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## ► To cite this version:

Christophe Amiot, Weihong Ji, Erle Ellis, Michael Anderson. Temporal and sociocultural effects of human colonisation on native biodiversity: filtering and rates of adaptation. *Oikos*, 2021, 130 (7), pp.1035-1045. 10.1111/oik.07615 . hal-03629381

**HAL Id: hal-03629381**

**<https://hal.science/hal-03629381>**

Submitted on 4 Apr 2022

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# Temporal and Sociocultural Effects of Human Colonisation on Native Biodiversity: Filtering and Rates of Adaptation

Running-title: human colonisation effects on native biodiversity

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Formatted for “forum” paper

25

26 **Acknowledgments**

27 We thank Andrew E. Hollis, James Dale, Dianne Brunton and the anonymous referees for their  
28 valuable comments and discussion on the paper. This project was supported by the Institute of  
29 Natural and Mathematical Sciences of Massey University.

30

31

32 **ABSTRACT**

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

41

42 **Keywords:** Human colonisation; Extinction / Extirpation; Native biodiversity; Evolutionary  
43 history; Sociocultural niche construction

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## 49 MAIN TEXT

50 Colonisation of habitats by modern human societies, have radically changed local and regional  
51 native species richness and the ecological and evolutionary processes of ecosystems (Koch and  
52 Barnosky 2006, Barnosky 2008, Ellis 2015, Malhi et al. 2016). As a hypothesis to explain these  
53 changes, we propose that the rates and types of changes in native species richness following modern  
54 human colonisation are mediated by the temporal dynamics and types of the coloniser's societies.  
55 Specifically, rates of extinction and extirpation following modern human colonisation can be  
56 understood as analogous to habitat filtering processes (Cornwell et al. 2006, Kraft et al. 2015). In  
57 this framework, time elapsed since colonisation, the number of times colonised by a different  
58 society type and its sociocultural regime at the time of colonisation all play significant roles in  
59 shaping the ecological and evolutionary responses to sociocultural filtering processes.

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

75 in Australia (Rule et al. 2012), Patagonia (Villavicencio et al. 2016), and in New Zealand  
76 (Holdaway et al. 2001, Trewick and Gibb 2010).

77

## 78 **Changes in human societies**

79 In this study, we consider the differing effects of human colonisation on species richness by three  
80 major types of human societies: hunter-gatherer, agrarian and industrial, each with profoundly  
81 different levels of societal complexity, subsistence regimes, resource use, ecological and material  
82 inheritances, and ecosystem engineering practices (Ellis 2015, Table 1). Admittedly archaeological,  
83 historical and ethnographic evidence has highlighted a strong correlation between these societies'  
84 complexities and the land productivity, the resource management, the human population size and its  
85 density, and the amount of nonhuman energy used per capita (Ellis et al; 2018, Freeman et al. 2020).  
86 Hunter-gatherer societies, while still present today represent the earliest forms of modern human  
87 societies (Ellis 2015). These societies generally depend on mobile to moderately sedentary social  
88 foraging strategies for subsistence (i.e. on primary and secondary productivity), which maximise the  
89 use of seasonally available local or regional food resources Typical patterns of resource  
90 exploitations are first by harvesting pressure (i.e. unsustainable hunting and overharvesting) on the  
91 most desirable large-sized fauna, then by broadening hunting (Stiner et al. 1999) and foraging  
92 strategies across taxa (niche broadening) as well as on flora with the used of wood for fuel or other  
93 parts of the plant for their antibacterial, antifungal, anti-inflammatory, antimicrobial or feeding  
94 properties (Esteban et al. 2020) and then later by the intentional use of fire to maintain more  
95 productive early- successional ecosystems (Hamilton et al. 2007, Ellis 2015, Ellis et al. 2016; Table  
96 1). The practice of this society has acted as a first anthropogenic and unnatural force transforming  
97 ecological pattern and process across the biosphere through the harvesting and the predation, and  
98 then by the burning practices (Braje and Erlandson 2013, Sullivan et al. 2017, Burger and Fristoe  
99 2018), that drove to first natural failure in the ecosystems functioning. These societies have shown  
100 the first major taxonomic turnover on biodiversity through the direct effect of harvesting pressures,

101 causing translocation, extinction, extirpation, range shifts and, through landscape modification and  
102 the use of fire, both intentionally and unintentionally (Grayson 2001, Barnosky et al. 2004, Koch  
103 and Barnosky 2006, Boivin et al. 2016). For example in some region of Chile ( Villavicencio et al.  
104 2015) or in Madagascar (Burns et al 2016), the arrival of hunter-gatherer communities have led to  
105 strong decline megafauna and some case some species extinction due to overhunting (see also  
106 Andermann et al. 2020) and the burning of human society. These societies generally mediated  
107 species introductions, through the intentional introduction of human commensals, species used as  
108 hunting aids (e.g., dogs), and the unintentional establishment of species (e.g., rats, mice; see table 1;  
109 Weissbrod et al. 2017). This first translocation of species might also have had an important impact  
110 on behavioural ecology and evolutionary biology of endemic taxa, like in insular system (e.g. in  
111 New Zealand avifauna, Whitwell et al. 2012). More than, the subsistence and habitat-modifying  
112 behaviours of this society, depending on the presence or absence of transition with pre-hominins  
113 societies, have mediated varying effects on the natural ecosystem as well as their contribution role  
114 in biodiversity extinction. The presence of Pre-hominins societies and the dietary change observed  
115 in some of them via the consumption of animal material, through the combination of hunting and  
116 passive or active scavenging, has already started pre-anthropogenic filtering by extirpating some  
117 wildlife, due to Pre-hominins diet pressure, as observed by Werdelin and Lewis (2013) on eastern  
118 Africa carnivore guilds. The pre-hominins-environment interactions through their harvesting  
119 strategies could have already mediated ecological changes (e.g. Werdelin and Lewis 2013), which  
120 would explain the divergent impact on cascading effect on local ecosystem function from Hunter-  
121 gatherer society in the different ecosystem (e.g. New Zealand vs. North America vs. Europe),  
122 leading to different starting points for modern human-environment filtering.

123 A transition from hunter-gatherer to early agrarian societies produces even greater  
124 alterations of native biodiversity (Table 1). Indeed, the cumulative cultural evolution observed into  
125 the hunter-gatherer societies through innovations has allowed pushing back some constraints that  
126 previously limited the geographic and population expansions of these societies and now favoured

127 the emergence of the agrarian society (Ellis et al. 2018). These culturally inherited and socially  
128 learned technologies, practices, and more productive strategies, led to an increase of human density  
129 on the order of 100 times higher than the most abundant period of hunter-gatherer society (Ellis et  
130 al. 2018, Freeman et al. 2020). With a change to Agrarian societies came a change in their  
131 associated impacts, through their intensive agricultural practices that systematically denuded  
132 vegetation from landscapes (e.g., grazing by livestock; Brigg et al. 2006) to increase the  
133 productivity of specific resources (e.g., horticultural and agricultural practices; Lightfoot et al.  
134 2013). Agrarian practices ranged from temporary shifting cultivation that , resembled burning by  
135 hunter-gatherers, to the continuous use of land by annual cultivation and the use of irrigation,  
136 causing permanent habitat loss and fragmentation (Ellis 2015, Boivin et al. 2016). Further impacts  
137 of agrarian societies include the introduction of domesticates, diseases, ruderals, and feral species  
138 (table 1), as well as additional pressures from larger, denser, and more rapidly growing human  
139 populations(Grayson 2001, Koch and Barnosky 2006, Ellis 2015, Boivin et al. 2016). The  
140 permanent settlements associated with these societies, has also shifted the hunting pressure to a  
141 more localized area, while also increasing the rate of exotic species introductions (e.g., weeds;  
142 Boivin et al. 2016; Table 1), ultimately leading to a loss of biodiversity at the local scale. Thus, the  
143 change in patterns of hunting pressure has caused a widening set of pressure on local biodiversity  
144 such as on the carnivore community to avoid human-carnivore conflict (i.e. competition on wild  
145 prey, predation on domestic livestock...; Galetti et al. 2018) or by the selection and protection of  
146 'noble game' species (e.g. deer, wild boar in Europe; Ashby 2002) for recreational hunting (Crees et  
147 al. 2019). This new human sociocultural niche construction through its different inheritance (e.g.,  
148 cultural, material, ecological ...) and its increasing population density has helped the cultural  
149 evolution of the human species to outpace the rate of biological evolution, putting humans as the  
150 major ecosystems engineer of the transformation causing the terrestrial biosphere (Ellis 2015) and  
151 significant impacts on global biodiversity (see Sullivan et al. 2017). This new societal evolution  
152 represents the second anthropogenic force to transform ecological patterns and processes across the



153 biosphere, through the intensification and the sophistication of ecosystem engineering. This has  
154 occurred via domestication and agriculture practices, by shaping new trajectories of environmental  
155 change and new ecological disturbances, and so by exerting new evolutionary pressures for  
156 biodiversity. These new transformations of ecological patterns and process, through the reduction  
157 and fragmentation of natural habitats and the development of a new anthropogenic habitat  
158 “cropland”, has caused a substantial reduction of native biodiversity, which were often replaced by  
159 a fewer number of domesticated species.

160         Most recently, the industrial revolution and the massive food requirements of growing  
161 human populations have led to an increase of agricultural productivity for commercial purposes, by  
162 the use of toxic agrichemicals, excess nutrients, mechanisation, loss of remaining habitat fragments,  
163 increased drainage of land, intensive grassland management, and the construction of transportation  
164 networks and movement of materials and biota across the planet (Ellis 2015, Boivin et al. 2016;  
165 Table 1). Modern agricultural techniques have therefore resulted in a further increase of land-use  
166 intensity the development of less suitable areas for agriculture (Benton et al. 2003), and the  
167 development of non-agricultural land use (i.e., urbanization; Ramalho and Hobbs 2012). This new  
168 Human sociocultural niche construction sustained the third anthropogenic force that transformed  
169 ecological patterns and processes across the biosphere. The new “industrial” phase resulted from the  
170 overharvesting of nonhuman energy (e.g. fossil biomass fuels, abiotic resources of energy) to  
171 support human populations and their subsistence regimes. This drove the decline in population of  
172 previously unaffected forms of biodiversity, both locally and regionally, caused by the creation of  
173 novel selective pressures. Furthermore, the sociocultural evolution that occurred during the  
174 industrial societies also resulted in new combinations of constraints, most notably via the  
175 appearance of new philosophical concepts, such as habitat alterations for the sake of  
176 ‘improvements’ or ‘aesthetics’ of the landscape. For example, these ideas led to the creation of the  
177 acclimatisation movement (Wallace 1911, Osborne 2000) that translocated familiar biodiversity into  
178 unfamiliar environments colonised by settlers (Carruthers et al. 2011, Boivin et al. 2016). This was

179 done to improve the productivity of the land for agriculture, hunting, or for nostalgic reasons  
180 (Osborne 2000). Thus, the appearance of this concept of acclimatisation was characterised at a local  
181 scale by an increase in species richness but was often detrimental to native ecological inheritance  
182 and its biodiversity. This effect was much greater on island ecosystems with species extinctions  
183 occurring after the introduction of exotic species at the start of each new sociocultural stage (Wood  
184 et al. 2017). Most recently, this cultural evolution has also led to the creation of game reserves and  
185 wildlife sanctuaries to improve survival of species and, maintaining and rationalising future hunting  
186 opportunity (Jepson and Whittaker 2002).

187

### 188 **Change in native biodiversity communities following filtering and adaptations**

189 Throughout each of these sociocultural regimes, human-induced habitat changes, such as  
190 altered land use, introduction of exotic species and exploitation of native species (Table 1), have  
191 acted as a ‘filter’ that some native species will pass through or persist, and others do not (Kraft et al.  
192 2015, Boivin et al. 2016, Andersmann et al. 2020), leading to associated extinctions and extirpations  
193 (Braje and Erlandson 2013). The number of surviving species after these filtering periods will be  
194 the result of three factors: 1) the numbers of species initially present (biogeographic principles), 2)  
195 the adaptive capacities of native species to cope and persist with altered environments and climate  
196 change, which will be determined by their species-specific traits (Cornwell et al. 2006), and 3) the  
197 response of human society to biodiversity decline (Welch et al. 2013, Lightfoot et al. 2013,  
198 Lepofsky and Caldwell 2013). So, following each filtering period, co-existing species sharing a trait  
199 or combination of traits, which allowed them to cope with anthropogenic change, tended to have a  
200 higher probability of survival; a process termed ‘inheritance ecology’ (Kraft et al. 2015). Thus, as  
201 human societies and their associated habitat alterations change through time, species with suitable  
202 life history strategies will tend to be selected and survive (Figure 1). Consequently, the current  
203 native species richness of an ecosystem and its community structure are the product of initial  
204 regional species richness mediated by a combination of phylogenetically conserved and convergent

205 traits that are adaptive in the face of anthropogenic pressures (Pavoine and Bonsall 2011,  
206 Andersmann et al. 2020).

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

219         Different types of societies act as different filters for native biodiversity and species traits,  
220 acting first to determine whether species go extinct or persist, and acting then on surviving species  
221 through extended periods of selection and adaptation within anthropogenic environments  
222 (Thompson et al. 2019). As the scale of societies has increased, so has human capacity for  
223 ecosystem engineering, such that anthropogenic filtering of biodiversity has changed substantially  
224 over human history, creating a cascading effect of different ecological constraints acting to filter the  
225 biological traits of persisting native species (Essl et al. 2015a). Mensing and Colleagues (2018)  
226 research have highlighted that the modern landscape shape of central Italy resulted from the  
227 legacies from multiple political regimes of forest ecosystem management. Each political regime or  
228 society have display different management of the forest ecosystem, through notably the use and  
229 selection of specific tree taxa, that drove in the persistence across the regime to the appearance of  
230 new forest type and led as a result of the subsequent regimes to the current forest ecosystem shape

231 (e.g. soft hardwoods were favour by Lombard's society, Oaks tree was favour by Carolingian's  
232 society for pig production, see Mensing et al. 2018)  
233

234 Native species richness within continents like Africa, Asia and Europe received the earliest selective  
235 pressure from behaviourally modern humans (Box 1). The earliest anthropogenic filtering processes  
236 caused the extinction of many species, in particular large-sized species that were hunted to  
237 extinction (with some exceptions like Africa), with cascading consequences across entire  
238 ecosystems (Grayson 2001, Barnosky et al. 2004, Barnosky 2008, Ellis 2015, Boivin et al. 2016).  
239 This was followed by the first adaptive responses to anthropogenic environmental changes and  
240 pressures. For example, mollusc populations of Cape turban shell *Turbo sarmaticus* in South Africa  
241 (Klein and Steele 2013, Sullivan et al. 2018) declined in size and altered age structure due to  
242 harvesting pressure from prehistoric humans (Grayson 2001, Boivin et al. 2016, Sullivan et al.  
243 2017). A similar evolutionary pattern was observed in other species of molluscs in Italy (Stiner et al.  
244 1999) as well as in north America (Erlandson et al. 2011). A comparable evolutionary response have  
245 also been reported in other terrestrial vertebrates, like the spur-thighed tortoises, *Testudo graeca*  
246 where humeral shaft diameter has decreased, which is a proxy for decreased body size (Stiner et al.  
247 1999). With agrarian and industrial societies, anthropogenic filtering pressures continue to increase  
248 and expand, driving continuing species extirpation and extinction, community shifts and increasing  
249 the rates, intensity and extent of anthropogenic ecological changes. Archaeological studies in Chile  
250 (Villavicencio et al. 2015) and in Madagascar (Crowley et al. 2016) have shown evidence that the  
251 settlement and the shift from a subsistence strategy to an agrarian regime, notably with associated  
252 land-use change, accelerated the loss of biodiversity (see table in supplementary material. The  
253 amount of time elapsed between major changes in society type also moderate the severity of  
254 filtering effects, by increasing or decreasing the time available for species to adapt to dynamic  
255 anthropogenic habitats. At the time of first colonisation of native habitats by Hominids, different  
256 types of human societies present different degrees of filtering (Balée 1998, O'Connell and Allen

257 2015), with larger scale societies (agrarian, industrial) tending to induce more rapid rates of  
258 environmental change and more extreme filtering than smaller scale societies (e.g., hunter-gatherer;  
259 Box 1).

260 Native species in African and European regions experienced the longest and most gradual  
261 forms of filtering pressures by preindustrial societies. This enabled traits adaptive to dynamic  
262 anthropogenic environments to become established and lessened rates of extinction both during  
263 societal regime transitions and during the period between the transitions (Box 1) as found by  
264 previous studies (Faubry et al. 2020, Andersmann et al. 2020). In North America, hunter-gatherer  
265 societies arrived much later than in Europe and Africa, driving a rapid phase of extinction at the  
266 time of first colonisation (Martin 1973, 1984, Faubry et al. 2020, Andersmann et al. 2020). This  
267 rapid filtering effect is even more pronounced in the very recent first arrival of hunter-gatherers to  
268 New Zealand, where the and their commensal introduced species (e.g., dogs, rats) (Barnosky et al.  
269 2004, Barnosky 2008, see Figure 2), where there had an absence of pre-sapiens Hominid societies.

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

277 To fully understand the long-term prospects for native species' persistence and adaptation in  
278 the face of anthropogenic pressures, rigorous comparative investigations of long-term  
279 anthropogenic filtering that focuses on the 1) timing and types of societal colonisations, 2)  
280 sociocultural regime shifts (Kinzig et al. 2006), and 3) the society response to biodiversity decline  
281 (Welch et al. 2013, Lightfoot et al. 2013, Lepofsky and Caldwell 2013), may serve as critical  
282 observational laboratories (Cartwright et al. 2014). While it seems fairly well established that more

283 recent colonisations are associated with higher rates of native biodiversity loss, the causes of this  
284 are not fully understood, nor are they necessarily generalisable to other species. Nevertheless, it is  
285 clear that failure to consider the effects of societal legacies and sociocultural transitions on native  
286 species loss and the presence of adaptations that might prevent future losses can have major  
287 consequences across history (Ramalho and Hobbs 2012).

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

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## 409 **Figure captions**

410

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

418

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

425

426

## 427 **Box 1. Case study**

428 Our planet has experienced a large mass extinction event caused by human activities over millennia through  
429 human interaction (e.g., hunting, harvesting) or transformation (e.g., human niche constructing activities like  
430 cleared lands, biotic exchange, erosion). Thus this model has been used in three different contexts of  
431 selective pressure from behaviourally modern human, (1) Europe and Africa, which had the earliest selective  
432 pressures from humans (> 45,000 years before present [YBP]; Fu et al. 2014, Suppl. 1), (2) North America  
433 (~10,000 YBP; Bourgeon et al. 2017, Suppl. 1) and (3) New Zealand, which observed a later selective  
434 pressure from humans (~737 YBP; Wilmshurst et al. 2008, Suppl. 1). The ultimate goal is to identify  
435 divergence between the change of human societies and their associated habitat alterations are affiliated to  
436 reduction of native large-sized fauna richness.

437 In these three contexts, similar process of sociocultural niche construction have been observed, also  
438 with similar sequences of changes sociocultural systems (i.e., hunter-gatherer, agrarian, industrial societies),  
439 but with different durations and overlaps between each type of system (Figure 2.2). Thus countries more  
440 recently colonised by humans have experienced shorter transitions times between sociocultural systems that  
441 could help explain the longer temporal delays in biodiversity responses to society change. The proportion of  
442 large-sized fauna species that went extinct following colonisation of hunter gatherer societies (Figure 2.2) in  
443 Europe (0.8% biodiversity reduction) and Africa (8.8%) were more fewer than those in North America  
444 (30.6%) and New Zealand (55.9%). Humans in Europe and Africa became established over a much longer  
445 period and had less impact on local large-sized fauna extinctions, a pattern that is clearly contrasted by North  
446 America and New Zealand. However, such extinction rates cannot fully be explained by human impacts  
447 alone, as other effects such as environmental impacts, either working alone or in tandem with human impacts  
448 can contribute to extinction or extirpation events. Similar results have also been observed during the later  
449 sociocultural niche construction during the onset of industrial societies (Figure 2.2), which are more  
450 characteristic of the Anthropocene period. Indeed, Europe (13.9%) and Africa (8.8%) had a lower extinction  
451 rate during the industrial period and the Anthropocene period than North America (18.7%) and New Zealand  
452 (25.0%) where extinction was more pronounced. The time-lagged between the onsets of a news human  
453 sociocultural system and the subsequent extinction events appears to vary with the duration of human  
454 association. In locations with longer periods of human association, the extinction rates of native biodiversity  
455 was lower (see Figure 2.2 for European and Africa) following transitions between sociocultural systems,

456 likely due to longer periods for evolutionary change to occur between transitions. However, in New Zealand,  
457 one of the last locations to be colonised by humans with particularly rapid transitions between sociocultural  
458 systems, the native community of large-sized fauna has undertaken a faster magnitude of extinction. So, the  
459 transition period between human sociocultural systems combined with climatic change may favour an  
460 evolutionary responses of biodiversity to anthropogenic impacts (i.e., past experience with humans provides  
461 the evolutionary history that could shape how biodiversity responds to human impacts; Sih et al. 2011).  
462 The importance of temporal dynamics in ecology has been well recognised. Our approach highlights the  
463 importance of temporal effect of human societies of the study of human impacts on biodiversity and  
464 landscape.

465 **Table 1:** Human sociocultural systems classified by primary subsistence regime, in order of historical emergence (based on Nolan and Lenski 2010, and Ellis 2015)  
 466 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]  
 467 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									
Sociocultural system	Subsistence regime	Technological innovation	Ecological impact	Introduced species	Flora		Fauna		General impact native ecosystems
					Observed	Potential traits	Observed	Potential traits	
						selected by humans		selected by humans	
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	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, reproducing higher ratio of production to respiration, loss of perennial plants, slower growing species decline.	Smaller sized, annually 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 herbivores [c], population size of large vertebrates and life reproduction species diversity.	Grazing selection of early 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.	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.
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,	Introduction of exotic predators, translocation of exotic species to enrich the diversity of the region (i.e.,	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	Sedentary, omnivorous, long life expectancy, importance parental care	Switch of biodiversity composition with appearance of introduced species replacing native species but increase of richness.

aridity, wetness area) marginal      acclimatisation  
lands due to their transportation      society).  
requirements, resource extraction  
increases, urban/industrial  
growth, drainage of wet area,  
flood control.

herbivore species      [f], pesticide  
remaining in      resistance [g].  
marginal habitats.



468 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.	- Lack of available data on early human colonisation history
	- Add new understanding to the evolution of genetic response and phenotype variation in biodiversity.	- Lack of understanding of the effect of human population growth and size on biodiversity.
	- Understand the ability of species or individuals to cope with anthropogenic habitats.	- Lack of knowledge about interactions of multiple stressor interactions (e.g., climate change, invasive species, and habitat clearance).
	- Develop conceptual framework to explain how past human history influences the evolution cue-responses relationships between organisms and environments.	
Conservation	- Probability of extinction or extirpation of native species.	- Current rate of habitat clearance.
	- Aid in the understanding of the causes of species population declines.	- Population size / propagule pressure of invasive species.
	- Further understanding of the factors that lead to the establishment of invasive species.	- Rate of invasive species introduction.
		- Vulnerability of native species (e.g. island species).
Ecology		- Lack of inclusion of interdisciplinary approaches.
	- Add to biogeographical parameter to help to refine the process of	- Uncertainty about the effect of climate change.

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.

- 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.

- 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.

- 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.

#### Anthroecology

469

470

Figure 1

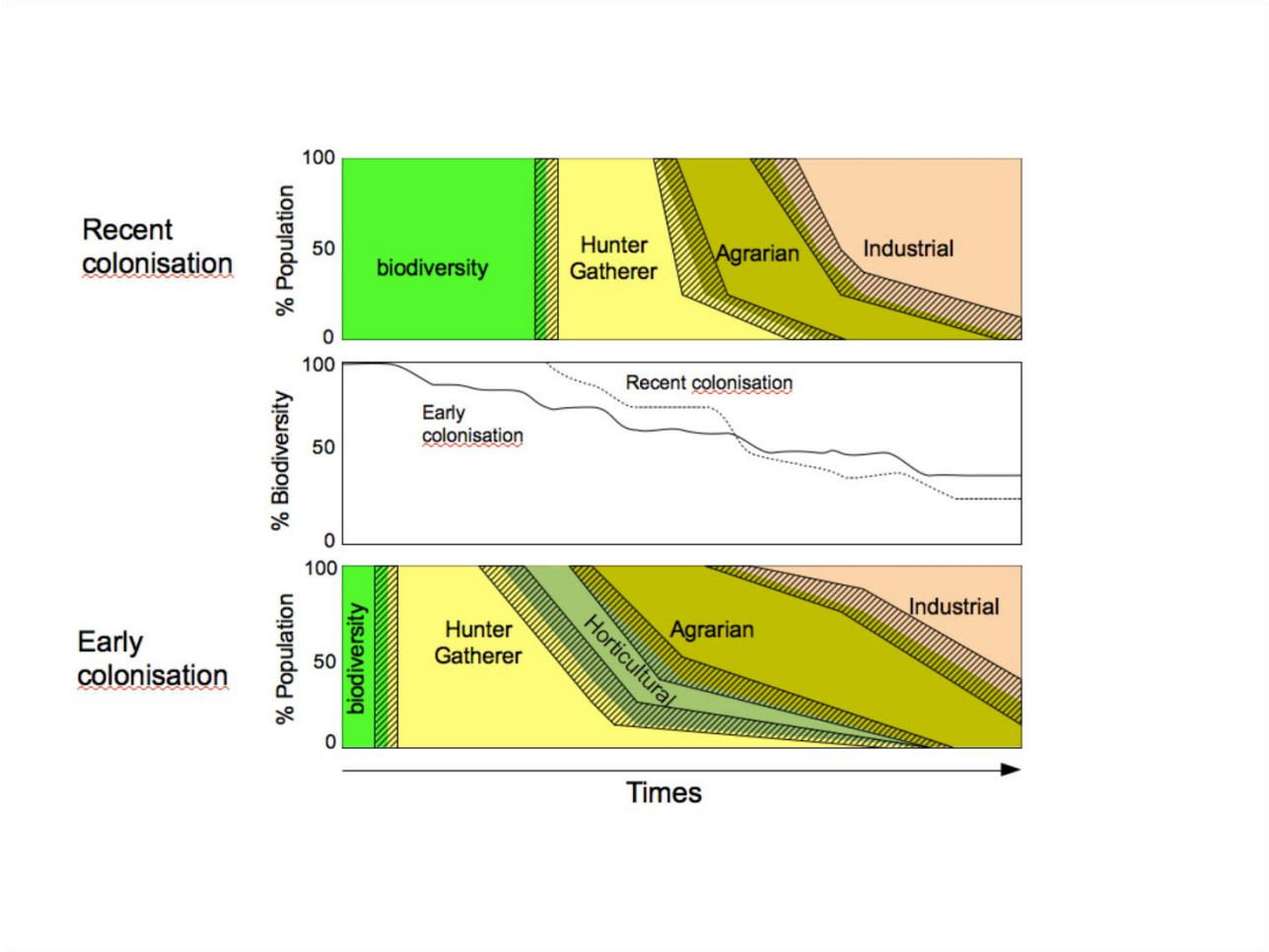


Figure 2

