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1 **Island biodiversity conservation needs palaeoecology**

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31 **Abstract**

32 The discovery and colonisation of islands by humans has invariably resulted in their
33 widespread ecological transformation. The small and isolated populations of many
34 island taxa, and their evolution in the absence of humans and their introduced taxa,
35 mean that they are particularly vulnerable to human activities. Consequently, even the
36 most degraded islands are a focus for restoration, eradication, and monitoring
37 programmes to protect the remaining endemic and/or relict populations. Here, we build
38 a framework that incorporates an assessment of the degree of change from multiple
39 baseline reference periods using long-term ecological data. The use of multiple
40 reference points may provide information on both the variability of natural systems and
41 responses to successive waves of cultural transformation of island ecosystems,
42 involving, for example, the alteration of fire and grazing regimes and the introduction of
43 non-native species. We provide exemplification of how such approaches can provide
44 valuable information for biodiversity conservation managers of island ecosystems.

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54 **Keywords:** Biodiversity conservation on islands, fire regime, fossils, herbivory, invasive
55 species, multiple baselines, palaeoecology.

56 **Introduction**

57 Island ecosystems have always played a leading role in conservation biology. They are
58 often described as natural laboratories, providing model systems for the testing of
59 evolutionary, ecological, and biogeographic theories^{1,2}. Remote island ecosystems are
60 hotspots of biodiversity, with legacies of relatively recent human impact and native
61 species' extinctions, and therefore provide significant challenges when considering how
62 to conserve biodiversity. They also offer some of the best-suited scenarios for rapidly
63 advancing our understanding of fundamental aspects of human relationships with
64 nature, and of conservation strategies, including restoration and eradication
65 programmes³⁻⁷. Examples of programmes specifically tailored to islands include The
66 Global Island Partnership, the International Union for Conservation of Nature (IUCN)
67 Island Initiative Program, and the Small Island Developing States Network.

68
69 The isolated nature of remote islands is both part of the problem, in creating 'naïve'
70 native ecosystems, especially vulnerable to outside contact, and a positive, in that the
71 natural barriers to colonisation can, for example, enable successful programmes
72 eradicating non-native vertebrates⁵ and/or translocating endangered species. However,
73 success in managing island ecosystems and conserving biodiversity, as well as invasive
74 species eradication, may be contingent upon a sound understanding of an island's
75 specific ecological history. Recent work within restoration ecology has highlighted that
76 ecological history is important, not only to determine the degree of change that has
77 occurred from baselines or reference conditions, but also the level of intervention
78 required to restore an ecosystem towards particular desired states⁸⁻¹⁰. Establishing
79 points in time (and accompanying baseline states) of first human impact can therefore

80 be important for decision-making and provide guidance on what to restore and where,
81 when managing both native and novel ecosystems¹¹⁻¹³.

82

83 Baselines are frequently derived from historical literature or from palaeoecological
84 studies based on biological proxy, fossil or sub-fossil evidence, especially pollen, spores,
85 plant macrofossils and charcoal records^{14,15}. Indeed, numerous decadal to millennial
86 scale time-series have been generated from islands (Figure 1). Collectively, these
87 records provide a rich picture of past environmental change and the ecological impacts
88 of initial and subsequent human settlement of island ecosystems globally (Figure 2)¹⁶⁻¹⁸.
89 Such studies can also provide information on the native/non-native status of particular
90 species, pre-human ecological conditions and how achievable restoration targets may
91 be^{8,11}. As most oceanic islands are relatively recently settled (many >10,000 yrs)
92 compared with continental regions, pre-human baselines can often be more clearly
93 distinguished and dated and such data can be of direct relevance to conservation
94 decisions. A good example is provided by the Hawaiian island of Kaua'i, where fossil
95 pollen data recovered from ancient caves and marshes revealed the character and scale
96 of human-induced ecological transformation and was used in refining a list of
97 appropriate native plants for forest restoration initiatives¹⁹.

98

99 Whereas ecological baselines can be conceived of as a referring to a single state, derived
100 from a particular point in time (e.g. a pre-human baseline), herein we discuss the
101 potential value of using palaeoecological techniques to determine multiple past
102 baselines. For instance, in addition to the consideration of pre-human states reflecting
103 natural variability and responses to environmental stressors (e.g. natural disturbances),
104 we may also identify key points in time where human cultures exerted different types of

105 influences on islands over time, and transformed ecosystems in distinct ways. Such
106 multiple baselines provide invaluable insights and opportunities for conservation
107 practitioners and policymakers and may also be particularly informative for restoration
108 programmes that take both an ecological and cultural perspective^{8,10,16}. The use of fossil
109 pollen data alongside other historical and pre-historical archives on Kaua'i again
110 provides illustration, as efforts have been made to develop management and
111 interpretive programmes for centuries-old working cultural landscapes owned by the
112 National Tropical Botanical Garden and on other privately owned sites¹⁹.

113

114 In this Perspective, we select three relevant topics that are closely related to human
115 colonisation and subsequent activities and each of which have been shown to have
116 profound impacts on island ecosystems (Table 1)^{1-7,19}: 1) invasive and non-native
117 species, 2) altered fire regimes and, and 3) altered grazing regimes. Using case studies
118 from islands that draw particularly upon plant microfossils and charcoal records, we
119 describe how palaeoecological data and the reconstruction of past baselines can be
120 applied to inform and improve management plans for island ecosystems.

121

122 **1. Invasive and non-native species**

123 The distinction between 'native' and '(alien) non-native' species and determination of
124 the 'natural range' of a species when considering longer timescales can become the
125 subject of much philosophical debate. Pragmatically, however, two approaches
126 dominate in the restoration ecology literature: 1) humans as the agency for introduction
127 and 2) the historic Holocene species' range²⁰. These distinctions can often be much
128 more clearly drawn on islands in contrast with continental ecosystems, as human
129 arrival times are generally both more recent and more precisely known. In the absence

130 of definitive data, the status determination of non-native plant species on islands is
131 often based on conjecture, derived from a combination of factors including: date and
132 site of first recorded presence (particularly post-European settlement); **non-native**
133 status designations in neighbouring regions; active change in current species
134 distributions; ability to transform habitats; individual species' characteristics, including
135 association with humans and history as a 'weed'^{21,22}.

136

137 Key questions in any ecological restoration programme are which species should be
138 conserved, which are priorities for eradication, and which should be closely monitored
139 for potential deleterious ecological future impacts⁵. Palaeoecological methodologies such
140 as the analysis of **plant macro- and microfossils (such as pollen and phytoliths)**, and
141 preserved DNA can be powerful tools, particularly when used in conjunction with
142 historical evidence, to determine the provenance of plant species on islands, e.g. to
143 determine whether they are native, historical or more recent introductions and to
144 provide insight to address conservation management questions^{e.g.20,23,24} through:

- 145 • Analysis of native species' ranges and historical distributions²⁵.
- 146 • Developing clear criteria for designation of **non-native** species status²⁶.
- 147 • Resolving the origin of 'cryptogenic species' (species which cannot be reliably
148 classed as either native or non-native)²⁷.
- 149 • Analysing the origin, dispersal, and rate of spread of invasive species over
150 time^{24,28}.
- 151 • Assessing the long-term impact of (invasive) **non-native** species on native
152 species.
- 153 • Predicting future outcomes of invasions and responses to environmental
154 change^{24,29}.

155

156 For example, Wilmshurst *et al.*²⁸ combined palaeoecological analyses and historical
157 records to confirm the **non-native** status of the daisy tree (*Olearia lyalli*) in the
158 Subantarctic Auckland Islands. Their results indicate that although endemic to the New
159 Zealand region, *O. lyalli* became established in these remote islands c. 1807–1810,
160 probably facilitated by localized habitat disturbances associated with European sealers
161 (Figure 3). Similarly, in an example from the Galápagos Islands, palaeoecological
162 analyses revealed that nine plant species presumed to be either introduced after
163 European discovery of the islands in 1597 or of doubtful native status were, in fact,
164 native to the archipelago^{21,30}. One of these species, *Hibiscus diversifolius*, an identified
165 ‘habitat transformer’ appearing to be expanding its distributional range, had previously
166 been considered for potential control or eradication. In addition, palaeoecological
167 analyses in Mauritius also recorded over a dozen plant species that are currently not
168 considered native to this Indian Ocean island³¹. Most of these taxa, including several
169 palm tree species, had been extirpated from the island prior to the first reliable
170 vegetation surveys of the island, less than two centuries following first human
171 colonisation. These species were abundant in pre-human ecosystems and illustrate a
172 considerable proportion of ‘unknown lost’ biodiversity^{e.g.31,32}.

173

174 In addition to recognition of ‘lost species’ through plant microfossil identification,
175 syntheses of palaeobotanical, historical, ecological and molecular evidence have also
176 been increasingly used to resolve the conservation status of species with cryptic
177 origins^{6,33-35} for example **Krauss’ clubmoss** (*Selaginella kraussiana*) in the Azores³³ and
178 eastern bluebirds (*Sialia sialis bermudensis*) on Bermuda⁶. However, many oceanic
179 islands now have high numbers and proportions of species that are considered to be

180 non-natives, in many cases outnumbering native species. Few would argue that all such
181 species should be targeted for control or eradication: many are valued by human
182 societies as food plants, for aesthetic reasons, or for their ecological functions, in some
183 cases replacing or supplementing extinct (or extirpated) native species e.g. 16.

184

185 From a biodiversity perspective, we may also use palaeo-data to address how human
186 colonisation and subsequent cultural phases, such as the introduction of livestock, crops
187 and new landuse techniques have influenced the abundance of particular island species
188 over time, recognizing that there may be winners as well as losers. Unique Island
189 species/subspecies may even have developed as a result of the genetic divergence of an
190 anthropogenically introduced or facilitated founder species. An example of this is the
191 Canarian Egyptian vulture, a genetically distinct, insular population of the Endangered
192 (IUCN) Egyptian vulture (*Neophron percnopterus*). Genetic analyses indicate that
193 vultures first colonized the Canary Islands 2500 years ago³⁶, a date coincident with the
194 timing of human colonisation of the archipelago determined from archaeological
195 remains. The vultures are believed to have colonised the islands naturally, but the
196 colonisation was likely facilitated by the introduction of domesticated livestock, as
197 previously suitable food sources were lacking³⁶.

198

199 The role of long-term ecological data (spanning palaeoecological and long-term
200 population monitoring studies) can thus be much more than simply determining
201 whether colonisation was anthropogenic, but also to include quantitative information
202 on changing abundances, distribution and response to environmental change within the
203 island system, and the processes explaining present-day island biodiversity.

204

205 2) Changes in fire regime

206 Humans have modified fire regimes in most ecosystem types around the world, as they
207 have colonised and increased in abundance over time³⁷. On islands, human
208 modifications of the fire regime typically occurred much later than in continental
209 regions, especially on islands where human presence is more recent (e.g. past 500/5000
210 years) and where natural ignitions were rare³⁸. Knowledge of long-term fire ecology is
211 fundamental to understanding the natural variability of fire regimes (fire history) and
212 the responses and resilience of ecosystems to fire (both natural and human ignited). On
213 islands where fire was a naturally occurring disturbance before human arrival, resource
214 managers face a complicated scenario. **They must consider whether fires should be**
215 **suppressed or prescribed in particular ecosystems, what the long-term ecosystem**
216 **responses to a particular fire regime will be, and whether post-fire restoration is**
217 **necessary**. Consequently, there is an increasing awareness among scientists and
218 managers that long-term research, including various forms of palaeoecological data,
219 holds significance for contemporary fire management policy³⁹.

220

221 Current management of forest fires consists mainly of prevention (management of fuel),
222 control (fire suppression), and recovery (ecosystem restoration). Palaeoecological
223 proxies such as charcoal, pollen, and fungal spores found in sediments, and tree rings
224 with fire scars, among other indicators, provide information on different spatial-
225 temporal resolutions of fire occurrence and fire regime characteristics³⁹. In addition,
226 these datasets allow reconstructions of both fire regimes and vegetation dynamics, and
227 can be used to address key issues related to fire-ecosystem interactions such as:

- 228 • Determining natural fire regimes on islands (i.e. caused by volcanism, lightning
229 strikes), providing a reference for resilience to fire on islands where fire was

230 uncommon or rare before human arrival, or to emulate fire suppression and
231 prescribed burning on islands where fire was an important and naturally
232 common form of disturbance before human arrival⁴⁰.

233 • Differentiating between natural and cultural fire regimes⁴¹, i.e. how have fire
234 regimes changed over time following human arrival?

235 • Determining ecosystem thresholds in response to fire (i.e. how or if species
236 recover after repeated fire) and the necessity to intervene through
237 restoration^{42,43}.

238 • Assessing the role of other anthropic disturbances on fire behaviour such as,
239 invasive species, climate change, forest logging, landscape fragmentation, and the
240 combined effects on ecosystems^{43,44}.

241

242 Several palaeoecological studies have shown the applicability of long-term
243 reconstructions in fire ecology and management on islands. For example, in New
244 Zealand, fossil charcoal records from lakes in the South Island indicate that severe fires
245 occurred soon after initial settlement by the indigenous Māori, resulting in significant
246 reduction of the native forest and subsequent soil erosion⁴⁵. Charcoal analysis of high
247 temporal resolution, from multiple sites, allowed the establishment of a robust fire
248 chronology before and after Māori arrival (in the 13th century). The reconstructions
249 showed that fire was rare and infrequent before human arrival, and rapidly increased in
250 frequency and extent following initial human arrival, with the development of a novel
251 anthropogenic fire regime, with fires every 50–100 years, a pattern sustained until
252 European contact, when fire frequency increased again⁴⁶. Some understanding of spatial
253 variation was also achieved, with key predictors of forest loss during the initial burning
254 period in New Zealand relating to gradients in moisture and topography rather than

255 human behaviour; the mere introduction of a novel anthropogenic ignition source made
256 deforestation of New Zealand and most of other Pacific islands inevitable⁴⁷. The virtual
257 absence of fires in the immediate period prior to human arrival (pre-Māori) and the
258 rapid replacement of trees by ferns, shrubs and grasses after the initial burning period,
259 indicate that although native forests were paradoxically highly flammable, they are not
260 adapted or resilient to frequent and repeated anthropogenic fires. There are other cases
261 where the charcoal record clearly shows different fire regimes associated with specific
262 periods of human occupation. For instance, in Hispaniola, the second largest island in
263 the Caribbean, there is evidence that natural fires occurred within dry forests, where
264 several tree species (e.g. *Pinus occidentalis*) are fire-adapted⁴⁸. This natural fire regime
265 was significantly modified from ca. 5400 cal. years BP, coinciding with the occurrence of
266 early settlers in the island. Following European settlement, fires became generally less
267 frequent than during the pre-Columbian phase. Another key example is provided by
268 pollen and charcoal data from Tenerife in the Canary Islands (Figure 4), where two
269 burning baselines can be linked with human arrivals: 1) **the first colonists from North**
270 **Africa** and 2) Europeans. Before human arrival the concentration of charcoal was
271 relatively low in Tenerife. After initial settlement fires increased in frequency, with an
272 associated decline and later extinction of some tree species (e.g. *Quercus* and
273 *Carpinus*)³².

274

275 Finally, there are **island** ecosystems that are known to be dependent on fire. Black pine
276 woodlands in Corsica are a key example of such a fire-dependent system: a high-
277 resolution charcoal record, together with plant macrofossils, has revealed that this fire-
278 prone ecosystem has persisted and very likely been favoured by frequent fires

279 occurring on the island during the last 13,200 years, both under naturally ignited and
280 human-induced fire regimes⁴⁹.

281

282 **3) Herbivore density over time**

283 The impacts of long-term herbivory by introduced taxa on island ecosystems remain the
284 subject of debate^{50,51}. Several authors have argued for the eradication of non-native
285 herbivores (e.g. feral goats and rabbits) to promote the conservation of native
286 vegetation⁵²⁻⁵⁴. Others have argued that herbivory provides the only means to preserve
287 certain cultural ecosystems, such as agroforestry systems that depart from the pre-
288 human baseline but nonetheless are valued for biodiversity and/or cultural values⁵⁵.
289 Herbivores can also be important ecosystem engineers on islands, altering fire and
290 disturbance regimes through changes in availability of biomass^{17,56,57}, or helping to
291 control plant invasions^{58,59}. It has been shown that eradication of introduced herbivores
292 can be successful in many islands⁵³ with significant conservation benefits^{5,60}. However,
293 in certain contexts, the eradication or exclusion of non-native herbivores may entail
294 some negative consequences, for example, through perverse outcomes such as the
295 increase in rat populations and their associated impacts upon e.g. nesting birds, seeds,
296 and invertebrates⁶¹, or unexpected cascading effects facilitating the increase of invasive
297 plant species⁵⁹. Therefore, techniques such as trapping, hunting, biocontrol, or any
298 combination of them to remove herbivores from a particular site may be unsuccessful if
299 not carefully coordinated and implemented^{62,63}. Finally, native herbivores occur also on
300 many islands worldwide and their decline or extinction after human arrival has had
301 consequences on ecosystem dynamics⁶⁴. Palaeoecological proxies (fossil pollen, fungal
302 spores, bones assemblages, aDNA in sediments, and coprolites) can provide information

303 to help understand and manage both native and **non-native** herbivores in island
304 ecosystems by:

305 • Determining whether large native herbivores (e.g. tortoises, rodents, birds) have
306 been extirpated in the past from some islands but introduced to others, and
307 whether population fluxes and extinctions have been anthropogenic and/or
308 natural in origin.

309 • Allowing the rate and pattern of herbivore introduction over time to be
310 assessed²⁵.

311 • **Demonstrating** the long-term impact of changes in herbivore population on
312 native ecosystems (e.g.⁶⁵).

313 **Determining when** herbivores were introduced to an island is also relevant to
314 understand the role of herbivory and its impact upon vegetation⁵⁶. In this context, the
315 coprophilous genus of fungi *Sporormiella* provides a powerful tool to trace changing
316 herbivory regimes and when coupled with fossil pollen records, the resulting impact on
317 plant diversity^{18,65,66}. Spores of these dung-affiliated taxa are considered to be one of the
318 most broadly applicable palaeoecological proxies for quantifying herbivore densities
319 because of their low dispersal capacity⁶⁶⁻⁶⁸. *Sporormiella* and other coprophilous dung
320 fungi are useful for tracing mammalian herbivores on islands (e.g.^{65,69}), as well as for
321 native avian and reptile herbivores on islands that were almost free of terrestrial
322 mammals before human arrival (for example all the Polynesian islands, Mauritius, and
323 Galápagos). *Sporormiella* has been successfully used to identify both native avian
324 herbivores, and introduced herbivore presence in New Zealand peat records¹⁸, **and it**
325 **has been used in studies** of the decline of giant tortoise populations in the Galápagos
326 Islands, **revealing the** previously unappreciated impact of this decline on wetland
327 **habitats**¹⁷. *Sphagnum* bogs currently found in the Galápagos uplands were revealed to

328 have developed only over the last 500 years, replacing former open-water wetland
329 habitats. *Sporormiella* data indicate that giant tortoises were formerly present at these
330 sites. The authors postulate that wallowing tortoises helped maintain open water
331 conditions; but as tortoise populations declined throughout the historic period, this led
332 to a series of cascading ecological impacts with the conversion of wetlands to *Sphagnum*
333 bogs and resultant deleterious impact on wetland-dependent species.

334

335 In many islands, early (pre-historic) human colonists introduced commensal mammals
336 such as pigs (*Sus domesticus*), goats (*Capra hircus*), sheep (*Ovis aries*), rats (*Rattus* spp.),
337 and rabbits (*Oryctolagus cuniculus*). These introductions typically had significant
338 negative impacts on the vegetation^{32,70}, promoting increased erosion, and sometimes
339 being implicated in the extinction of native fauna as, for example, species of avifauna in
340 Macaronesia (e.g.⁷¹), and of many small birds on Pacific islands^{72,73}. Native island
341 herbivores usually fulfil an important role in their ecosystems, mostly by control of
342 biomass, influencing landscape heterogeneity, seed-dispersal and nutrient cycling³.
343 Whereas remote oceanic islands mostly lacked terrestrial mammals prior to human
344 colonisation, many less remote or past land-bridge islands did possess their own
345 indigenous assemblages of terrestrial mammals (see⁷⁴). Many of these island herbivores
346 experienced reduction of their population size, population collapse, and extinction
347 following human colonisation. On theoretical and empirical grounds, we know that the
348 removal (or addition) of a major trophic level or function has wide-ranging impacts on
349 ecosystem process and form, often out of proportion to the number of extinctions
350 initially involved. For example, palaeoecological studies from Mauritius show that the
351 now extinct dodo and two species of giant tortoise lived in dense populations in the
352 coastal lowlands⁷⁵. These populations experienced regular environmental hazards from

353 tropical storms and seasonal droughts⁷⁶. A prolonged drought 4200 years ago caused a
354 mass death in the Mare aux Songes⁷⁶. This wetland was the primary source of drinking
355 water in the southwest of the island, as open freshwater is scarce in the Mauritian
356 lowlands due to its recent basaltic nature. In excess of 100,000 giant tortoise and dodos
357 died within 100 years when decreased precipitation caused **salinization** and algal
358 blooming. In another example from an Alaskan island, it has been shown that the
359 extinction of the mammoth population on St. Paul also related to diminished freshwater
360 availability combined synergistically with shrinking island area and regional climate
361 change, in this case entirely independently of and before human colonisation⁷⁷. These
362 examples show how larger vertebrate species, especially those of **former** land-bridge
363 islands, have been subject to fluctuations in resources (especially related to water and
364 island size), of large ecological impact, independent of human action. This also serves to
365 highlight the importance of developing longer-term chronologies of changing island
366 environments and carrying capacities in order to develop understanding of the
367 resilience of insular fauna and systems to environmental change.

368

369 **Future directions: towards the integration of palaeoecological data in**
370 **conservation frameworks for island ecosystems**

371 It is apparent from the examples we have provided that the choice of baseline or
372 reference condition could have **significance for conservation targets and strategy, and**
373 **hence that identification of multiple baselines and assessment of natural variability in**
374 **response to past change should be important goals of conservation palaeoecologists^{8,19}.**

375 The complexity of managing island ecosystems varies depending on what baseline(s)
376 **is/are** used, and **what goals are prioritized**, e.g. 1) a functioning and biodiverse
377 ecosystem; 2) a particular cultural landscape, or 3) **restoration of** a pre-human

378 ecosystem. This complexity opens an important knowledge gap, as in many island
379 ecosystems management decisions usually occur without knowledge of their pre-
380 human vegetation and faunal baselines, and without a direct measure of ecosystem
381 change through time¹⁴. In this context, the potential level of intervention and the
382 associated implementation costs are unknown. For example, in figure 3 we illustrate the
383 case of Poor Knights islands in New Zealand where a complete compositional turnover
384 from the pre-human baseline was reported, including the extirpation of a dominant
385 conifer from the Podocarpaceae family (*Dacrydium cupressinum*) and a palm tree
386 (*Rhopalostylis*). On this island, a novel (but native) and successional angiosperm-
387 dominated forest (*Metrosideros*) is currently dominant and there is no modern
388 equivalent of the pre-human conifer- and palm- dominated forests on any other
389 northern offshore New Zealand island¹⁶. Although fossil pollen and aDNA data show
390 that the current ecosystem is significantly altered from the pre-human baseline, in this
391 case the analyses can be used to suggest that accepting the novel successional
392 ecosystem with no further intervention may be more beneficial and cost-effective than
393 trying to restore the vegetation to its pre-human baseline.

394

395 In addition, the notion that multiple baselines may each be valued and part of the
396 cultural and biological heritage of an island and its peoples, and thus worthy of
397 consideration by managers in a conservation and landscape management (and tourist
398 and recreation) context is one that arguably deserves wider attention. Lyver *et al*
399 (2015)¹⁰ present an example where palaeoecological data about past ecological states
400 was integrated with traditional knowledge to help island managers inform their
401 restoration goals. This is relevant if we aim to recognise the long-term role of humans in
402 re-shaping island ecosystems and that managing to conserve particular cultural

403 landscapes may have a place within an overarching conservation strategy. Multiple
404 baselines can guide managers interested in restoring some parts of their islands to pre-
405 human vegetation baselines in order to enhance native biodiversity, while also allowing
406 other areas to be developed for cultural purposes such as harvesting or traditional
407 activities, which can also often be compatible with healthy populations of native species.

408

409 Palaeoecological records and the multiple baseline framework also help to inform the
410 likely trajectories of future natural successions and to evaluate pre-human responses of
411 the vegetation to natural disturbances⁷⁸. For example, detailed Holocene plant
412 microfossils and sediment records can document the response of vegetation to a range
413 of natural disturbances over time and allow these to be compared with the more recent
414 impacts of human arrival on an island. As such records can reveal the time taken for
415 successions to take place and for ecosystems to recover to their pre-disturbed state
416 after a natural disturbance (e.g., fire, storms, volcanism, etc.), they can provide
417 important information about ecosystem resilience, especially when they have occurred
418 under similar climatic conditions to the present⁷⁹. This is illustrated in the Poor Knights
419 Island records, where the pre-human vegetation had a high beta-diversity and the forest
420 composition remained tightly homogeneous despite disturbance from volcanism¹⁶. In
421 contrast, following human arrival, beta-diversity declined and the vegetation
422 composition not only diverged completely away from its pre-human baseline, but
423 became highly variable, suggesting decreasing resilience to disturbance.

424

425 On Alexander Selkirk Island (Juan Fernández Islands, Chile), the palaeo-pollen records
426 show that although the vegetation communities (e.g. subalpine heath-shrubland) were
427 highly dynamic over millennial to decadal timescales, all taxa persisted through periods

428 of rapid and significant climate change, including the lowering of sea level by c. 135 m at
429 the last glacial maximum. However, following European arrival in the 16th century, the
430 next four centuries have seen drastic reductions in native species abundance and
431 diversity as a result of a novel fire regime and the introduction of goats, and of invasive
432 plant species (e.g. *Rumex acetosella*)⁸⁰. Finally, Wood *et al*⁶⁵ identified a clear link
433 between introduced mammalian herbivores and vegetation change in the dune system
434 on the uninhabited sub-Antarctic Enderby Island, in the Auckland Island archipelago⁶⁵.
435 Here, in the 19th century, after humans introduced rabbits, pigs, goats, cattle, and sheep,
436 intense grazing pressure caused a rapid decline of palatable native tussock grasses (*Poa*
437 *litorossa*) and megaherbs, which were replaced with an exotic sward community. As the
438 dates of introduced animal eradications from the islands are known, and could be
439 pinpointed in the age–depth profiles of the pollen and dung fungal spore records, cattle
440 and rabbits could be identified as the key drivers of vegetation change. The records also
441 showed that the native palatable species re-established within years of their removal
442 from the island. These examples and many others appear to suggest a consistent impact
443 on vegetation variability when humans settle islands. However, outcomes are varied
444 and thus further research is needed to understand the links between vegetation change
445 and specific drivers of change (e.g. fires, invasive plant species, herbivory or a
446 combination).

447

448 We have reviewed examples where palaeoecological records can, and should, be used to
449 complement conservation strategies and management frameworks. Good sources of
450 palaeoecological information are the online databases such as Neotoma
451 (<http://www.neotomadb.org>) and the European Pollen Database
452 (<http://www.europeanpollendatabase.net/index.php>). These datasets are continually

453 growing as new data are organized and made available. Although the availability of
454 palaeoecological records for smaller and more remote endemic-rich islands is limited,
455 the information can provide a solid first step to determine, for example, pre-human
456 floral and faunal states, the category of invasive and native species, fire regimes, and the
457 impacts of **non-native** herbivores. By our estimation, at least 155 fossil pollen datasets
458 are currently publically available from island ecosystems and there are many more
459 faunal reconstructions from sediment and cave deposits. In addition, there is also a
460 Global charcoal database (<https://www.paleofire.org/>) that includes 35 “palaeofire
461 datasets” from islands (Figure 1).

462

463 To maximize the value of palaeoecological data in island conservation we need to
464 incorporate **the following considerations**: 1) how to more effectively disseminate
465 knowledge about the legacy of a landscape in a manner that will influence the design of
466 planning frameworks for biodiversity conservation; and 2) the limitations of each
467 palaeoecological proxy, such as low taxonomic and temporal resolution, and potential
468 bias towards islands with suitable conditions for fossil preservation. Finally, we
469 advocate establishing routine palaeoecological investigations involving fossil proxies
470 and other biomarkers, as a key step in developing science-based evidence for
471 biodiversity conservation plans for island ecosystems, whether focused on restoration,
472 eradication, or the acceptance of novel ecosystems⁸¹⁻⁸³. Such data can lead to a more
473 flexible view on the management of future ecosystems that now include humans and
474 their introduced taxa, and to better-informed debate on the type of nature to be
475 conserved or restored.

476

477

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495

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497 S.N. lead the review and wrote the paper together with all authors: L.d.N., C.F., J.M.W.,
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499

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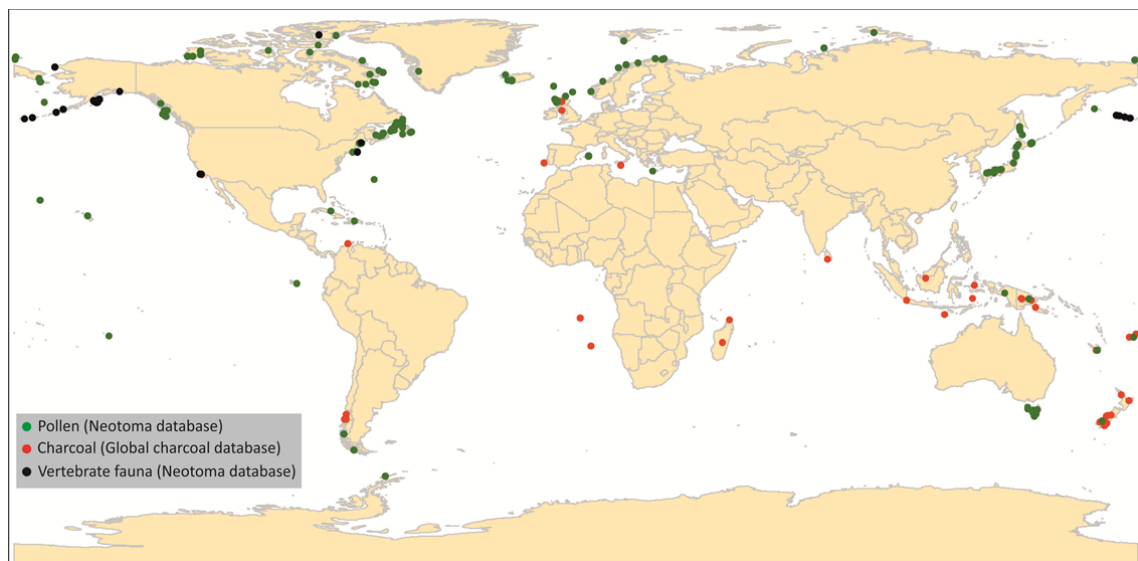
764 . The set of biological proxies, management questions and informed conservation
 765 actions used within the text to track back human impacts on island ecosystems. Note
 766 that some biological proxies can be used to characterise different impacts. * Not
 767 discussed in the text.
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Impact	Biological proxy	Management questions	Informed Conservation action
Invasive and non-native species	plant microfossils, plant macrofossils, ancient DNA	1) Timing of species introduction 2) Resolving the species provenance 3) Rate and pattern of spread 4) Assessment of the impact on native ecosystems	Eradication Restoration Monitoring
Fire	plant microfossils, charcoal (macro-and micro), tree ring fire-scars*, charred plant macrofossils*	5) Determine natural vs. human induced fire regimes 6) Determine ecosystem thresholds in response to fire 7) Assessing the interaction with other anthropogenic disturbances	Fire suppression Fire prevention Restoration
Herbivory	fungal spores (e.g. <i>Sporormiella</i>), Plant microfossils, ancient DNA, faunal remains (e.g. bones)	8) Determine the origin of the herbivores 9) Analyse the rate and pattern of the introduction 10) Assessment of the impact on native ecosystems	Eradication Restoration Monitoring

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774 **Figure 1.** To encourage the use of palaeoecological datasets in conservation we ideally
775 need freely available online datasets. This figure shows the geolocation for fossil pollen
776 (indicators of past vegetation change), bone assemblage (presence of vertebrates), and
777 fossil charcoal (indicators of past fires) datasets currently available from islands around
778 the World in the Neotoma database and the Global charcoal database (last accessed
779 January 2017).

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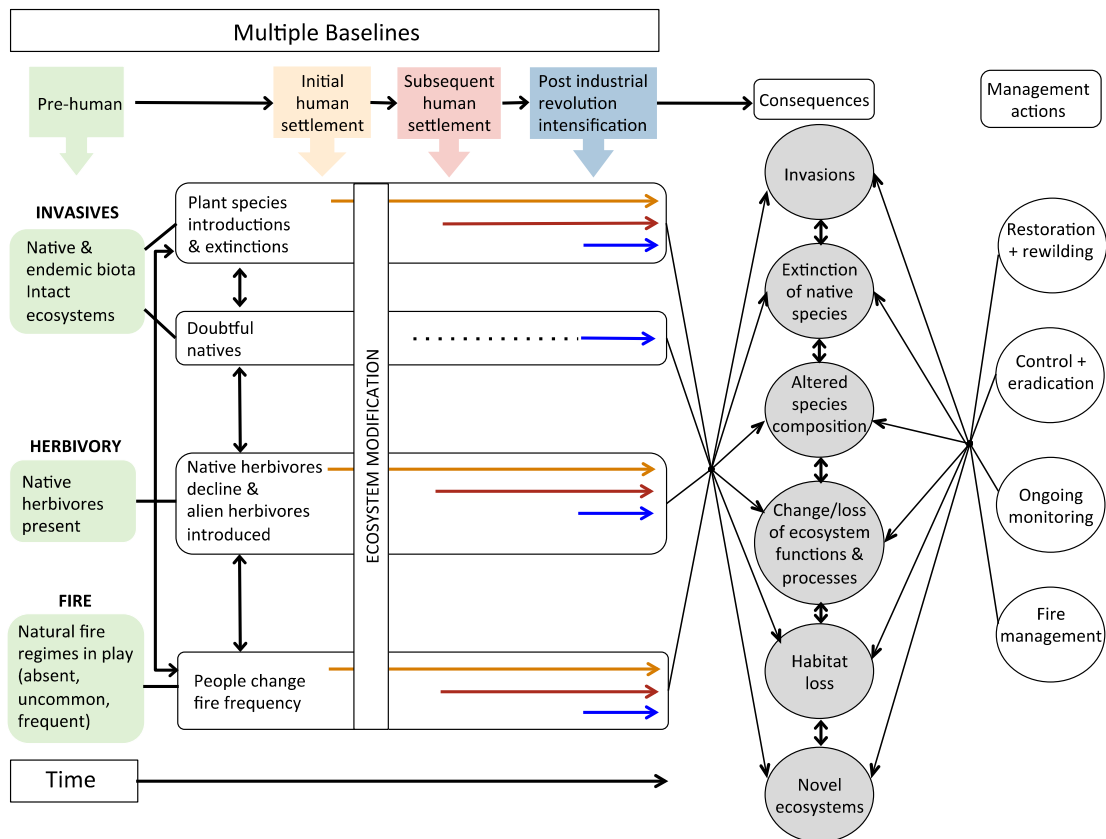
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789 **Figure 2:** Conceptual diagram summarising the main concepts discussed within the
 790 text and the suggested management actions. The diagram focuses on the degree of
 791 change and main human impacts on island ecosystems over time, taking into
 792 consideration multiple baselines (indicated by orange, red, and blue arrows). We show
 793 how the introduction of invasive species, herbivores, and human-induced changes of the
 794 fire frequency may impact the native and endemic island biota and **lead to varied**
 795 **management actions.** Colour of the arrows are related to the relevant baseline above.

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800 **Figure 3.** This figure assumes a context where the most desired state is the least altered
801 by humans: although we recognize that this may not always be the key goal of
802 conservation managers in practice. We are showing a modified framework by Jackson
803 and Hobbs (2009)⁸ applied to two palaeoecological examples in New Zealand, Poor
804 Knight Islands¹⁶ and the Auckland islands²⁸. In the first example, the pollen shows that
805 the current vegetation composition on the Poor Knights is completely different to the
806 pre-human state, and the level of intervention required to return it to its undisturbed
807 state would be prohibitive. Furthermore, palaeoecological insights from the Poor
808 Knights have revealed that the native *Metrosideros* forest is not a good analogue for a
809 pre-human restoration endpoint on other more degraded islands in northern New
810 Zealand. In the second example, pollen and charcoal analyses were able to resolve the
811 non-native status of a tree daisy on Subantarctic Auckland Islands, and show that
812 although its establishment was facilitated by anthropogenic disturbance, the tree has
813 been slow to spread. Pollen and charcoal records suggest this non-native tree poses a
814 low risk to the Auckland Island's ecological integrity, and the level of intervention
815 required to return the invaded sites to a pre-invaded state would be relatively modest.
816 However, current management practices of ongoing monitoring and no intervention are
817 also appropriate.

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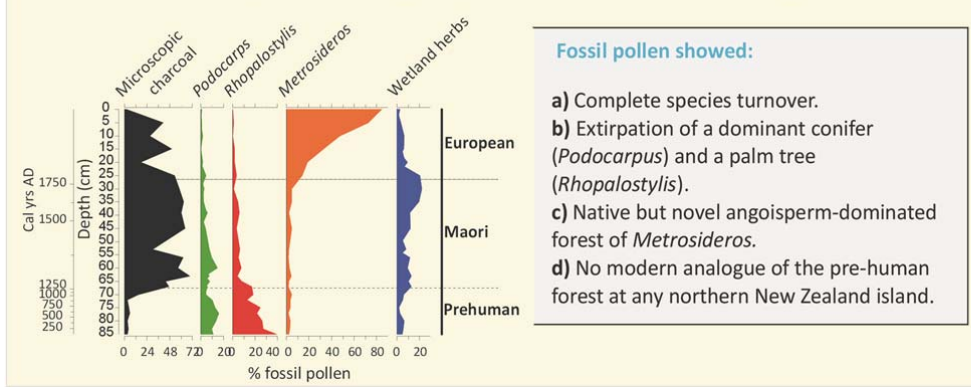
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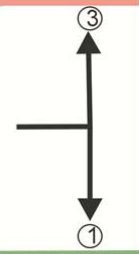
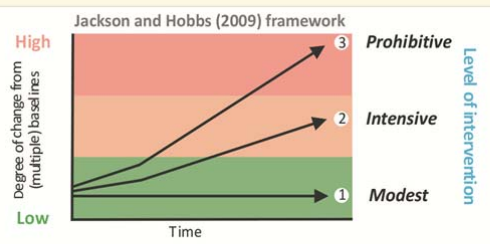
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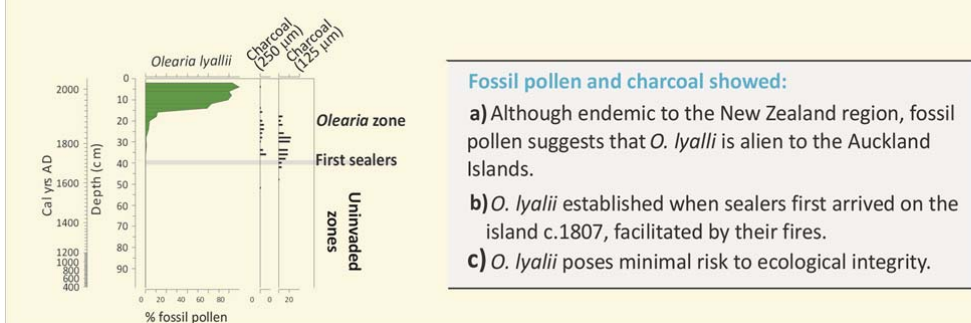
Example 1: Restoring to a pre-human baseline in Poor Knights Islands?



The degree of change is high.
 Level of intervention prohibitive.
 Restoration programmes prohibitive.
Acceptance of novel ecosystems



Example 2: Managing the alien status of the daisy tree *Olearia lyallii*



The degree of change is low.
 Level of intervention is modest.
Monitoring/eradication.

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831 **Figure 4.** Summary time-series from a sedimentary sequence from Tenerife (Canary
 832 Islands). We show the long-term dynamics of main Canarian vegetation types: extinct
 833 trees (e.g. *Quercus* and *Carpinus*), Laurel forest (e.g. *Morella* and *Erica*), Pine forest (e.g.
 834 *Pinus canariensis*), thermophilous forest (e.g. *Juniperus* and *Phoenix*), and shrubs and
 835 herbs (e.g. Poaceae). In addition, we show micro- charcoal counts to depict fire regimes.
 836 We have highlighted in red bars two obvious points for calculation of alternative
 837 baselines for La Laguna (Tenerife). See de Nascimento *et al.* ³² for full details.

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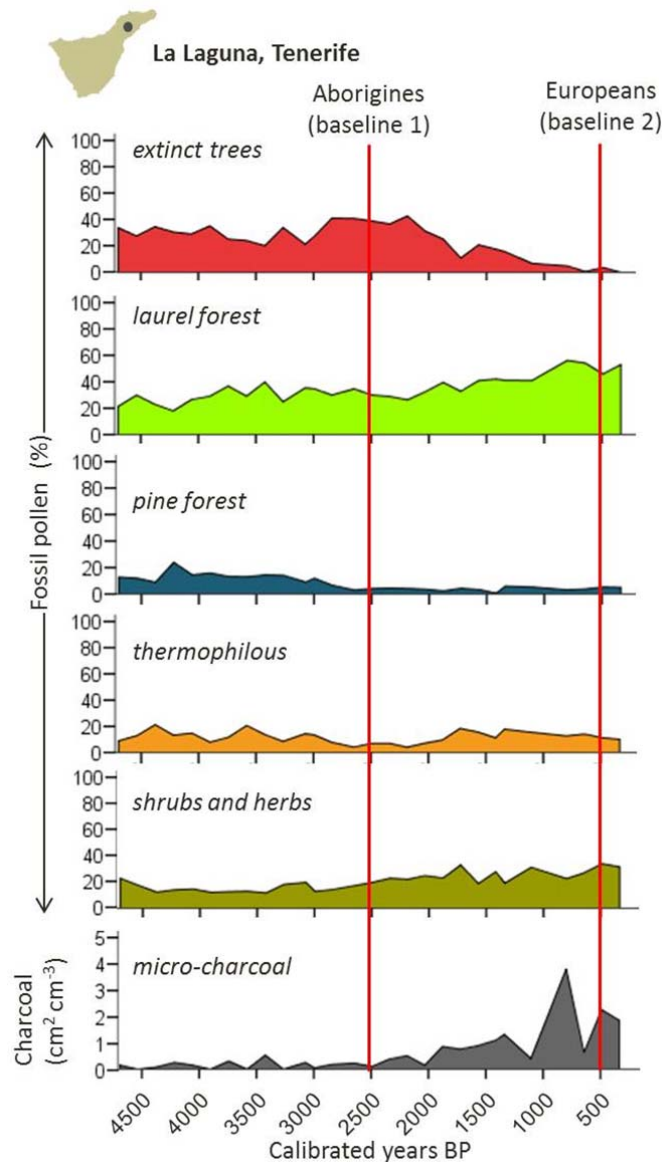
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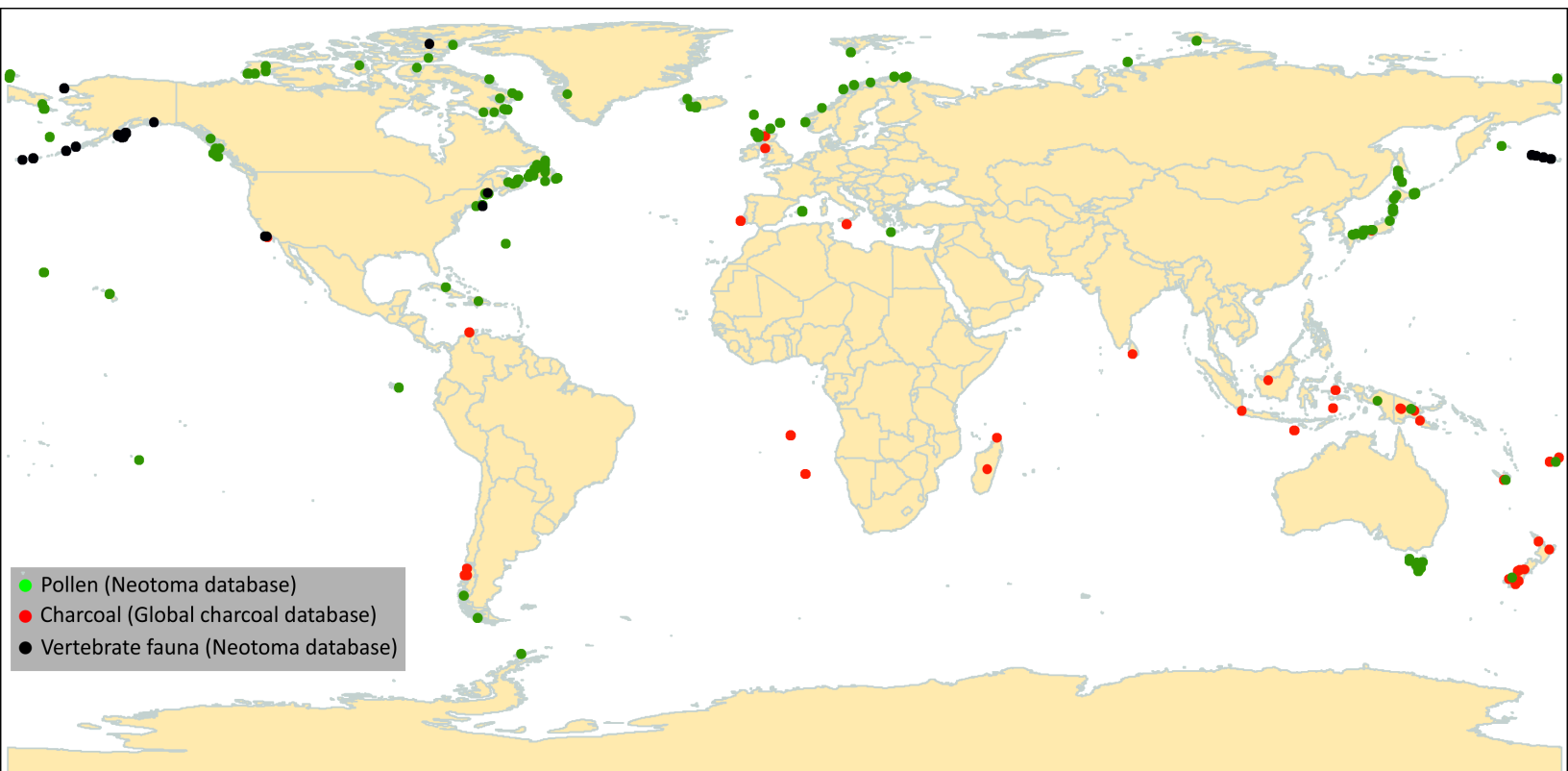
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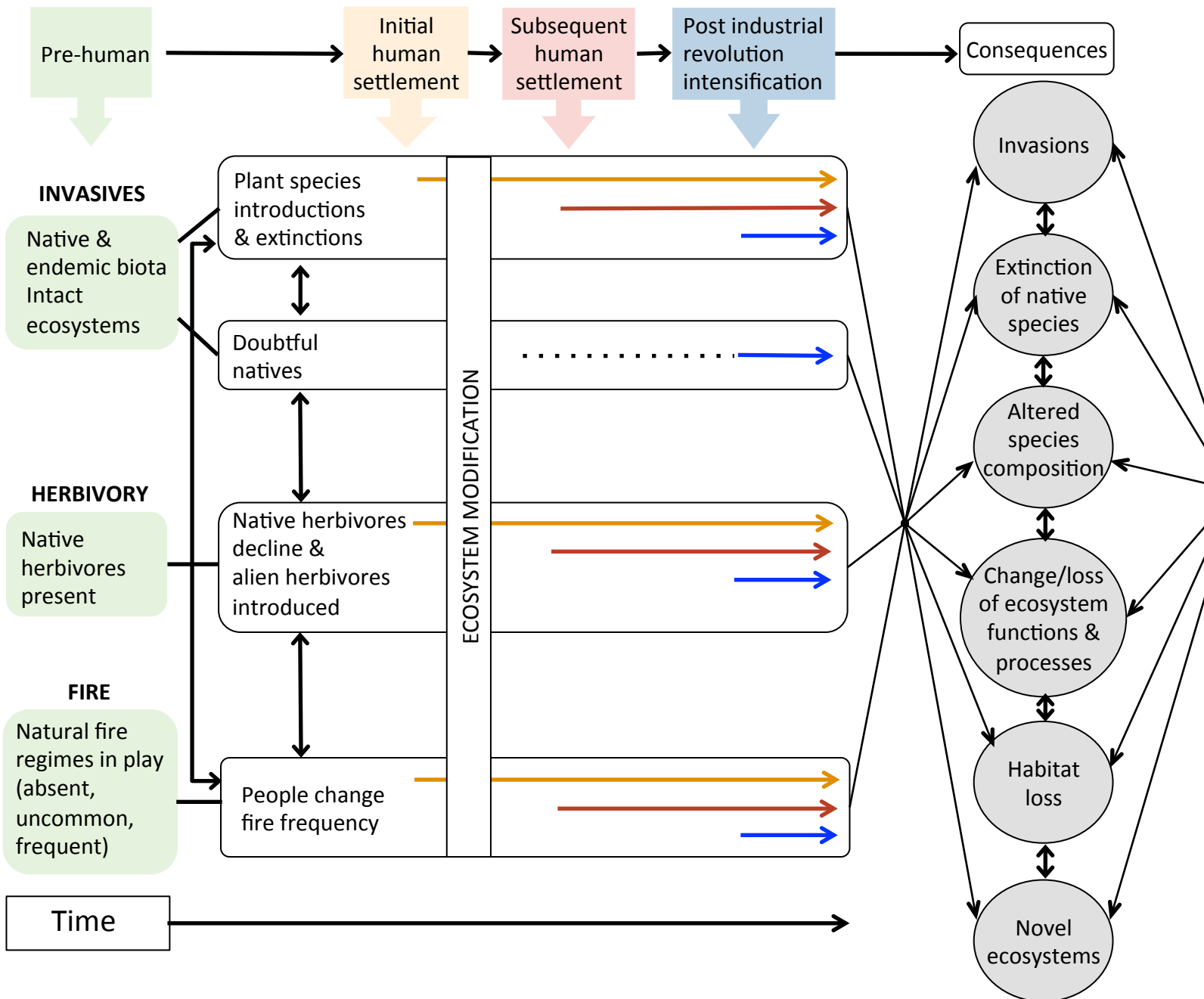
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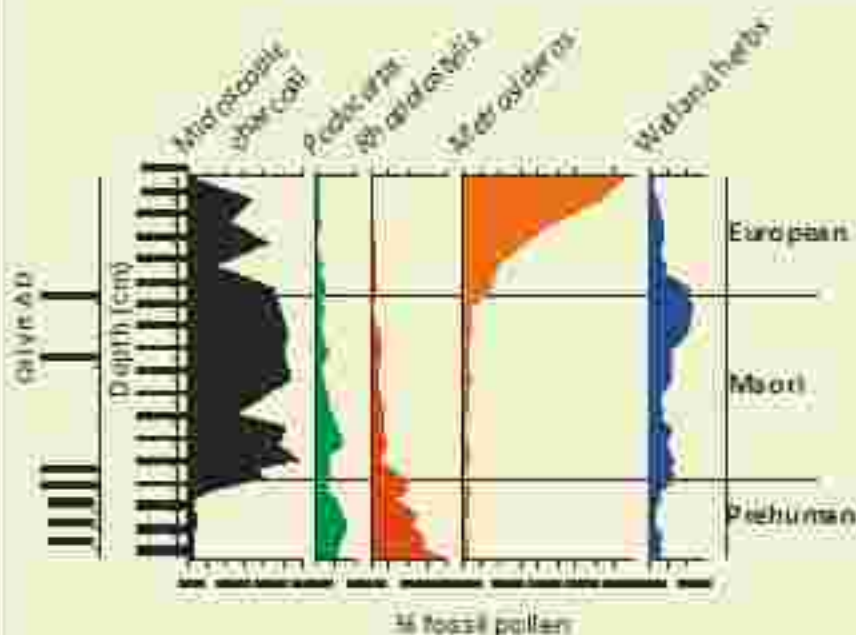




Multiple Baselines

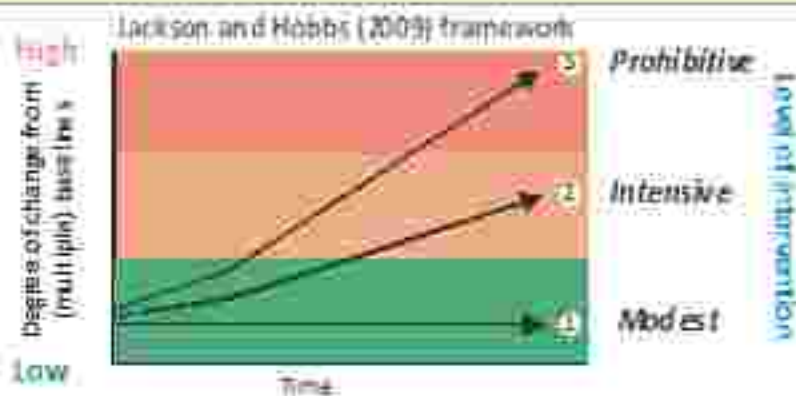


Example 1: Restoring to a pre-human baseline in Poor Knights Islands?

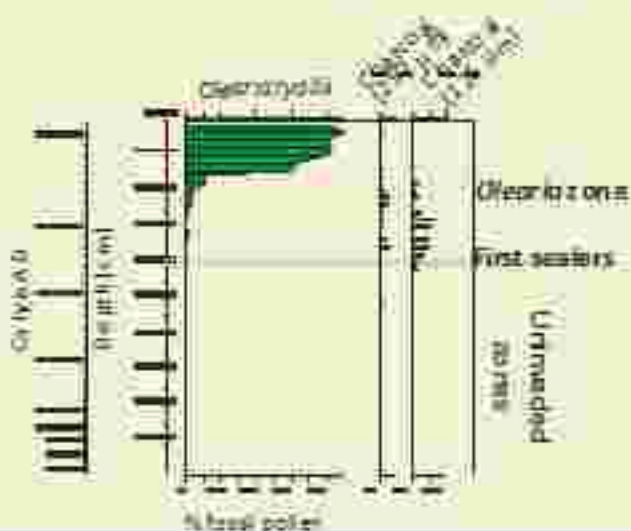


Fossil pollen showed:

- Complete species turnover.
- Extirpation of a dominant conifer (*Podocarpus*) and a palm tree (*Rhopalostylis*).
- Native but novel angiosperm-dominated forest of *Metrosideros*.
- No modern analogue of the pre-human forest at any northern New Zealand island.



Example 2: Managing the alien status of the daisy tree *Olearia lyallii*



Fossil pollen and charcoal showed:

- Although endemic to the New Zealand region, fossil pollen suggests that *O. lyallii* is alien to the Auckland Islands.
- O. lyallii* established when sealers first arrived on the island c.1807, facilitated by their fires.
- O. lyallii* poses minimal risk to ecological integrity.



La Laguna, Tenerife

