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Research

General patterns of niche construction and the management of 'wild' plant and animal resources by small-scale pre-industrial societies

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Niche construction efforts by small-scale human societies that involve 'wild' species of plants and animals are organized into a set of six general categories based on the shared characteristics of the target species and similar patterns of human management and manipulation: (i) general modification of vegetation communities, (ii) broadcast sowing of wild annuals, (iii) transplantation of perennial fruit-bearing species, (iv) in-place encouragement of economically important perennials, (v) transplantation and in-place encouragement of perennial root crops, and (vi) landscape modification to increase prey abundance in specific locations. Case study examples, mostly drawn from North America, are presented for each of the six general categories of human niche construction. These empirically documented categories of ecosystem engineering form the basis for a predictive model that outlines potential general principles and commonalities in how small-scale human societies worldwide have modified and manipulated their 'natural' landscapes throughout the Holocene.

Keywords: human niche construction; resource management; indigenous knowledge small-scale societies; ecosystem engineering; predictive modelling

1. INTRODUCTION

> *What is certain is that the forest dwellers . . . were not passive in their environment but actively altered it.* Groube [1, p. 289]

Humans have a long history of niche construction—of modifying their environments in a wide range of different ways, large and small, through behaviour patterns that are both deliberate and inadvertent [1–20]. Although the consequences of human niche construction are not always anticipated, one of the primary goals of environmental engineering by human societies has been to increase their share of the annual productivity of the ecosystems they occupy by increasing both the abundance and reliability of the plant and animal resources they rely on for food and raw materials. Using fire and simple technology in the modification of vegetation communities, our distant ancestors were shaping environments more to their liking in ways that we can see in the archaeological record back perhaps as far as 40 000 years ago [1,8].

Human manipulation of ecosystems intensified at the end of the Pleistocene, when societies in different regions of the world began to independently domesticate a broad spectrum of plant and animal species. Clearly separated in space and time, these multiple independent domestication events occurred, it has been argued, within a broader behavioural context of niche construction [16]. As world climates and environments stabilized by about 12 000–10 000 years ago, human societies worldwide were actively auditioning many wild species of plants and animals, and intervening in their life cycles in a variety of different ways that would reshape local biotic communities and ecosystems. Some of these human management efforts led to the domestication of plants and animals, and genetic and archaeological research in recent years has substantially expanded our understanding of the temporal and spatial context of initial domestication of an increasing number of species worldwide [21].

While human manipulation and management of some species resulted in genetic and morphological changes associated with their domestication, other human niche construction efforts have targeted a broad spectrum of species that would remain 'wild' in terms of an absence of obvious genetic and morphological modification. Nakao [2] coined the term '*hansaibai*' (*han* and *saibai*, i.e. half and cultivation) to refer to such species that are neither domesticated nor wild [22,23]. Although they lack both the morphological markers and the higher profile accorded domesticates, these numerous manipulated species have been, throughout the Holocene, the subject of sustained human attention and energy, and have represented

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important long-term resources for pre-industrial human subsistence economies worldwide.

Along with obtaining a much more accurate and complete picture of where and when different species of plants and animals were domesticated worldwide, research has also substantially expanded our understanding of many of the basic underlying rules that define and shape the various developmental contexts and pathways that have led to domestication—the general characteristics that make particular plants and animals attractive targets for domestication—why some taxa are independently domesticated multiple times in different world regions, while others are not, and the basic general strategies used by human societies to create and sustain relationships of domestication [21].

In comparison, relatively little attention has been focused on looking for underlying principles or general patterns of niche construction exhibited by small-scale human societies worldwide during the Holocene in their utilization of wild or non-domesticated plants and animals. Are there certain sets of characteristics, and certain taxa of wild plants and animals that are logical targets for human engineering? And are there a finite number of general solutions or strategies for management and manipulation of these targeted taxa that can be documented in the past and present day across different world areas? In this article, I present an overall framework of understanding, a predictive model, for human niche construction focused on wild species by small-scale societies during the Holocene which parallels that which has been developed for domesticates.

The initial step in developing this model involved an explicitly inductive search for, and identification of, descriptions of potential human niche construction strategies involving wild plant and animal resources. This search was primarily focused on North America, which has both a rich diversity of different environmental zones and a substantial empirical corpus of archaeological, ethnohistoric and ethnographic descriptions of how indigenous small-scale societies manipulated the 'natural' world.

Following this initial continent-wide search, a simple 'pattern recognition' process was employed in an effort to organize the identified examples of human niche construction into a coherent and all-inclusive set of distinct categories of management of different segments of natural biotic communities. This resulted in the identification of six general categories of human niche construction, based both upon the shared characteristics of the target species and upon generally similar patterns of human intervention in their life cycle.

— *General modification of vegetation communities*: creating mosaics and edge areas, and resetting successional sequences.
— *Broadcast sowing of wild annuals*: creating wild stands of seed-bearing plants in river and lake edge zones exposed by receding high water.
— *Transplantation of perennial fruit-bearing species*: creating 'orchards' and berry patches in proximity to settlements.
— *In-place encouragement of perennial fruit and nut-bearing species*: creating landscapes patterned with point resources.
— *Transplantation and in-place encouragement of perennial root crops*: creating root gardens and expanding the habitat of wild stands.
— *Landscape modification to increase prey abundance in specific locations*: enhancing salmon streams and creating clam gardens, fish ponds and weirs, and drive lines.

Characterization of each of these six general categories of environmental manipulation in the following sections of this article in turn provides the basis for a concluding formulation of a general predictive model of human niche construction efforts involving wild components of natural biotic communities. The primary purpose in developing such a predictive model or abstract explanatory framework is to encourage further efforts to identify both additional specific examples, and perhaps additional general categories, of human niche construction involving wild species in other world areas, while also providing a better understanding of the underlying general principles and commonalities in how human societies worldwide have modified and manipulated their natural landscapes throughout the Holocene.

For a number of reasons, recognition of human niche construction involving wild as opposed to domesticated species of plants and animals can often prove difficult. Management and manipulation of free-living plant and animal populations and non-agricultural ecosystems are often carried out by small-scale societies. These hunter–gatherers and farmers, numbering a few hundred to a few thousand people [24], characteristically leave a relatively light footprint on the landscape. In addition, human niche construction involving non-domesticated or wild species often mimics natural events and processes, making it difficult to differentiate between the two. And finally, there has been a notable absence of shared terminology employed in the documentation of human management of wild plants and animals (table 1), and a corresponding lack of linkage to an appropriate overarching conceptual framework and paradigm for comparative analysis and pattern recognition of different general forms of human ecosystem engineering, worldwide. This final problem is easily addressed by adopting the concept of *human niche construction*, which provides a general unifying perspective for integrating consideration of human efforts at management and modification of ecosystems [30,31].

For well over a half century, scholars have been providing accounts of how small-scale pre-industrial societies situated in a variety of different ecosystem settings, from tropical and temperate forest zones to semi-arid grassland environments, modify non-agricultural landscapes and natural biotic communities in favour of particular target species that are valued as sources of food or for the manufacture of a range of material culture categories (e.g. clothing, tools, structures). These 'ecosystem improvement' efforts take a variety of different forms, target a wide range of species and vary considerably in terms of their

Table 1. Twenty five different terms for human niche construction.

aboriginal agronomy [25]
aboriginal land management [5,18]
anthropogenic environment [18]
anthropogenic ecology [12,18]
anthropogenesis [26]
anthropogenic forest [18]
anthropogenic landscape [18]
disturbance regime [18]
domesticated landscape [6,27]
domestication of the environment [25]
engineered environment [18]
environmental manipulation [1,12]
forest management [1]
hansaibai ('half cultivation') [2]
forest modification [18]
humanized landscape [1]
human-modified environments [18]
Indian environmental management [5]
indigenous management [12,28]
indigenous human intervention [18]
indigenous resource management [15]
semi-cultivation [29]
taming of the forest [1]
traditional resource management [14]
woodland management [22]

scope or focus, from very general attempts to shift vegetation communities towards earlier successional stages (and their higher representation of economically valued species), to very specific activities focused on a particular species or species group. Given the range of different societies and environments that have been considered, worldwide, by scholars from different generations and different disciplinary perspectives, and the rich variety of different human ecosystem improvement behaviour strategies that have been encountered, it should not be surprising that a multitude of different terms and phrases have been coined to characterize human manipulation of environments (table 1).

While certainly reflective of broad geographical, temporal and behavioural coverage, this profusion of different descriptive terms, unfortunately, has also served to focus attention on individual region-specific and often species-specific case study examples and has emphasized their seeming distinctively different and unique character. As a result, attention has been drawn away from broader more inclusive consideration of what all of these human behaviour patterns have in common—they all represent human strategies of ecosystem engineering or niche construction. With the adoption of niche construction as a unifying concept, all of these different human strategies for environmental manipulation, and all of the various descriptive terms that have been employed, come into broader focus as comprising a large and coherent category. This in turn opens the way to look for broad patterns and general categories of resource management and manipulation, as well as the underlying general principles of how small-scale human societies go about shaping their environments to their advantage.

2. GENERAL MODIFICATION OF VEGETATION COMMUNITIES: CREATING MOSAICS AND EDGE AREAS, AND RESETTING SUCCESSIONAL SEQUENCES

By far the most commonly documented form of human niche construction by small-scale societies, worldwide, is a general effort to alter the overall composition of vegetation communities in order to increase the relative abundance of early successional stage plants that provide a source of food for either humans or animals that play a role in human economies, at the expense of other species of plants of lesser economic value [26]. This overall modification of vegetation communities is directed towards disrupting the reproductive rate of slowly growing 'climax' vegetation, enhancing the short-term productivity of herbaceous plants, and increasing in-patch diversity [6]. In contrast to the variety of different efforts that are directed towards selectively enhancing individual plants or clusters of plants of known location, which will be discussed below, general strategies for shaping vegetation communities represent more diffuse efforts designed to result in larger scale patterns of modification. Interestingly, such general efforts to modify vegetation communities appear to be the primary way in which human societies attempt to increase biomass levels of animal species of economic importance [32]. As will be discussed later in this article, when compared with plants, relatively few species of wild animals are the subject of tightly focused human niche construction efforts, and the majority of these involve aquatic resources (fishes and bivalves).

Fire has long provided small-scale societies with a relatively easy, low-cost and effective way of generally reshaping vegetation communities in ways that increase the relative abundance of a range of different plant and animal food resources. Small-scale, moderate-impact burning of open grassland and shrub communities as well as forest environments is directed towards creating and maintaining a mosaic of small patches of habitat at different stages of regeneration [14,32–39]. The vegetation patches at early stages of regeneration, and the edge or interface zones between them, support higher biomass levels of plant and animal species of economic importance to humans than do later successional communities. Food plants used by humans (and other species) across a broad range of environments often have a competitive advantage early in a successional sequence, but decline in abundance over time. This general strategy of establishing mosaic landscapes with a variety of early-stage vegetation communities and extensive interface edge areas also represents a very effective strategy for humans to employ in order to increase the carrying capacity of their environments for terrestrial prey species. In both tropical and deciduous forest environments, for example, clearing of the overstorey canopy and the creation of open areas increase the carrying capacity and density levels for a wide range of grazing and browsing species [32]. In the eastern woodlands of North America, intermediate-impact forest clearance, both pre-Columbian and present day, has resulted in an increase in white-tailed deer (*Odocoileus virginianus*) populations [5,39]. Small-scale mosaic burning in more open grassland habitats has also been documented as increasing the abundance of game animals. In the spinifex (*Triodia* spp.) sandplains and dune fields in western Australia, for example, controlled fires have been shown to result in greater habitat heterogeneity at the spatial scale of the human day range, with the increase in landscape diversity resulting in an increase in small-animal hunting productivity [40].

Along with being a widely employed and relatively easy way of shifting vegetation communities towards earlier successional stage species and maintaining habitat heterogeneity within human resource catchment zones, fire is also the form of human niche construction that is most easily seen in past environmental and archaeological records. Although it is not always easy to distinguish between natural and anthropogenic fires, charcoal, pollen and fire scar tree ring records from a range of different environments, worldwide, have been cited in a steady stream of studies documenting the widespread practice of deliberate burning of vegetation by human societies throughout the Holocene [5,9,17,26,36,40–53]. While increasingly sophisticated analyses of fire records that combine different approaches and multiple datasets are improving our ability to establish the scale, frequency and causes (natural versus humans) of past burn episodes, other forms of human niche construction are much more difficult to document in the archaeological record.

3. BROADCAST SOWING OF WILD ANNUALS: CREATING NEW STANDS OF SEED-BEARING PLANTS IN RIVER AND LAKE EDGE ZONES EXPOSED BY RECEDING HIGH WATER

Along with using fire as a relatively low-cost way of opening up landscapes to colonization by early successional stage plant species, small-scale human societies in different world regions also facilitated, with relatively little labour investment, the colonization by early succession annual seed plants of unoccupied habitat areas that opened up predictably on an annual basis—the river and lake edge zones exposed each year by receding high water. This effective filling-up of empty habitat patches by establishing new stands of wild seed-bearing plant species could be accomplished through the simple practice of broadcast sowing of harvested seed.

Take, for example, the description provided by Le Page du Pratz in the early 1700s of Natchez women and children scattering the seeds of a plant he called *choupichoul* along the sandbank margins of the lower Mississippi River that had been newly exposed by receding spring floodwaters [54]. Following seed dispersal, the planters casually pushed sand over the seeds with their feet. No other investment of labour was involved. Today the plant in question, *Chenopodium berlandieri* (chenopod, lamb's quarters, goosefoot), remains a commonly occurring pioneer of river valley settings in the eastern woodlands of North America. It colonizes a variety of open and disturbed soil environments, both anthropogenic and natural, but it is most frequently found in open sand bank settings exposed by the receding floodwaters of spring. Dependent upon a variety of poorly documented vectors of seed dispersal in river valley settings, and impacted by modern herbicides and introduced European chenopods, *C. berlandieri* today is usually found only in small patches, often mixed with introduced chenopods, or as isolated plants, rather than in extensive stands. In full sun settings, individual free-living *C. berlandieri* plants can grow to six feet in height and produce up to 50 000 small seeds, and would have required very little, if any, attention from humans during the growing season [54]. In contrast to the small patches and isolated individual plants of today, the Natchez, through their concerted and well-timed human seed dispersal by broadcast sowing onto open sandbank situations, could have created large and very productive wild stands of this economically important annual seed plant with an investment of relatively little effort. It is interesting to note that such efforts would not have occurred in exactly the same locations from year to year. Spring floodwaters would have reshaped river valley topography, and shifted the locations of prime sandbank real estate on an annual basis, necessitating the relocation of anthropogenic chenopod stands each year.

Unfortunately, it is not possible to establish whether the seeds scattered by the Natchez had been harvested from local wild stands of chenopod the preceding autumn, or whether they represented the seed stock of the domesticated *C. berlandieri* that had been grown in eastern North America for more than 3000 years [55]. Nor have any good archaeological markers of this form of niche construction yet been identified, so the time depth of broadcast sowing in river or lake edge habitats, in eastern North America or any other world areas, remains undocumented.

Broadcast sowing following spring floods, however, could have had considerable time depth and could have been employed along many of the river valleys of the eastern woodlands, and could have involved a number of other wild floodplain pioneering seed plants in addition to chenopod, including marshelder (*Iva annua*), sunflower (*Helianthus annuus*), erect knotweed (*Polygonum erectum*) and cucurbits (*Lagenaria secaria, Cucurbita pepo* ssp. *ovifera*).

Broadcast sowing of small-seeded annuals in areas recently exposed by receding floodwaters has also been described in a number of other locations in North America, including the Southwest and Great Basin [11,56]. In one of the best-documented examples [29], Cocopa societies of the lower Colorado are described as broadcast sowing in 'décrue' fashion seeds that they had harvested the previous autumn, on thin, muddy nutrient-rich river-bank soils exposed by the receding floodwaters of the Colorado [56]. These floodplain plots were up to 50–100 m wide and could extend several kilometres along the river. They received no further attention prior to harvest, and included any of five different identified species. Three of these were historic-period introductions of Eurasian origin, while two species of panic grass (*Panicum*) were indigenous and known to have been grown at least as far back as 1541, leading Castetter & Bell [29] to raise the possibility that this human environmental modification or 'semi-cultivation' of grasses may have preceded maize–bean–squash agriculture in the region. Although involving different plant species, and located in very different environmental settings, the Natchez & Cocopa case study examples of décrue sowing of annual seed crops are similar in that human niche construction efforts in both situations took advantage of naturally occurring and reliably predictable open areas that held the additional dual benefits of high ground water levels for early seedling growth and fertile soils owing to nutrient-rich annual floodwaters.

These attractive aspects of seasonally flooded floodplain settings (planting areas clear of competing vegetation, and having fertile soil and adequate soil moisture) also played a role, it is interesting to note, in other examples of broadcast sowing of wild seed-bearing annuals by small-scale societies in North America. The broadcast sowing of a number of seed-bearing annuals, including chenopod, Indian rice grass and busy blazingstar (*Mentzelia dispersa*), by Western Shoshone groups has been documented in the Great Basin near springs and seeps (locales with high soil moisture) [57,58]. Areas to be sown were also frequently burned over in preparation, thereby both returning some nutrients to the soil and clearing competing vegetation. Similar décrue niche construction strategies have also been described for other world areas [6].

4. TRANSPLANTATION OF PERENNIAL FRUIT-BEARING SPECIES: CREATING ORCHARDS AND BERRY PATCHES IN PROXIMITY TO SETTLEMENTS

In a form of niche construction that reflects several of the same principles at work in the creation of dense stands of annual seed plants adjacent to river and lake margins, small-scale human societies also establish new stands of fast-growing perennial fruit-bearing trees and bushes in proximity to settlements and other frequently visited locales (e.g. major trails, active and fallow garden plots). Rather than planting seeds in naturally occurring open areas, this form of human niche construction involves digging up seedlings or young trees that are found scattered through the forest and transplanting them in anthropogenic disturbed habitat openings in closer proximity to human settlements, and in much greater density than they occur in the wild.

Eastern North America again provides a good case study example of the key aspects of this fruit tree transplantation strategy. As Gremillion [59] has noted, the peach (*Prunus persica*) was one of the European domesticates most rapidly and widely adopted by indigenous societies of the eastern woodlands, owing in large measure to its key similarities to native wild trees that were already subject to transplantation and tending by indigenous societies. Along with the peach, these native species targeted for transplantation all share a number of key attributes: they are weedy colonizers and require a minimum of labour investment for transplantation or tending; they mature rapidly, bearing fruit within *ca* 3–5 years; and they are perennials with life spans of several decades or more, ensuring a sustained harvest of fruit each year with minimal maintenance.

The eastern woodlands of North America have a dozen or more native fruit-bearing trees that flourish in open sunny forest edges and clearings, including honeylocust (*Gleditsia triacanthos*), gum (*Nyssa* spp.), elderberry (*Sambucus canadensis*), mulberry (*Morus rubra*), hackberry (*Celtis occidentalis*), sugarberry (*Celtis laevigata*), hawthorn (*Crataegus* spp.), plum and cherry (*Prunus* spp.) and persimmon (*Diospyros virginiana*), all of which were potential targets for transplantation [60]. William Bartram and other early travellers through the East mention plums, peaches, persimmons, beautyberry and red mulberry, among other species, growing in orchards adjacent to old Indian settlements [5,61].

Many early historical accounts in the eastern woodlands of North America also describe a variety of different berry crops growing in 'old fields' around Indian settlements [5,11,61]. Gremillion [60] lists wild strawberry (*Fragaria virginiana*), groundcherry (*Physalis* spp.) and *Rubus* species (dewberry and blackberry) as often observed thriving in open areas adjacent to settlements, with understorey shrubs that produced edible fruits such as blueberry and cranberry (*Vaccinium* spp.), serviceberry (*Amelanchier alnifolia*) and huckleberry (*Gaylussacia* spp.) recorded as commonly present in overgrown fields [60,62–63]. Similarly, Doolittle [11] summarizes early European descriptions from the Northeast of raspberries and strawberries growing close to settlements, with accounts often mentioning their abundance in overgrown fallow fields, and occasional reports of transplanting.

Transplantation of fruit and berry species adjacent to settlements has also been documented on the Plains of North America. Adair & Drass [64] discuss the greater abundance of fruit- and berry-producing perennial plants within the fields and on the margins of permanent and semi-permanent settlements on the Plains, and reference both the Pawnee transporting American plums (*Prunus americana*) with them to their Oklahoma reservations, and the descriptions and maps of fruit thickets adjacent to Hidatsa settlements. They also suggest that higher quantities of fruit remains in archeobotanical assemblages from late prehistoric sites (e.g. plum, chokecherry) may reflect an increased occurrence of perennial fruit-bearing species in association with large aggregate villages and accompanying farm fields.

Documentation of indigenous societies in North America transplanting economically important species in proximity to their settlements is not, however, limited to the Plains and eastern woodlands, or to perennial fruit and berry crops. There are records of people relocating plants of economic value in the subarctic [65], Northwest Coast, California, Great Basin, Southwest and Mexico. A variety of tuberous species are frequently mentioned in the literature, for example, as potential transplants. Deur [66] discusses the transplanting of springbank clover (*Trifolium wormskjoldii*) and other estuarine root crops along the Northwest Coast, and onions (*Allium*) are mentioned as target species for transplantation in both eastern North America [11] and California. Similarly, Jerusalem artichoke, the perennial cousin of the sunflower, is described as a frequent invader of old fields, and a possible target for transplantation throughout its broad geographical range across the Plains and eastern North America. In addition, the Hopi are noted as having relocated the cattail (*Typha angustifolia*) closer to their settlements [11], and plants of a ritual nature, including tobacco and, in the Southeast, *Ilex vomitoria*, are also documented as having been transplanted close to settlements. The Kumeyaay in California have also been described as having an extensive and far-reaching programme of transplantation and tending of a select yet broad assemblage of wild perennial food plants, including oaks, pines, palms, mesquite, agave, yucca, wild grapes and cacti [56,67]. Similarly, Bye & Linares [68] describe the relocation of dead trunks of morning glory trees adjacent to settlements in the Valley of Mexico to ensure a reliable harvest of a highly prized mushroom (*Pleurotus ostreatus*).

As Gremillion [59] and Doolittle [11] both note, this general practice of transplanting long-lived species, from fruit trees to fungi, adjacent to settlements allowed for easier harvesting and shorter travel time. It would also have strengthened perceptions of ownership of the resources, reduced unwanted harvesting of crops by human and non-human interlopers and have facilitated the monitoring and harvesting of fruits, berries and other plant parts as they matured.

As is the case with human broadcast sowing of annual seed plants, the establishment of transplantation orchards of fruit-bearing perennials has been difficult to document in the archaeological record. Transplantation of parthenocarpic fig trees (*Ficus carica*) in proximity to 11 000 year old settlements in the Jordan Valley has recently been proposed, providing the oldest potential evidence for transplantation of a fruit-bearing species [69]. Witness tree records obtained within a decade or two of initial abandonment of Native American settlements in the Southeast United States, before the re-establishment of an overstorey canopy, have also shown higher than expected frequencies of fruit-bearing trees, indicating either transplantation or selective culling [70]. Although quite unusual species characteristics such as parthenocarpy in figs, as well as witness tree records (which can reach back only a few decades) are of limited use as archaeological markers of transplantation of economically important plant species, pollen analysis targeting samples recovered from archaeological contexts holds much greater potential for documenting the transplantation of economically important perennials by past societies, worldwide. At the SGang Gway Midden site in British Columbia, for example, six samples from a 13 cm sequence of litter and shell midden debris provided a record of the vegetation composition within the village, and based on the high amounts of rose family pollen, Hebda *et al.* [71] suggest that fruit-producing members of the rose family such as salmonberry and perhaps Pacific crabapple may have been grown in the village. Similarly, using pollen samples taken from several Jomon period sites in Japan, Kitagawa & Yasuda [22,23] document an increase in abundance of pollen from two economically important tree species—chestnuts (*Castanea* spp.) and horse chestnuts (*Aesculus* spp.)—beginning at *ca* 7000–4500 BP, suggesting selective encouragement and perhaps transplantation by Jomon groups.

5. IN-PLACE ENCOURAGEMENT OF PERENNIAL FRUIT- AND NUT-BEARING SPECIES: CREATING LANDSCAPES PATTERNED WITH POINT RESOURCES

Along with identifying and transplanting young fruit-bearing perennials closer to settlements, small-scale human societies could also, with minimum effort, practice in-place encouragement of established, mature fruit trees, as well as those nut-bearing tree species that were not good candidates for transplantation because of the long delay that would separate replanting of seedlings and first harvest. The economically valuable fruit- and nut-bearing perennials could be selectively spared as competing trees were culled or harvested for building material and firewood, as well as during general vegetation clearance in the creation of mosaic patches and edge areas.

As settlements were periodically relocated, the established orchards of abandoned settlements could also be revisited, and competing vegetation could be cleared away from the human-created stands of fruit trees and berry bushes. Over time, as old settlements were abandoned and new ones established, this sustained practice of removing competing tree species in proximity to habitation sites, while maintaining old orchards and creating new ones, could substantially alter the species composition of vegetation communities over relatively large resource catchment areas.

Turning again to the woodlands of eastern North America, slower growing, larger and later successional stage nut- and mast-bearing trees, such as oaks, hickories and walnut, while sometimes mentioned as occurring among the fruit- and berry-producing species of close-in transplanted orchards [59], are more often described as being scattered both within abandoned fields and beyond, reflecting a niche construction strategy involving selective in-place encouragement. Hammett [5,61], for example, outlines a general abstract pattern of landscape management by pre-European societies of North America that has settlements and their adjacent small gardens encircled by two resource catchment zones—a close-in area of actively cultivated and fallow fields, orchards and berry patches, and surrounding it, a wooded zone containing mast-, nut- and fruit-bearing trees as well as trees for construction and firewood, along with white-tailed deer and other prey species (see [3] for a similar abstract catchment zone pattern for Japan). Selective retention of overstorey nut- and mast-bearing trees during field clearance could have resulted in their scattered distribution in the close-in zone of active and fallow fields, with their relative abundance in outlying forest zones increased by a lower level of selective encouragement and culling of competitors in the absence of substantial clearing. Controlled burning in forest resource zones, along with other methods of thinning both understorey and canopy species, could have encouraged larger and higher yielding nut- and mast-bearing trees [5,61,72,73], and such a broad-scale niche construction practice has been suggested as having a deep time depth in eastern North America [46]. At the same time, as settlements and their concentric resource catchment zones were periodically relocated throughout forest zones of North America, they would have left behind a legacy of fallow-cycle vegetation communities that were substantially enriched in forest species of economic value in comparison to their composition prior to clearing. Following settlement abandonment, as overstorey canopies encroached on, and reduced the habitat of, early successional species, the larger, later successional stage trees of economic value that had been the target of earlier selective encouragement would have sustained their increased abundance in the restructured forests over a longer period of time [51,74].

Similar strategies of selective culling of competing species and encouragement of nut- and fruit-bearing trees have been documented in a number of different past and present-day low-latitude tropical forest environments [8,28,75], as well as in temperate forest and more open environments. Fowler [57], for example, documents the clearing away of vegetation from piñon trees in the Great Basin, as well as 'knocking' branches and pinching growth tips to encourage additional cone development. In Japan, Kitagawa & Yasuda's [22,23] analysis of pollen samples from Jomon period sites, as well as prior studies showing an increase in the size of nuts, provides evidence of selective encouragement of both chestnut (*Castanea* spp.) and horse chestnut (*Aesculus* spp.) as early as 5000 BP, and Nishidha [3] outlines broader patterns of management of wild plants in contemporary villages in rural Japan.

In-place management and manipulation of long-lived perennials also, of course, includes those species that can be harvested for raw material rather than food. A variety of different species in different environments are coppiced and pollarded (pruned) to maintain them in a physiologically young state, producing new growth each year to be used for firewood and a range of manufactured items, including baskets [57,68].

6. TRANSPLANTATION AND IN-PLACE ENCOURAGEMENT OF PERENNIAL ROOT CROPS: CREATING ROOT GARDENS AND EXPANDING THE HABITAT OF WILD STANDS

Along with the transplantation and in-place encouragement of fruit- and nut-bearing perennial species, small-scale pre-industrial societies also direct similar niche construction efforts towards perennial plants of a different sort—those with starch-rich underground storage organs (roots, rhizomes, culms). These perennial 'root' crops differ from fruit-, berry- and nut-bearing species, however, in three notable respects. Since it is the roots of the plants themselves that are of interest rather than 'renewable' products (fruits, nuts, berries, branches), the entire plant is harvested, requiring periodic addition of new replacement plants. In addition, unlike fruit- and nut-bearing species, where human niche construction efforts are primarily directed towards removal of competing plants, modifying the target species, and ensuring adequate sunlight, management of root crops usually focuses instead on issues of water management. And finally, in contrast to management of fruit- and nut-bearing species, niche construction strategies for perennial root crops often involve considerable investments of human labour in habitat improvement features (e.g. dams, canals, rock mulching, soil retention walls, etc.). Three examples of human niche construction focusing on perennial root crops by small-scale societies located in different regions of North America help to illustrate these three points.

One of the most remarkable examples of high-investment human niche construction involving perennial root crops has been documented in the Owens Valley of the Great Basin area of California [57,58]. Owens Valley Paiute groups constructed an irrigation system that carried and dispersed water across extensive tracts of swampy low-lying floodplain meadows adjacent to the Owens River.

The vegetation of these waterlogged, river valley resource zones included a number of bulbous hydrophytic food plant species that had long been an important component of Owens Valley subsistence economies (e.g. blue dicks or purplehead brodiaea (*Dichelostemma capitatum* ssp. *capitatum*), chufa flat sedge (*Cyperus esculentus*) and possibly spikerush (*Eleochari* spp.) [58]. This enhancement and expansion of the natural habitat of the water-meadow root crops was carried out on a large scale in several locations. Each year, construction and subsequent removal of temporary diversion dams along some of the tributary creeks of the Owens River called for the labour of all of the men of communities. Feeder ditches up to 6.5 km long carried nutrient-rich, early summer mountain run-off from dams to the river valley plots, the largest of which were 5.2–10.4 km^2 in size [76]. No efforts were made at planting, tilling or tending either the wild root crops of these water meadows or the adjacent downstream stands of wild seed plants (including sunflower, chenopod and lovegrass) that also benefited from the irrigation efforts. Unfortunately, it is probably not possible to determine how far back in time prior to the 1840s these labour-intensive water management practices were carried out [58].

Like the Owens Valley groups, small-scale societies along the Northwest Coast of North America also invested considerable effort in enhancing and expanding the saturated soil habitats of indigenous starchy root crops. They encountered different challenges from those faced by Owens Valley groups, however. In the Owens Valley, the central hurdle in expanding and enhancing water meadow root crop production involved ensuring a reliable water supply. This was accomplished, with considerable human labour, through the construction of irrigation canals. Relatively little labour appears to have been invested in tilling the soil or weeding the water meadows themselves.

Along the Northwest Coast, in contrast, human ecosystem engineering efforts focused not on water-delivery systems, but on the artificial expansion of the habitat zone of a number of estuarine food plant species, along with active and sustained efforts to improve the soil and selectively remove competing grasses within these expanded tidal 'garden' plots [66]. The root crop species in question, including springbank clover (*Trifolium wormskjoldii*), pacific silverweed (*Potentilla anserine* ssp. *pacificia*), northern riceroot lily (*Fritillaria camschatcensis*) and Nootka lupine (*Lupinus nootkatensis*), which all produce dense concentrations of thin, long starchy roots and rhizomes, have a particularly narrow range of distribution within the tidal column in undisturbed high salt marsh estuarine settings. Interestingly, this high marsh habitat zone, like the open sandbank settings selected for broadcast sowing of annuals discussed above, represents an 'externally powered' ecosystem. Just as floodwaters carry new soil and nutrients to riverbank settings, peak tides and floods deposit marine, riverine and estuarine sediments and organic debris into this high marsh habitat zone, dramatically increasing the nutrient composition of the soils, and making it one of the most productive environments in the world in terms of carbon produced per unit of area [66].

Both historical descriptions and recent research provide evidence for widespread ecosystem engineering of this high marsh zone by Northwest Coast societies, with substantial human effort invested in expanding the very narrow band in which the plant species with edible starchy root crops can grow. This was accomplished by the downslope mounding of soils and the construction of rock and wood reinforcing walls, which effectively extended the habitat of the target species [66]. Within these extended garden plots, the soil was periodically churned. This churning created a texturally diverse soil while also mixing in the most recent deposits of fresh organic matter. It also increased the porosity of the soil, thereby encouraging the growth of the larger, longer and straighter roots so highly prized by Northwest Coast societies. In addition to churning the soil, human management of these expanded cultivation areas also involved sustained weeding of grasses and other unwanted invaders throughout the growing season, and the vegetative replanting of root fragments and small plants at the time of harvest, in order to ensure future abundant yields.

The Owens Valley and Northwest Coast examples of in-place enhancement and expansion of natural stands of perennial plants share a number of similarities. In both areas, the targeted species are all components of natural wet-soil communities, and human niche construction efforts are directed towards the deliberate and sustained enrichment and expansion of the habitat zones of these plant communities. Rather than focusing on a single species, a variety of perennials were involved in both regions.

In the Southwest, a third example of considerable human labour being invested in wild perennial root crops involves human niche construction efforts to increase soil moisture in order to mimic the natural habitat of agave (*Agave* spp.). One of the best-documented examples of this form of niche construction consists of a checkerboard pattern of linear rock-bordered grid features (each square roughly 10 m on a side) situated on the broad cobble and boulder terraces adjacent to the alluvial plain of the Gila River in southern Arizona. A total of 36 grid clusters covering an a area of 82 hectares were mapped within 1 km on either side of Spring Wash, a tributary of the Gila River [77]. Constructed between about AD 750 and 1300, these rock grids were water control features that captured rainfall, retained surface runoff and created a mulch, reducing evaporation and increasing soil moisture levels (soil moisture within and adjacent to these liner rock features today measures twice that recorded outside of the features). Although still far below what would have been needed to grow maize or other domesticated crop plants, the increase in soil moisture resulting from these rock grid features was significant in terms of supporting indigenous perennials such as agave that could withstand seasonal moisture shortfalls. A series of roasting pits situated along Spring Wash and several other tributaries transecting the rock grid area yielded agave processing tools along with monocot tissue compatible with agave, as well as cf. agave leaf base fragments, confirming the large-scale cultivation of this wild plant for food and fibre. It is estimated that this rock grid system could have supported an estimated 44 500 agave plants at any one time. Small 'offsets' or 'pups' of mature parent plants were probably initially collected from relatively distant stands and then transplanted to the prepared rock grid mulch fields. Once established, mature plants within the rock grids could produce all the pups needed for the perpetuation of the cultivated stands of wild agave.

This is only one of a growing number of locations across the Southwest where transplantation and cultivation of agave in rock mulch contexts have been identified. In the Phoenix, Tonto and Tucson Basins, more than 550 individual locations where agave plants were transplanted by Hohokam societies at *ca* AD 600–1350 have been documented [77].

Evidence of early human niche construction efforts involving water management is not, of course, limited to North America. Drainage canals associated with the cultivation of tree crops and dating to *ca* 7000 BP have been documented in the highlands of New Guinea [78], and artificial walls or 'bunds' designed to retain floodwaters and thereby expand the natural habitat of wild and early cultivated rice crops and dating as early as 7700 BP have been documented in the Yangtze Delta region of China [17].

7. LANDSCAPE MODIFICATION TO INCREASE PREY ABUNDANCE IN SPECIFIC LOCATIONS: ENHANCING SALMON STREAMS AND CREATING CLAM GARDENS, FISHWEIRS AND DRIVE LINES

As mentioned earlier in this paper, while efforts by small-scale pre-industrial societies to increase the availability of economically important wild animals in their resource catchment areas primarily involve general and indirect efforts to enhance carrying capacity through vegetation modification, there are also scattered examples of human niche construction that are directly focused on specific animal species and particular locations on the landscape. These management strategies are of two general types: those designed to enhance and/or expand the habitat of particular species, and those designed to channel and constrain the movement of prey for easier harvesting.

An excellent example of this first form of niche construction, habitat expansion and enhancement, is the 'clam gardens' of the Northwest Coast of North America. Employing a strategy analogous to that used to construct the root gardens discussed earlier, downslope rock walls, sometimes up to a metre in height, are constructed at extreme low tide lines adjacent to extant clam beds, and soil and shell 'hash' is filled in behind them, effectively extending the extant natural clam bed farther out from shore. Often situated in favourable locations adjacent to settlements, clam gardens have been mapped from Vancouver Island north to Alaska, with more than 400 being recorded on Vancouver Island alone [79]. The time depth of these ecosystem engineering efforts is not yet known. Interestingly, the bivalves that are 'cultivated' are more similar in several respects to the Northwest Coast root crops than they are to other species of animals. They are essentially a stationary resource, with specific and clearly discernible requirements in terms of water depth and nutrient flow, and as a result are worthwhile targets for location-specific habitat expansion and enhancement.

Such location-specific niche construction efforts can also be employed for prey species that, while mobile, also have very predictable seasonal movements and specific habitat locations that can be enhanced through human intervention. Salmon streams can be enhanced through removing debris, and fish eggs can be transplanted between water systems [80] (J. Jones 2002, unpublished MA thesis).

In contrast to niche construction meant to expand and enhance particular habitat locations, which are relatively poorly documented, examples of human alteration to the landscape designed to channel and constrain the movement of prey for easier harvesting are much more abundant, and primarily fall into two similar forms of construction: fishweirs—designed to direct fishes into enclosures for capture, and fences—placed to facilitate the driving of large herbivores into corrals for killing.

The use of fishweirs has been documented in many inland and coastal areas, worldwide. In a comprehensive summary of fishweirs in North America, Connaway [81] describes three basic categories of fishweirs: flowing stream weirs, tidal weirs and longshore weirs. Constructed of both stone and wooden stakes, flowing stream fishweirs are usually 'V' shaped and are placed in shallow areas or shoals, with the downstream apex of the V acting as a funnel to direct fishes into a trap. In the Northwest, flowing stream Salmon weirs often take the form of a straight fence-like barricade, which blocks the fish running upstream and subjects them to spears and dip nets. Tidal or ebb weirs also take the form of bank to bank stone and wooden post barriers that are placed along the coast in tidal inlets and along streams subject to tidal flow and ebb. At high tide, fishes pass easily over the barrier, but are then trapped behind the barrier as the tide recedes. Longshore weirs consisted of a fence or a single wing extending out perpendicular from the shore in non-tidal inlets, river mouths, on the edges of lakes and along saltwater shorelines. Fishes swimming parallel to the shore will encounter the barrier and are then diverted along it into traps or pens.

Generally comparable to fishweirs in function, game fences were constructed by small-scale societies in a variety of settings to facilitate the driving of large herbivores into corrals for killing. Drive lines designed for bighorn sheep and pronghorn antelope in the Great Basin date back more than 3000 years, including one pronghorn fence, constructed of dwarf cedars and bound together in some places by willow withes, which was more than 8 km long [82]. Similar pronghorn drive lines have been documented in the Southwest, and drive line fences were also employed for corralling bison at *ca* 3000 BP on the Great Plains. A caribou drive line submerged beneath the waters of Lake Huron and dating *ca* 10 000 BP has also recently been detected [83].

Small-scale societies also recognize and take advantage of the drawing power of edge areas, fields and garden plots close to their settlements in attracting prey species to them. The practice of 'garden hunting' where hunters take advantage of deer, waterfowl and other species' efforts to browse on the early successional species of anthropogenic habitats is well documented in many regions of North America [66,84].

8. DISCUSSION: A PREDICTIVE MODEL

The formulation of a predictive model for the management of wild resources by small-scale pre-industrial societies draws both on the broader theoretical perspective and paradigm provided by niche construction theory (NCT) [31], and on the numerous real-world examples of human niche construction briefly outlined above. These two seemingly disparate foundational influences or sources—derived theory on the one hand and inductively collated empirical examples on the other—are in fact interrelated in a number of important respects.

Since small-scale human societies represent a subset of the larger set of species encompassed by the more inclusive general conceptual framework of NCT, it logically follows that the core principles and basic assumptions of NCT are applicable to the smaller nested subset. Note that these basic tenets and core principles, as applied to small-scale human societies, are derived and not deduced from NCT (see the discussion of universal laws, probabilistic laws and law-like statements in [85,86]). As is often the case with theoretical models and explanatory frameworks in the biological and behavioural sciences, the concepts and ideas embodied in NCT fall under the heading of law-like statements rather than either universal or probabilistic laws, and as a result, their relative explanatory strength or utility rests entirely on their track record in accounting for or predicting events—how well they can be shown to fit the real world [85].

The predictive model outlined here for niche construction by small-scale human societies thus derives support from the general conceptual framework of

NCT not because of some radiant theoretical purity or elegance embodied in NCT (although that may certainly be present), but rather because it carries with it a large and diverse array of empirical examples that appear to conform to its predictions or test implications. The extensive documentation of niche construction activities by a wide range of different species that is presented by Odling-Smee *et al.* [31] illustrates and underscores the basic and obvious necessity of continually testing the relative strength of any proposed framework of explanation through assessing its ability to account for empirical reality.

In a similar manner, the case study examples of human niche construction described above, and their organization into six general categories, which together form the second source or foundational element for the predictive model presented here, also reflect the basic cyclical nature of scientific inquiry, this time at the subset level. These case study examples further shape and support a framework of explanation specifically tailored to a particular nested subset of environmental engineering—the efforts by small-scale pre-industrial human societies to modify their natural surroundings. In both this small-scale human society subset and in the larger set of species encompassed by NCT, the seeking out and compiling of specific empirical examples from the real world with which to formulate, test and refine theoretical models represents an essential aspect of the scientific cycle. It is of course necessary to avoid the circularity of exclusively employing the same empirical data that were used in formulating a predictive model in subsequently assessing its utility—additional, independent datasets provide the true and ongoing measure of the strength of any explanatory framework in the biological and behavioural sciences. Future testing of this model will involve assessing the extent to which its predictions or test implications are confirmed in other regions of the world and in other cultural and environmental contexts.

This predictive model of niche construction by small-scale human societies worldwide during the Holocene in their utilization of wild or non-domesticated plants and animals has a number of core principles or tenets. The most basic of these, as eloquently articulated in the quotation at the beginning of this article, is that humans have been intensive and extremely successful ecosystem engineers for more than 10 000 years: 'What is certain is that the forest dwellers . . . were not passive in their environment but actively altered it.' [1]. This simple observation might seem both obvious and non-controversial—that throughout the Holocene and for an unknown preceding span of time, *Homo sapiens* have not been simple passive components of biotic communities, with their diet choices constrained by the structure of extant pristine natural environments, but rather that they actively and sometimes extensively shaped their ecosystems. In fact, however, it directly calls into question a number of still quite popular conceptual models of human resource selection that lack consideration of the human capacity for ecosystem engineering, most notably the diet breadth and patch choice models of human behavioural ecology [87].

A second basic tenet of the model is that one of the central goals of environmental engineering by human societies is to increase their share of the annual energy produced by the ecosystems they occupy by increasing the accessibility, abundance and reliability of the plant and animal resources they rely on for food and raw materials (see [11] for detailed descriptions of ecosystem engineering associated with agricultural landscapes). As seen in the North American case study examples briefly presented above, the timing and duration of human energy invested in such environmental modification efforts can vary widely between target species, from annually repeated and behaviourally imbedded low-cost activities (e.g. controlled burning and selective culling of vegetation) to the less frequent but higher initial investment construction (and maintenance) of longer lasting environmentally imbedded structures (e.g. fishweirs and drive lines, diversion dams, rock mulching and clam beds). But in all of these examples, a basic goal of the human niche construction initiatives by small-scale societies is to restructure the food web within their local resource catchment in ways that strengthen their position and their network of energy sources [88].

This predictive model also proposes that just as there are general characteristics that make particular plants and animals attractive targets for domestication, there are also certain sets of characteristics and certain taxa of wild plants and animals that are logical targets for human engineering, as well as a finite number of general solutions or strategies for management and manipulation of these targeted taxa. Each of the six strategies of niche construction described above identifies such a set of resources with particular characteristics that make them good targets for human manipulation, along with the general outline of the basic human strategy for how they can be successfully managed.

Human niche construction intended to increase the abundance and harvest of wild animal species of economic importance to small-scale human societies is limited to two quite different strategies. On the one hand, burning and other low-cost efforts at general vegetation modification, and their influence in different environments (e.g. release of nutrients into the soil, reduced woody biomass, breaking of overstorey forest canopies, increased edge areas and a more mosaic vegetation landscape, shift to earlier successional sequence vegetation communities) all result in an increase in the plant foods relied on by prey species, and a corresponding potential increase in prey abundance. At the same time, structural modifications to the landscape (drive lines, fishweirs) serve to channel and constrain the movement of prey for easier harvesting.

General niche construction strategies targeting plant species, in contrast, span a range of different approaches, depending on the characteristics of the species groups involved. Stand expansion of annual seed plants of economic importance is accomplished by human-mediated seed dispersal into areas recently cleared by burning or by the receding of seasonally high water. Transplantation of economically important species closer to settlements primarily involves perennial understorey berry- and fruit-bearing herbaceous and woody plants with a short time span to maturity, while overstorey nut- and fruit-bearing species with a longer growth to yield time span are selectively encouraged in place through culling of competing species. Finally, the availability of perennial species with underground storage organs is increased by habitat enhancement and expansion, and sustained transplantation, with specific strategies addressing environmentally variable soil moisture requirements.

The composition and the structure of these general categories of human ecosystem engineering in turn reflect the obvious underlying challenges that human societies face in reshaping local plant and animal communities more to their liking. The essential recipe for the advantageous restructuring of plant communities includes: (i) the removal of unwanted vegetation that competes for sunlight, soil moisture and nutrients, (ii) increasing the localized abundance or patch size of desirable food plants by expanding their existing habitats, transplanting (perennials) or planting (annuals) in either anthropogenic or naturally created habitats, and (iii) ensuring that these resource patches, either already existing or newly created, receive sufficient sunlight, moisture and nutrients. Ecosystem engineering directed towards wild animal species involves both habitat improvement and the construction of fences designed to facilitate more dependable and higher yield harvests of fishes and wildlife.

Future testing of this model will involve the seeking out of additional examples of management of wild plant and animal species by small-scale human societies worldwide, and establishing the extent to which they comfortably fall into the six categories. This may not be an easy exercise, since many of the specific methods of human niche construction outlined here represent anthropogenic analogues to events, processes and landforms that occur in nature—fire clearance of trees and grasslands, forest clearings owing to windfalls, flood-scoured sand banks, natural traps and drive line features, seasonal stranding of fishes in oxbow lakes, etc. This mimicking of natural processes will constitute a major challenge in continuing efforts to expand the list of documented small-scale human niche activities and general categories, particularly in the archaeological record.

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