently, the industrial revolution and the massive food requirements of growing human populations have led to an increase of agricultural productivity for commercial purposes, by the use of toxic agrichemicals, excess nutrients, mechanisation, loss of remaining habitat fragments, increased drainage of land, intensive grassland management and the construction of transportation networks and movement of materials and biota across the planet (Ellis 2015, Boivin et al. 2016, Table 1). Modern agricultural techniques have therefore resulted in a further increase of land-use intensity the development of less suitable areas for agriculture (Benton et al. 2003), and the development of non-agricultural land use (i.e. urbanization; Ramalho and Hobbs 2012). This new human sociocultural niche construction sustained the third anthropogenic force that transformed ecological patterns and processes across the biosphere. The new 'industrial' phase resulted from the overharvesting of nonhuman energy (e.g. fossil biomass fuels, abiotic resources of energy) to support human populations and their subsistence regimes. This drove the decline in population of previously unaffected forms of biodiversity, both locally and regionally, caused by the creation of novel selective pressures. Furthermore, the sociocultural evolution that occurred during the industrial societies also resulted in new combinations of constraints, most notably via the appearance of new philosophical concepts, such as habitat alterations for the sake of 'improvements' or 'aesthetics' of the landscape. For example, these ideas led to the creation of the acclimatisation movement (Wallace 1911, Osborne 2000) that translocated familiar biodiversity into unfamiliar environments colonised by settlers (Carruthers et al. 2011, Boivin et al. 2016). This was done to improve the productivity of the land for agriculture, hunting or for nostalgic reasons (Osborne 2000). Thus, the appearance of this concept of acclimatisation was characterised at a local scale by an increase in species richness but was often detrimental to native ecological inheritance and its biodiversity. This effect was much greater on island ecosystems with species extinctions occurring after the introduction of exotic species at the start of each new sociocultural stage (Wood et al. 2017). Most recently, this cultural evolution has also led to the creation of game reserves and wildlife sanctuaries to improve survival of species and, maintaining and rationalising future hunting opportunity (Jepson and Whittaker 2002).

Change in native biodiversity communities following filtering and adaptations

Throughout each of these sociocultural regimes, human-induced habitat changes, such as altered land use, introduction of exotic species and exploitation of native species (Table 1), have acted as a 'filter' that some native species will pass through or persist, and others do not (Kraft et al. 2015, Boivin et al. 2016, Andermann et al. 2020), leading to associated extinctions and extirpations (Braje and Erlandson 2013). The number of surviving species after these filtering periods will be the result of three factors: 1) the numbers of species initially present (biogeographic principles), 2) the adaptive capacities of native species to cope and persist with altered environments and climate change, which will be determined

by their species-specific traits (Cornwell et al. 2006) and 3) the response of human society to biodiversity decline (Lepofsky and Caldwell 2013, Lightfoot et al. 2013, Welch et al. 2013). So, following each filtering period, co-existing species sharing a trait or combination of traits, which allowed them to cope with anthropogenic change, tended to have a higher probability of survival; a process termed 'inheritance ecology' (Kraft et al. 2015). Thus, as human societies and their associated habitat alterations change through time, species with suitable life history strategies will tend to be selected and survive (Fig. 1). Consequently, the current native species richness of an ecosystem and its community structure are the product of initial regional species richness mediated by a combination of phylogenetically conserved and convergent traits that are adaptive in the face of anthropogenic pressures (Pavoine and Bonsall 2011, Andermann et al. 2020).

The adaptive capacity of a species in responding to dynamic anthropogenic environments depends on life history and other complex genetic traits (Helm et al. 2009). Natural selection for life history and other traits under earlier environmental conditions (i.e. initial human arrival), therefore, shape evolutionary responses to later environmental changes (Sih et al. 2011). Species face three main outcomes in responding to rapid environmental change: 1) survival through adaptive traits already selected through evolutionary history without further evolutionary change, 2) survival without an evolutionary history of selection for adaptive traits or phenotypic plasticity or 3) extirpation or extinction in the absence of adaptive traits or phenotypic plasticity (Hendry et al. 2011, Sih et al. 2011). Similar adaptive patterns have been observed in environments undergoing urbanization and are categorised as exploiter, adapter and avoider (Blair 1996). Thus, the evolutionary past shapes the persistence of native species in rapidly changing anthropogenic habitats (Pavoine and Bonsall 2011, Essl et al. 2015a, Figueiredo et al. 2019).

Different types of societies act as different filters for native biodiversity and species traits, acting first to determine whether species go extinct or persist, and acting then on surviving species through extended periods of selection and adaptation within anthropogenic environments (Thompson et al. 2019), as observed on Mauritius kestrel in Madagascar (Cartwright et al. 2014). As the scale of societies has increased, so has human capacity for ecosystem engineering, such that anthropogenic filtering of biodiversity has changed substantially over human history (e.g.

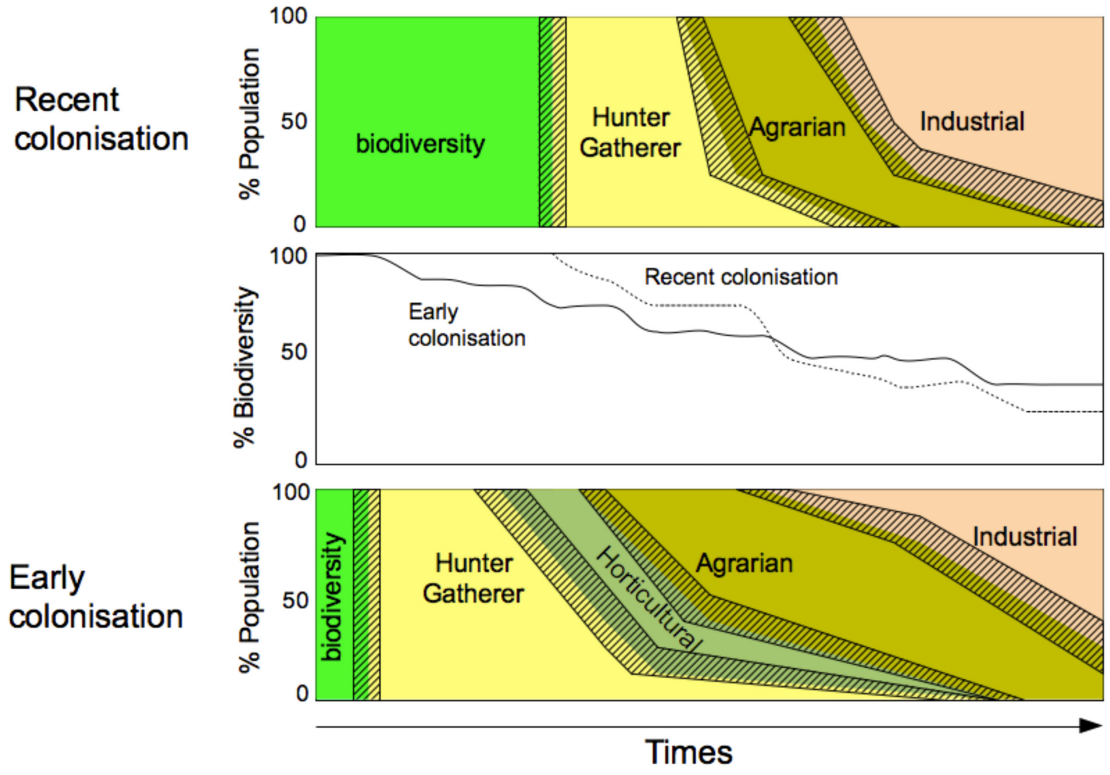

Figure 1. A stylised depiction illustrating differing temporal impacts of human colonisation patterns on native species richness and their evolutionary response under two colonisation patterns (early and recent) using three major colonisation periods of human sociocultural system: 1) hunter–gatherers, 2) agrarian societies and 3) industrial societies. Hatched zones represent filtering events during the transition period between sociocultural regimes. Extinction events may occur because of filtering during transition periods or failing to adapt within each sociocultural niche. Shorter transition periods and shorter duration of each cultural development stage may result in more rapid extinction or extirpation rates of native species.

Box 1. Case study

Our planet has experienced a large mass extinction event caused by human activities over millennia through human interaction (e.g. hunting, harvesting) or transformation (e.g. human niche constructing activities like cleared lands, biotic exchange, erosion). Thus this model has been used in three different contexts of selective pressure from behaviourally modern human, 1) Europe and Africa, which had the earliest selective pressures from humans (> 45 000 years before present [YBP]; Fu et al. 2014, Supporting information), 2) North America (~10 000 YBP; Bourgeon et al. 2017, Supporting information) and 3) New Zealand, which observed a later selective pressure from humans (~737 YBP; Wilmshurst et al. 2008, Supporting information). The ultimate goal is to identify divergence between the change of human societies and their associated habitat alterations are affiliated to reduction of native large-sized fauna richness.

In these three contexts, similar process of sociocultural niche construction have been observed, also with similar sequences of changes sociocultural systems (i.e. hunter–gatherer, agrarian, industrial societies), but with different durations and overlaps between each type of system (Fig. 2). Thus countries more recently colonised by humans have experienced shorter transitions times between sociocultural systems that could help explain the longer temporal delays in biodiversity responses to society change. The proportion of large-sized fauna species that went extinct following colonisation of hunter gatherer societies (Fig. 2) in Europe (0.8% biodiversity reduction) and Africa (8.8%) were more fewer than those in North America (30.6%) and New Zealand (55.9%). Humans in Europe and Africa became established over a much longer period and had less impact on local large-sized fauna extinctions, a pattern that is clearly contrasted by North America and New Zealand. However, such extinction rates cannot fully be explained by human impacts alone, as other effects such as environmental impacts, either working alone or in tandem with human impacts can contribute to extinction or extirpation events. Similar results have also been observed during the later sociocultural niche construction during the onset of industrial societies (Fig. 2), which are more characteristic of the Anthropocene period. Indeed, Europe (13.9%) and Africa (8.8%) had a lower extinction rate during the industrial period and the Anthropocene period than North America (18.7%) and New Zealand (25.0%) where extinction was more pronounced. The time-lagged between the onsets of a news human sociocultural system and the subsequent extinction events appears to vary with the duration of human association. In locations with longer periods of human association, the extinction rates of native biodiversity was lower (Fig. 2 for European and Africa) following transitions between sociocultural systems, likely due to longer periods for evolutionary change to occur between transitions. However, in New Zealand, one of the last locations to be colonised by humans with particularly rapid transitions between sociocultural systems, the native community of large-sized fauna has undertaken a faster magnitude of extinction. So, the transition period between human sociocultural systems combined with climatic change may favour an evolutionary responses of biodiversity to anthropogenic impacts (i.e. past experience with humans provides the evolutionary history that could shape how biodiversity responds to human impacts; Sih et al. 2011).

The importance of temporal dynamics in ecology has been well recognised. Our approach highlights the importance of temporal effect of human societies of the study of human impacts on biodiversity and landscape.

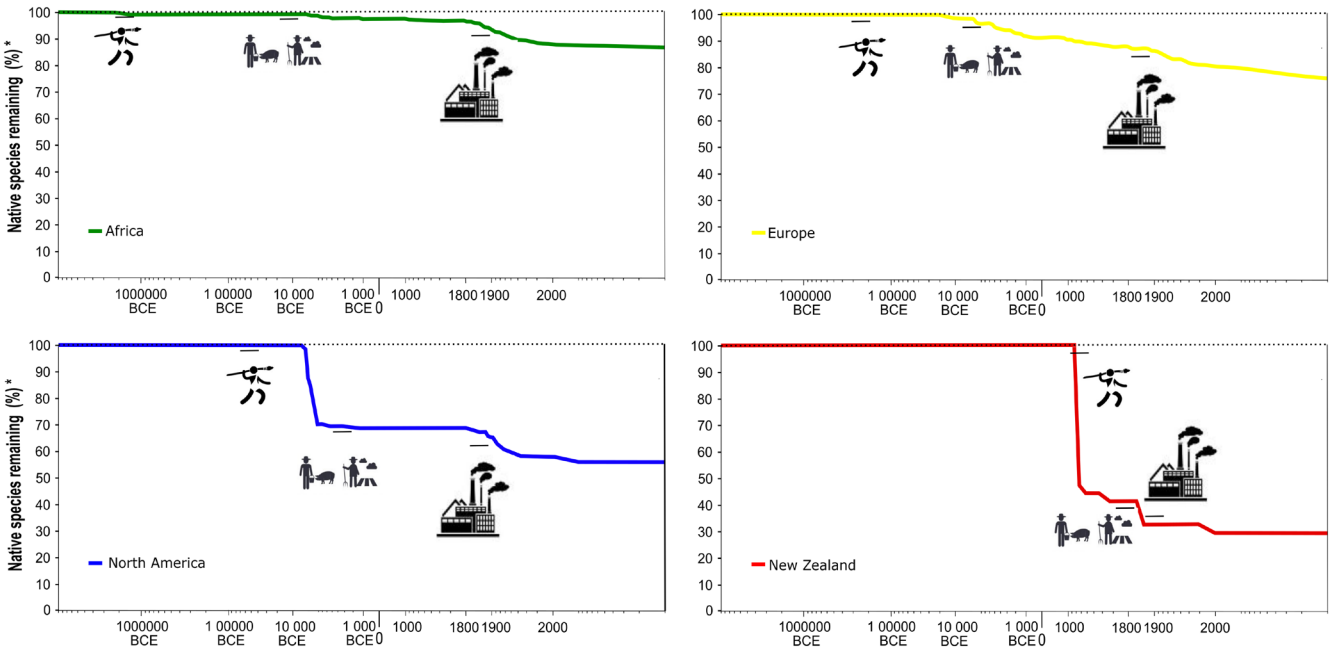

Figure 2. Long-term global changes based on the percentage of pre-human anthropocene large-sized fauna (mammal and avifauna weighing > 0.7 kg, Dirzo et al. 2014) that went extinct as a function of estimated times of major categories of human sociocultural systems in Africa (green), Europe (yellow), North America (blue) and New Zealand (red) (supplementary form for methodology). The x-axis is a logarithmic scale (year), trend-lines shows temporal changes of extant large-sized fauna species for each location, and the onset of human population exhibiting major categories of sociocultural systems are indicated by symbols.

Table 2. Potential applications and additional considerations following our framework.

Research fields	Suggested applications	Additional consideration (limitation, alternative hypothesis, other factors)
Evolution	– Understanding of how human society affects species adaptation rate. – Add new understanding to the evolution of genetic response and phenotype variation in biodiversity. – Understand the ability of species or individuals to cope with anthropogenic habitats. – Develop conceptual framework to explain how past human history influences the evolution cue-responses relationships between organisms and environments.	– Lack of available data on early human colonisation history. – Lack of understanding of the effect of human population growth and size on biodiversity. – Lack of knowledge about interactions of multiple stressor interactions (e.g. climate change, invasive species and habitat clearance).
Conservation	– Probability of extinction or extirpation of native species. – Aid in the understanding of the causes of species population declines. – Further understanding of the factors that lead to the establishment of invasive species.	– Current rate of habitat clearance. – Population size / propagule pressure of invasive species. – Rate of invasive species introduction. – Vulnerability of native species (e.g. island species). – Lack of inclusion of interdisciplinary approaches.
Ecology	– Add to biogeographical parameter to help to refine the process of species extinction. – Understand biodiversity dynamic and response to novel cues. – Understand behavioural response flexibility of species to anthropogenic habitats. – Understand the behavioural response to ecological change.	– Uncertainty about the effect of climate change. – Habitat loss and fragmentation. – Introduction of novel enemies (e.g. diseases, predator or parasites). – Lack of knowledge about interaction of multiple stressors. – Problem of interpretation due to complexity of biodiversity response and individual potential adaptations.
Anthroecology	– Understand human-induced ecological pattern changes and their influence on the complexities of socioecological systems. – Understand the dynamic interplay between human society and ecological systems. – Aid in understanding the evolution of the anthropogenic global-warming system and its effect on biodiversity. – Understand the relation between human sociocultural systems transitions, landscape alteration and their long-term impact.	– Required the time depth accessible on the area on human societies. – Lack of knowledge of major anthropogenic roles in shaping biodiversity in each societies. – More multidisciplinary research required with ecologists and archaeologists.

shift of ungulate extinction wave in the Southern Levant, Tsahar et al. 2009), creating a cascading effect of different ecological constraints acting to filter the biological traits of persisting native species (Essl et al. 2015a). Mensing et al. (2018) research have highlighted that the modern landscape shape of central Italy resulted from the legacies from multiple political regimes of forest ecosystem management. Each political regime or society have display different management of the forest ecosystem, through notably the use and selection of specific tree taxa, that drove in the persistence across the regime to the appearance of new forest type and led as a result of the subsequent regimes to the current forest ecosystem shape (e.g. soft hardwoods were favour by Lombard's society, Oaks tree was favour by Carolingian's society for pig production, Mensing et al. 2018).

Native species richness within continents like Africa, Asia and Europe received the earliest selective pressure from behaviourally modern humans (Box 1). The earliest anthropogenic filtering processes caused the extinction of many species, in particular large-sized species that were hunted to extinction (with some exceptions like Africa), with cascading consequences across entire ecosystems (Grayson 2001, Barnosky et al. 2004, Barnosky 2008, Ellis 2015, Boivin et al. 2016). This was followed by the first adaptive responses to anthropogenic environmental changes and pressures. For example, mollusc populations of Cape turban shell *Turbo sarmaticus* in South Africa (Klein and Steele 2013, Sullivan et al. 2017) declined in size and altered age structure due to harvesting pressure from prehistoric humans (Grayson 2001, Boivin et al. 2016, Sullivan et al. 2017). A similar evolutionary pattern was observed in other species of molluscs in Italy (Stiner et al. 1999) as well as in north America (Erlandson et al. 2011). A comparable evolutionary response have also been reported in other terrestrial vertebrates, like the spur-thighed tortoises, *Testudo graeca* where humeral shaft diameter has decreased, which is a proxy for decreased body size (Stiner et al. 1999). With agrarian and industrial societies, anthropogenic filtering pressures continue to increase and expand, driving continuing species extirpation and extinction, community shifts and increasing the rates, intensity and extent of anthropogenic ecological changes. Archaeological studies in Chile (Villavicencio et al. 2016) and in Madagascar (Crowley et al. 2016) have shown evidence that the settlement and the shift from a subsistence strategy to an agrarian regime, notably with associated land-use change, accelerated the loss of biodiversity (Supporting information). The amount of time elapsed between major changes in society type also moderate the severity of filtering effects, by increasing or decreasing the time available for species to adapt to dynamic anthropogenic habitats. At the

time of first colonisation of native habitats, different types of human societies present different degrees of filtering (Balée 1998, O'Connell and Allen 2015), with larger scale societies (agrarian, industrial) tending to induce more rapid rates of environmental change and more extreme filtering than smaller scale societies (e.g. hunter–gatherer; Box 1).

Native species in African and European regions experienced the longest and most gradual forms of filtering pressures by preindustrial societies. This enabled traits adaptive to dynamic anthropogenic environments to become established and lessened rates of extinction both during societal regime transitions and during the period between the transitions (Box 1) as found by previous studies (Andersmann et al. 2020, Faurby et al. 2020). In North America, hunter–gatherer societies arrived much later than in Europe and Africa, driving a rapid phase of extinction at the time of first colonisation (Martin 1973, 1984, Andersmann et al. 2020, Faurby et al. 2020). This rapid filtering effect is even more pronounced in the very recent first arrival of hunter–gatherers to New Zealand and their commensal introduced species (e.g. dogs, rats) (Barnosky et al. 2004, Barnosky 2008, Fig. 2).

Species exposed to shorter periods between anthropogenic filtering events (Fig. 1) would be expected to experience higher risks of extinction when faced with a subsequent filtering event, owing to inadequate prior evolutionary shifts in adaptive traits (Essl et al. 2015a, b, Figueiredo et al. 2019). This may explain why North America's more recent establishment of larger scale agrarian and industrial societies is related to higher extinction rates than in Europe, as native species have had less time to adapt to anthropogenic environmental changes in the Americas (Fig. 2, Box 1).

To fully understand the long-term prospects for native species' persistence and adaptation in the face of anthropogenic pressures, rigorous comparative investigations of long-term anthropogenic filtering that focuses on the 1) timing and types of societal colonisations, 2) sociocultural regime shifts (Kinzig et al. 2006) and 3) the society response to biodiversity decline (Lepofsky and Caldwell 2013, Lightfoot et al. 2013, Welch et al. 2013), may serve as critical observational laboratories (Cartwright et al. 2014). While it seems fairly well established that more recent colonisations are associated with higher rates of native biodiversity loss, the causes of this are not fully understood, nor are they necessarily generalisable to other species. Nevertheless, it is clear that failure to consider the effects of societal legacies and sociocultural transitions on native species loss and the presence of adaptations that might prevent future losses can have major consequences across history (Ramalho and Hobbs 2012).

We propose a framework to outline the importance to understand the sociocultural legacy role in shaping current biodiversity patterns. Indeed, we argue that current biodiversity and ecosystems are the outcomes of human sociocultural filtering and transitions and not only result from ecological or climatological processes. By integrating this framework, we hope to contribute to our understanding of biodiversity evolution patterns overtimes, as well as the context in which sociocultural filtering and transitions act on species. By presenting an integrated framework for investigating the processes of native species extinction and adaptation in response to anthropogenic filtering will further advance our understanding of native species' adaptations to anthropogenic environments (see potential applications and additional considerations, Table 2).

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Author contributions

Christophe Amiot: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Writing – original draft (lead); Writing – review and editing (lead). **Weihong Ji**: Formal analysis (supporting); Funding acquisition (lead); Project administration (supporting); Supervision (supporting); Visualization (supporting); Writing – original draft (supporting). **Erle C. Ellis**: Visualization (supporting); Writing – original draft (supporting). **Michael G. Anderson**: Supervision (lead); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.xwdbrv1d2> (Amiot et al. 2021).

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