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Paper:

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1   **Island biodiversity conservation needs palaeoecology**

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Abstract

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

Introduction

Island ecosystems have always played a leading role in conservation biology. They are often described as natural laboratories, providing model systems for the testing of evolutionary, ecological, and biogeographic theories[1,2]. Remote island ecosystems are hotspots of biodiversity, with legacies of relatively recent human impact and native species' extinctions, and therefore provide significant challenges when considering how to conserve biodiversity. They also offer some of the best-suited scenarios for rapidly advancing our understanding of fundamental aspects of human relationships with nature, and of conservation strategies, including restoration and eradication programmes[3-7]. Examples of programmes specifically tailored to islands include The Global Island Partnership, the International Union for Conservation of Nature (IUCN) Island Initiative Program, and the Small Island Developing States Network.

The isolated nature of remote islands is both part of the problem, in creating 'naïve' native ecosystems, especially vulnerable to outside contact, and a positive, in that the natural barriers to colonisation can, for example, enable successful programmes eradicating non-native vertebrates[5] and/or translocating endangered species. However, success in managing island ecosystems and conserving biodiversity, as well as invasive species eradication, may be contingent upon a sound understanding of an island's specific ecological history. Recent work within restoration ecology has highlighted that ecological history is important, not only to determine the degree of change that has occurred from baselines or reference conditions, but also the level of intervention required to restore an ecosystem towards particular desired states[8-10]. Establishing 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 ecosystems[11-13].

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 initiatives[19].

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

4

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 sites[19].

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' range[20]. 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

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

Key questions in any ecological restoration programme are which species should be conserved, which are priorities for eradication, and which should be closely monitored for potential deleterious ecological future impacts[5]. Palaeoecologial methodologies such as the analysis of plant macro- and microfossils (such as pollen and phytoliths), and preserved DNA can be powerful tools, particularly when used in conjunction with historical evidence, to determine the provenance of plant species on islands, e.g. to determine whether they are native, historical or more recent introductions and to provide insight to address conservation management questions[e.g.20,23,24] through:

- Analysis of native species' ranges and historical distributions[25].
- Developing clear criteria for designation of non-native species status[26].
- Resolving the origin of 'cryptogenic species' (species which cannot be reliably classed as either native or non-native)[27].
- Analysing the origin, dispersal, and rate of spread of invasive species over time[24,28].
- Assessing the long-term impact of (invasive) non-native species on native species.
- Predicting future outcomes of invasions and responses to environmental change[24,29].

155

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

173

In addition to recognition of 'lost species' through plant microfossil identification, syntheses of palaeobotanical, historical, ecological and molecular evidence have also been increasingly used to resolve the conservation status of species with cryptic origins[6,33-35] for example Krauss' clubmoss (*Selaginella kraussiana*) in the Azores[33] and eastern bluebirds (*Sialia sialis bermudensis)* on Bermuda[6]. However, many oceanic 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 ago[36], 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 lacking[36].

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

2) Changes in fire regime

Humans have modified fire regimes in most ecosystem types around the world, as they have colonised and increased in abundance over time[37]. On islands, human modifications of the fire regime typically occurred much later than in continental regions, especially on islands where human presence is more recent (e.g. past 500/5000 years) and where natural ignitions were rare[38]. Knowledge of long-term fire ecology is fundamental to understanding the natural variability of fire regimes (fire history) and the responses and resilience of ecosystems to fire (both natural and human ignited). On islands where fire was a naturally occurring disturbance before human arrival, resource managers face a complicated scenario. They must consider whether fires should be suppressed or prescribed in particular ecosystems, what the long-term ecosystem responses to a particular fire regime will be, and whether post-fire restoration is necessary. Consequently, there is an increasing awareness among scientists and managers that long-term research, including various forms of palaeoecological data, holds significance for contemporary fire management policy[39].

Current management of forest fires consists mainly of prevention (management of fuel), control (fire suppression), and recovery (ecosystem restoration). Palaeoecological proxies such as charcoal, pollen, and fungal spores found in sediments, and tree rings with fire scars, among other indicators, provide information on different spatial-temporal resolutions of fire occurrence and fire regime characteristics[39]. In addition, these datasets allow reconstructions of both fire regimes and vegetation dynamics, and can be used to address key issues related to fire-ecosystem interactions such as:

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

9

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 arrival[40].

233   • Differentiating between natural and cultural fire regimes[41], 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 erosion[45]. 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 again[46]. 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 inevitable[47]. 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-adapted[48]. 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 regimes[49].

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   vegetation[52-54]. 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 values[55].

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 islands[53] 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 invertebrates[61], or unexpected cascading effects facilitating the increase of invasive

297   plant species[59]. 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 dynamics[64]. 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:

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

- Allowing the rate and pattern of herbivore introduction over time to be
  assessed[25].

- Demonstrating the long-term impact of changes in herbivore population on
  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 vegetation[56]. 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 capacity[66-68]. *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 records[18], 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 cycling[3].

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 (see[74]). 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 lowlands[75]. These populations experienced regular environmental hazards from

353 tropical storms and seasonal droughts[76]. A prolonged drought 4200 years ago caused a

354 mass death in the Mare aux Songes[76]. 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 colonisation[77]. 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 time[14]. 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 island[16]. 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

16

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 disturbances[78]. 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 present[79]. 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 volcanism[16]. 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 archipelago[65].

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

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

To maximize the value of palaeoecological data in island conservation we need to incorporate the following considerations: 1) how to more effectively disseminate knowledge about the legacy of a landscape in a manner that will influence the design of planning frameworks for biodiversity conservation; and 2) the limitations of each palaeoecological proxy, such as low taxonomic and temporal resolution, and potential bias towards islands with suitable conditions for fossil preservation. Finally, we advocate establishing routine palaeoecological investigations involving fossil proxies and other biomarkers, as a key step in developing science-based evidence for biodiversity conservation plans for island ecosystems, whether focused on restoration, eradication, or the acceptance of novel ecosystems[81-83]. Such data can lead to a more flexible view on the management of future ecosystems that now include humans and their introduced taxa, and to better-informed debate on the type of nature to be conserved or restored.

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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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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. *Sporormiella*), 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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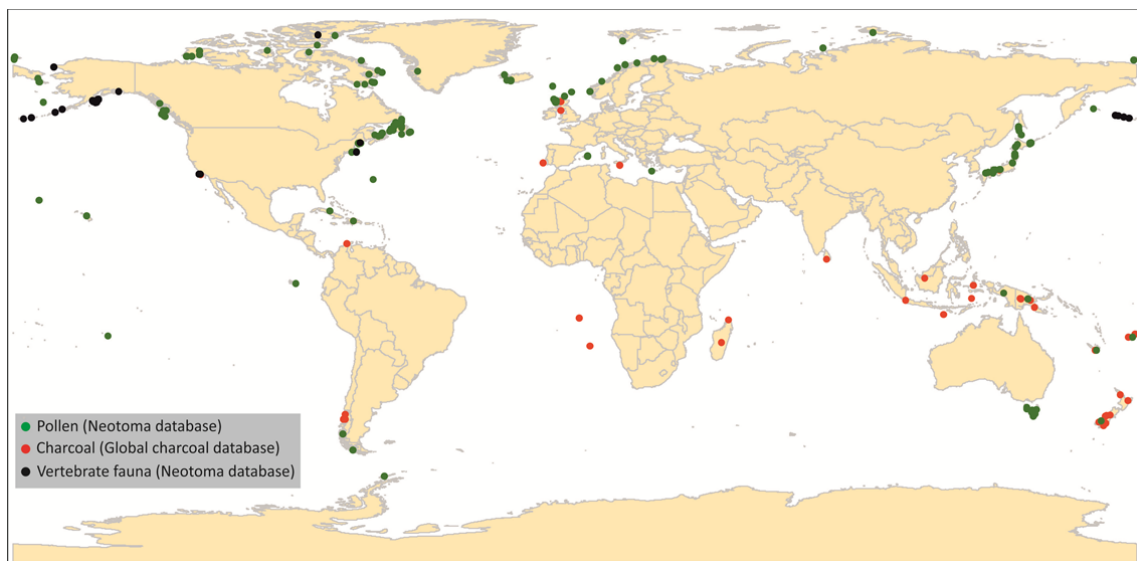
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789 **Figure 2:** Conceptual diagram summarising the main concepts discussed within the
790 text and the suggested management actions. The diagram focuses on the degree of
791 change and main human impacts on island ecosystems over time, taking into
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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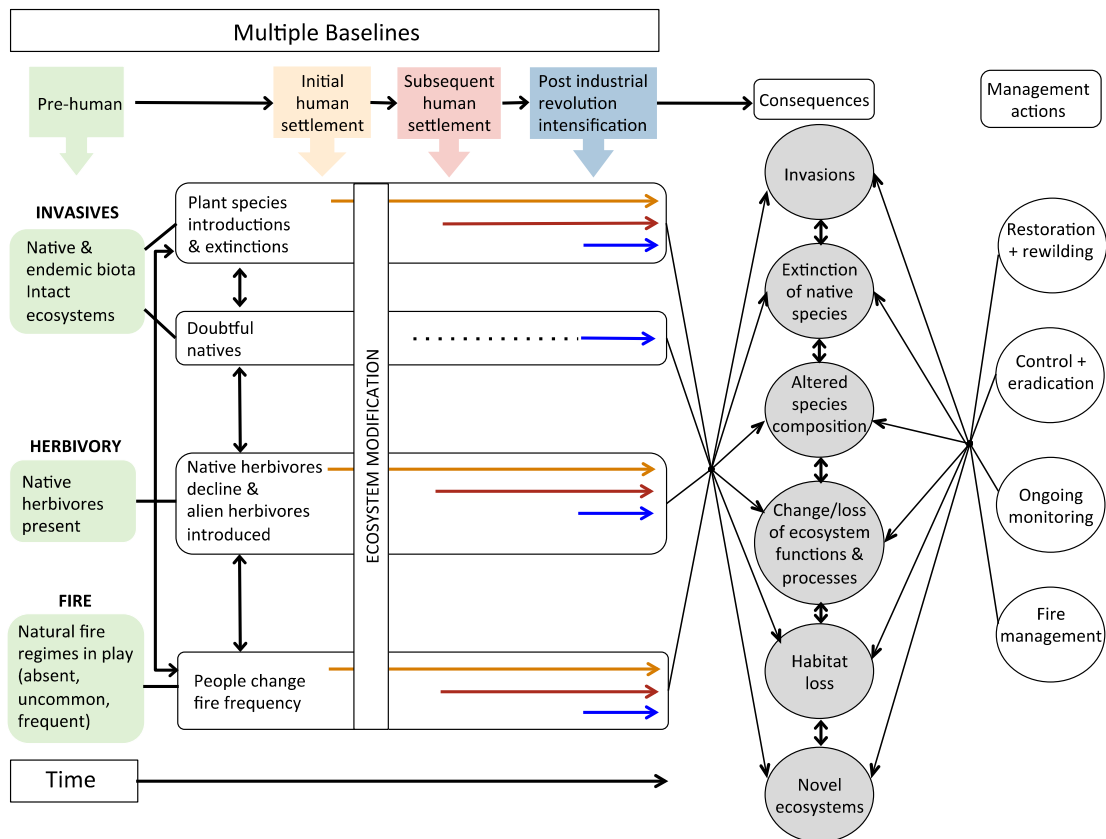
Figure 3. This figure assumes a context where the most desired state is the least altered by humans: although we recognize that this may not always be the key goal of conservation managers in practice. We are showing a modified framework by Jackson and Hobbs (2009)[8] applied to two palaeoecological examples in New Zealand, Poor Knight Islands[16] and the Auckland islands[28]. In the first example, the pollen shows that the current vegetation composition on the Poor Knights is completely different to the pre-human state, and the level of intervention required to return it to its undisturbed state would be prohibitive. Furthermore, palaeoecological insights from the Poor Knights have revealed that the native *Metrosideros* forest is not a good analogue for a pre-human restoration endpoint on other more degraded islands in northern New Zealand. In the second example, pollen and charcoal analyses were able to resolve the non-native status of a tree daisy on Subantarctic Auckland Islands, and show that although its establishment was facilitated by anthropogenic disturbance, the tree has been slow to spread. Pollen and charcoal records suggest this non-native tree poses a low risk to the Auckland Island's ecological integrity, and the level of intervention required to return the invaded sites to a pre-invaded state would be relatively modest. However, current management practices of ongoing monitoring and no intervention are also appropriate.
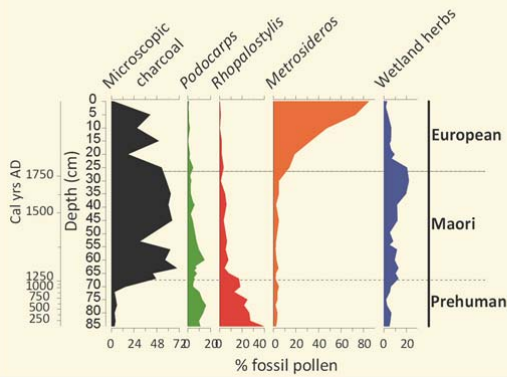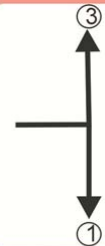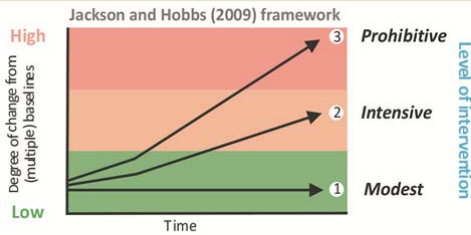
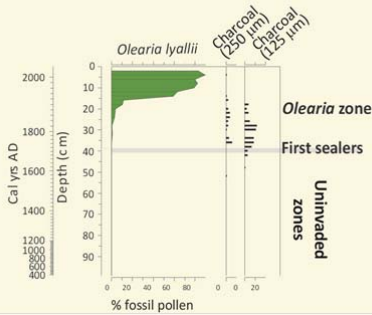**Example 1: Restoring to a pre-human baseline in Poor Knights Islands?**

Fossil pollen showed:

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

Two examples in New Zealand

Jackson and Hobbs (2009) framework

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

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

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

Fossil pollen and charcoal showed:

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

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Figure 4. Summary time-series from a sedimentary sequence from Tenerife (Canary

Islands). We show the long-term dynamics of main Canarian vegetation types: extinct

trees (e.g. *Quercus* and *Carpinus*), Laurel forest (e.g. *Morella* and *Erica*), Pine forest (e.g.

Pinus canariensis), thermophilous forest (e.g. *Juniperus* and *Phoenix*), and shrubs and

herbs (e.g. Poaceae). In addition, we show micro- charcoal counts to depict fire regimes.

We have highlighted in red bars two obvious points for calculation of alternative

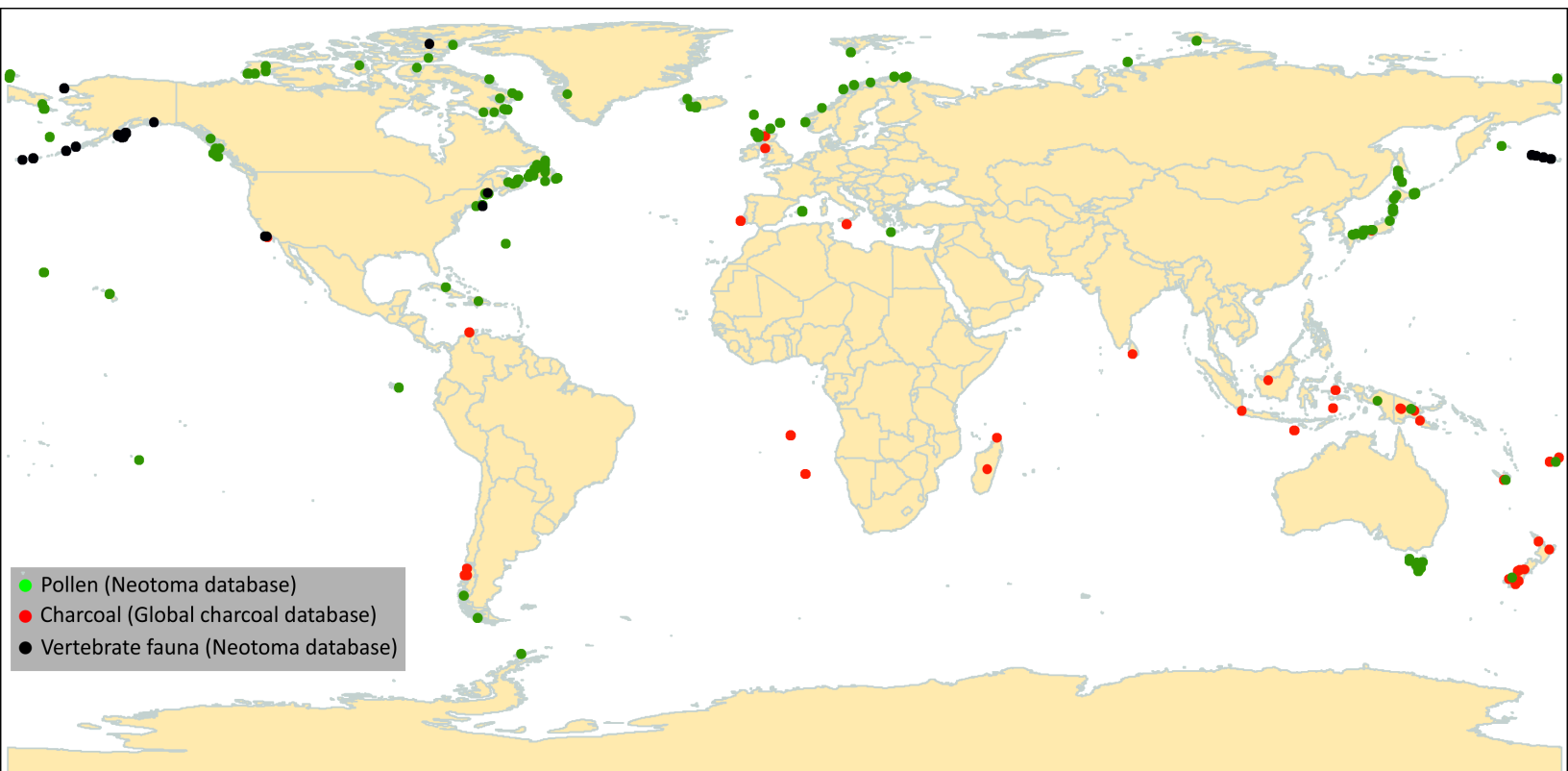baselines for La Laguna (Tenerife). See de Nascimento *et al.* [32] for full details.

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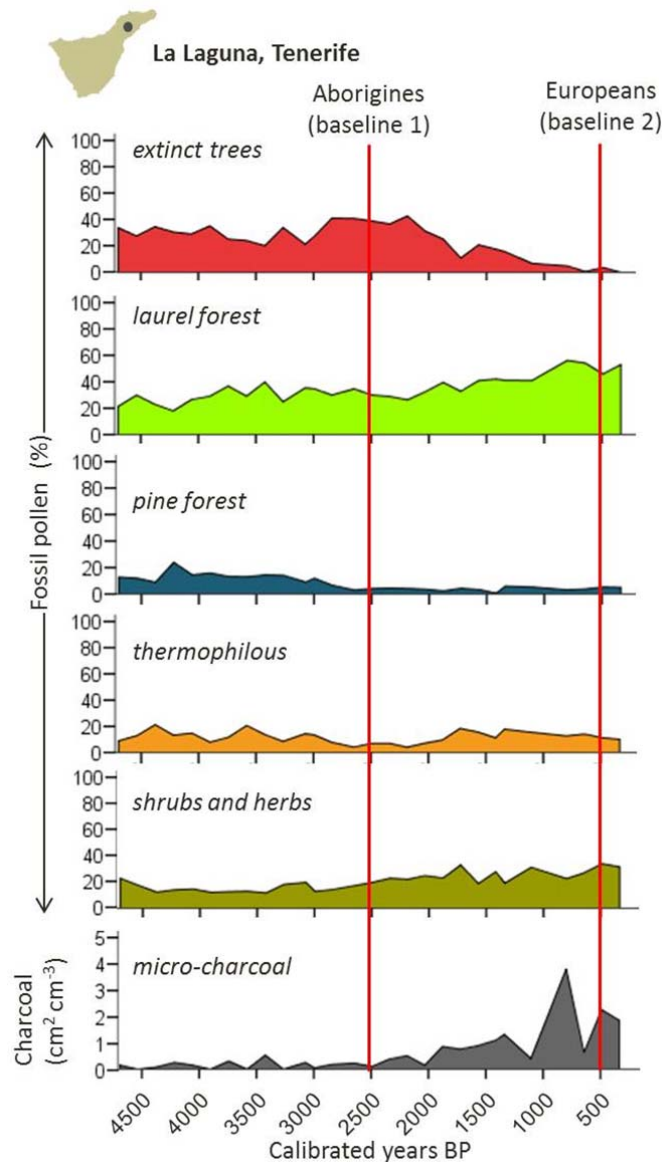
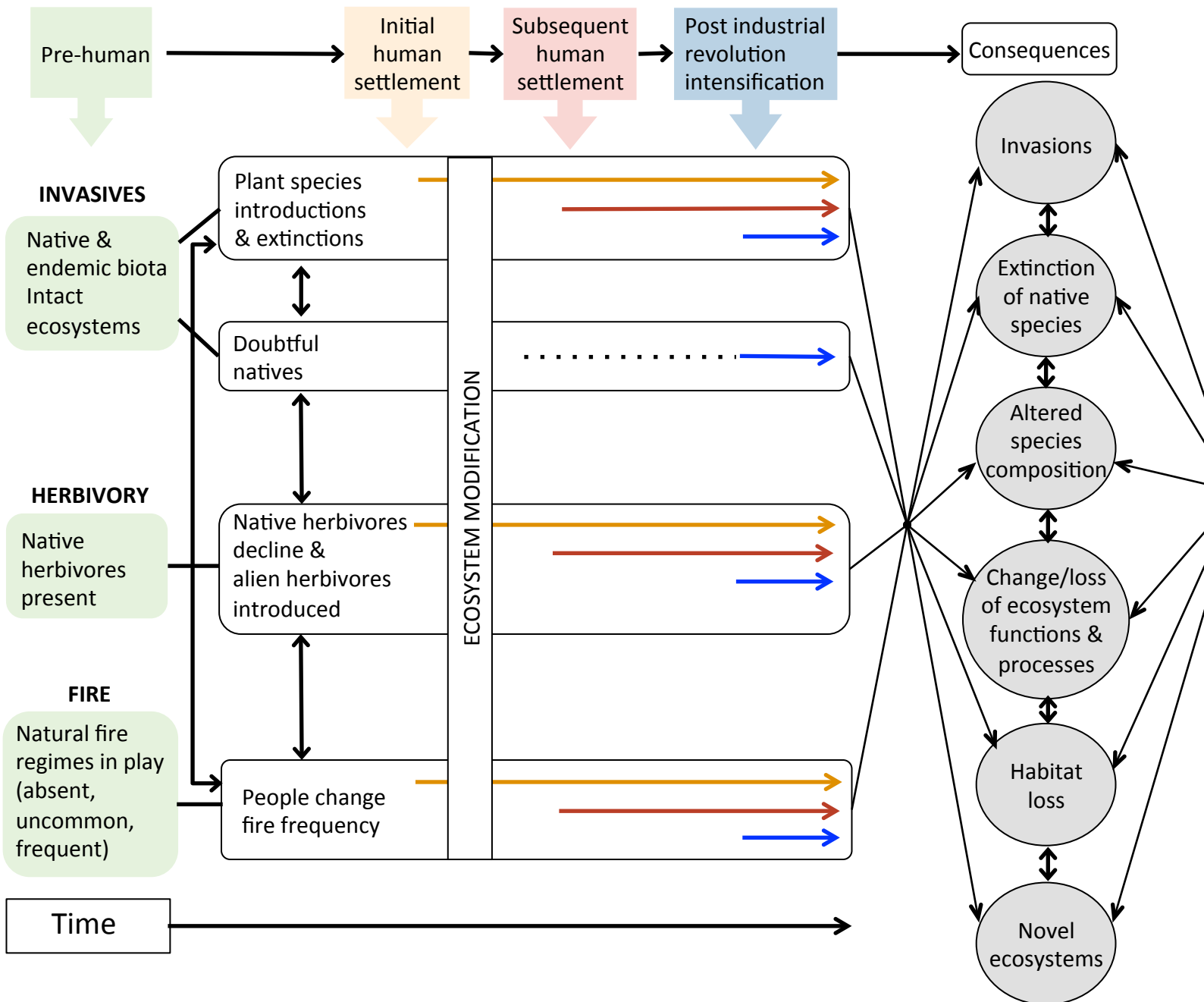Pollen (Neotoma database)
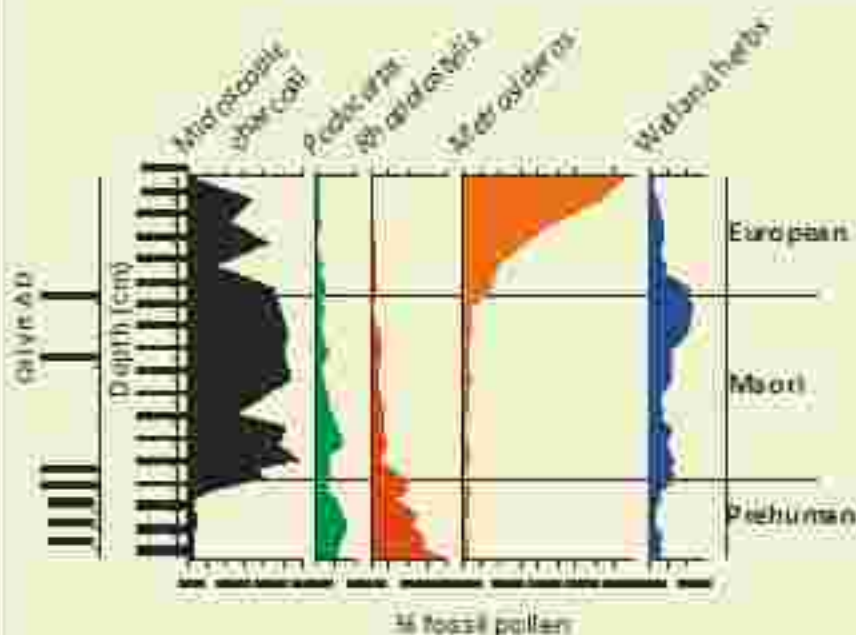Charcoal (Global charcoal database)
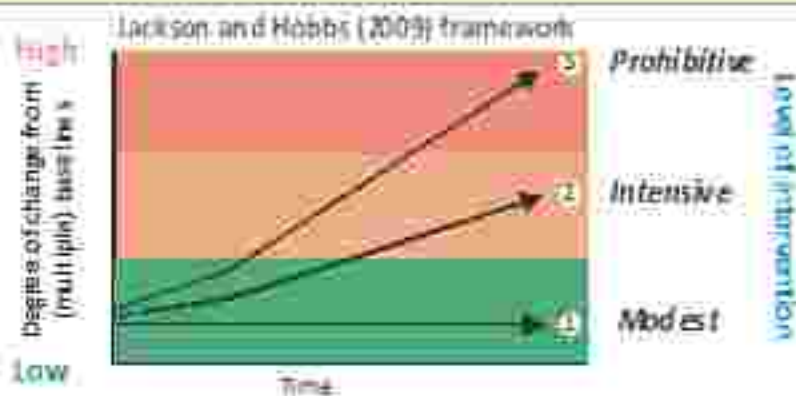Vertebrate fauna (Neotoma database)

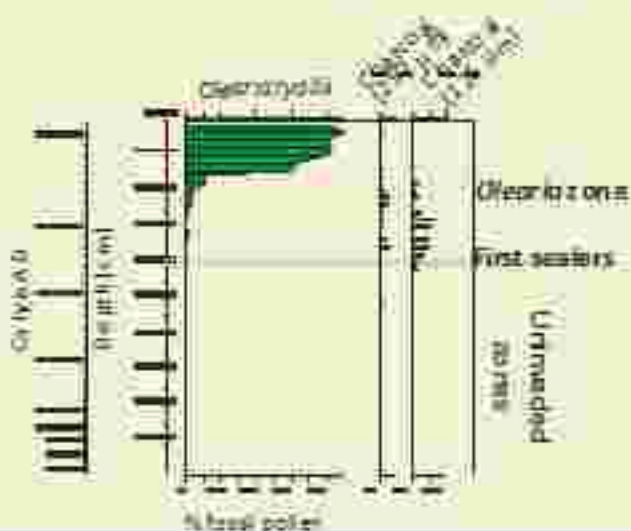# Example 1: Restoring to a pre-human baseline in Poor Knights Islands?

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Two examples in New Zealand

Poor Knights Islands

① Auckland Island

Jackson and Hobbs (2009) framework

Prohibitive

Intensive

Modest

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

Fossil pollen and charcoal showed:

a) Although endemic to the New Zealand region, fossil pollen suggests that *O. lyallii* is alien to the Auckland Islands.

b) *O. lyallii* established when sealers first arrived on the island c.1807, facilitated by their fires.

c) *O. lyallii* poses minimal risk to ecological integrity.

La Laguna, Tenerife