

Article

Adventive Vertebrates and Historical Ecology in the Pre-Columbian Neotropics

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Abstract: The arrival of Europeans in the Western Hemisphere (ca. AD 1500) is generally used as a convenient reference point for signaling the early appearance of invasive faunas. Although use of this date embraces an implicit belief in benign landscape management by pre-Columbian inhabitants of the Americas, substantial evidence for the anthropogenic movement of domesticated, wild, and synanthropic vertebrates throughout the Neotropics suggests that it may be an exaggerated and erroneous reference point for the aims of ecological restoration and biological conservation.

Keywords: invasive fauna; Neotropics; historical ecology; archaeology; zooarchaeology; ecological restoration; conservation biology; prehistoric Indians

1. Introduction

Invasive species are one of the major anthropogenic factors contributing to decline in contemporary biological diversity [1]. Globally, over a half million invasive species annually account for more than \$1.4 trillion in economic damage, or about 5% of the world's gross national product. However, the specter of invasives is simultaneously complicated by the fact that up to 99% of the world's food system, annually valued at approximately \$30 trillion, is largely derived from introduced species [2]. Clearly, their management requires arbitrary decisions. One essential task is defining exactly what we mean by invasive organisms, which involves the timing of their arrival or dispersal.

Precisely how long must a species exist in any given environment before it can be considered native, or conversely what is the maximum temporal depth required to regard it as invasive? The decision is a necessarily arbitrary one; however, despite the fact that humans have long been recognized as

important agents for disseminating plants and animals, AD 1500 tends to be the common reference point for assigning native/invasive status in the Western Hemisphere [3-8]. It might be best to view this date as an expedient convention for designating the onset of massive global biological exchange that took place between the hemispheres after discovery and colonization by Europeans. Nonetheless, the arbitrary AD 1500 end/starting point normally embraces an ingrained belief that humans practiced a relatively benign landscape management in the Western Hemisphere before that time. Although this may seem to be a relatively obvious assertion in light of the contemporary dilemma of invasives, it is nonetheless an exaggerated claim that may be entirely faulty. This is particularly important if we define a desired conservation and restoration target that manages biota and landscapes toward some seemingly natural benchmark that we think may have existed before AD 1500 [5]. We also frequently assume that depressed richness or extirpation automatically coincide with the arrival of humans, pre-Columbian or otherwise. These automatic assumptions are rejected by historical ecology, which recognizes the variable impact of humans on their environments in time and space, the different responses of local species richness to human action, and the importance of historical trajectory to the production of unique landscapes [6].

This paper summarizes evidence for anthropogenic movement of adventive vertebrate faunas throughout Neotropical landscapes. The term adventive refers both to intentionally introduced species and unintentional immigrants [9,10] that can accompany anthropogenic movement and indicate human landscape occupation and modification [6]. They are important for discussions of biodiversity because large portions of the Neotropics are characterized as remote remnants of surviving global wildernesses that are relatively insensitive to biotic exchange and little affected by human intervention [11,12]. A brief introduction examines the nature and interpretation of pertinent data, after which this article summarizes the evidence for possible human movement of adventive vertebrates throughout the pre-Columbian Neotropics, with particular attention on the Caribbean archipelago. A concluding section discusses issues related to anthropogenic extinction, animal domestication in the Neotropical lowlands, and broader implications for contemporary ecological restoration and conservation.

2. Identification of Adventive Vertebrates in the Buried Record

With the exception of fortuitous and often anecdotal observations written by early Europeans after AD 1492, most of our evidence for adventive vertebrates in the pre-Columbian Neotropics includes preserved and identified specimens recovered from buried contexts. Paleontological specimens that were unambiguously accumulated, deposited, and buried in contexts prior to the initial appearance of humans can provide evidence for native or naturally introduced faunas. However, most specimens are recovered from archaeological contexts which tend to be palimpsests of cultural and natural deposition. In both cases, the relationship between the recovered sample and the originally deposited assemblage changes, sometimes radically, in the time between deposition and recovery. It is crucial to gauge the reliability and validity of the data used to support inferences about the past. This is often assessed during specimen analysis and identification, and is frequently prone to equivocal results (similar outcomes from different events) due to partial recovery, differential specimen preservation and modification, and the disjuncture between surviving evidence and the criteria used by systematists to

identify taxonomic categories. It is crucial to establish the circumstances surrounding assemblage accumulation and to recognize the patterned biases introduced by different accumulating agents during assemblage formation [13]. Moreover, although analysis of buried assemblages can reveal contextual evidence in the form of spatial and temporal associations, it rarely establishes cause and effect. An identified bone specimen recovered from a dated archaeological context might establish its presence in spatial and temporal association with other materials; however, it does not necessarily represent evidence that the animal once lived in the immediate vicinity, nor does it necessarily represent a breeding population, or extirpated species. These secondary inferences are regularly generated from sources other than contextual association.

The recovery and analysis of dated associations contribute important information about the spatial distribution of animal taxa through time. However, retrodiction of spatial patterning is also prone to equivocal results because vertebrate species can diffuse about their landscapes in different ways. Gradual diffusion across hospitable terrain may occur over the course of generations; it can also proceed at such a slow pace that evolutionary changes take place during dispersion. In contrast, jump dispersals of organisms across great distances and inhospitable terrain occur within the span of a single generation. Distributional changes are produced by any combination of diffusion and local extinction. A once continuous range that now appears as disjunct populations of allopatric sister populations may be the patterned result of different processes that can act in combination, including vicariance through changes in geomorphology and climate, or evolutionary differentiation associated with migration. Range extensions may also be the product of natural or human-aided long distance jump dispersal, or they may simply reflect incomplete knowledge or errors in data collection. Unfortunately, “clear patterns seldom emerge; one can do little more than search for, and almost certainly find, support for one’s pet theory in data whose almost every item is idiosyncratic [14]”.

3. Adventive Vertebrates in the Pre-Columbian Neotropics

The decision to include human-caused population disjunctions with “natural” disjunctions or to exclude them as “unnatural” is entirely arbitrary; however, it can be easy to confuse as natural that which was anthropogenic [14]. Although contemporary studies of invasive species regularly demonstrate the key role played by humans in altering the distributions and numbers of biological organisms, this often remains unrecognized or underestimated in pre-Columbian America. The following sections review evidence for the movement of domesticated and non-domesticated vertebrates and/or their products around continental and insular Neotropical landscapes, and conclude with some speculations about the place of synanthropic taxa and human migrations.

3.1. Human Movement of Domesticated Animals

Humans likely entered the Western Hemisphere with the domesticated dog (*Canis familiaris*) which they subsequently distributed and bred throughout most of the American continental land masses. Dogs eventually reached the insular Caribbean where all canids are either attributed to human introductions or closely associated with unequivocally cultural contexts [15-18]. Over the subsequent millennia

humans domesticated relatively few autochthonous vertebrates, including two large birds, a medium-sized rodent, and two closely related camelids.

The turkey (*Meleagris gallopavo*) may originally have been domesticated in the western highlands of Mexico, but Europeans found it widely distributed throughout Mexico and Central America. It may have been independently domesticated from a localized wild bird in the American Southwest; however, today's commercial variety is a hybrid of wild varieties in eastern North America and the original Mexican domesticate re-introduced by Europeans into the eastern United States during the 17th century [19]. The Muscovy duck (*Cairina moschata*) is a poorly known domesticate with a broad distribution in the wild from Mexico to northern Argentina and Uruguay, and northward possibly into Trinidad. The area and circumstances surrounding its early domestication are unknown, yet archaeology records its presence from western South America and Panama, eastern Bolivia, northwestern Argentina, Venezuela, and Trinidad. Early accounts identify it in the Lesser Antilles, along the Caribbean shores of South America, and into Honduras and Mexico. Feral populations are widely distributed today throughout the Americas and Europe [20,21].

When Europeans arrived in the New World, the cuy or guinea pig (*Cavia porcellus*) was broadly dispersed throughout the Andes from northwestern Venezuela to central Chile and northern Argentina. Early documents also suggest its presence in Central America and the Caribbean. Although much of its early domestication is poorly known, the longest record of its prehistoric association with humans is found in the central Andes where it is first recorded in the ninth millennium before Christ. From here it was distributed by humans throughout its expansive pre-Columbian distribution on the continent and Caribbean islands. Today, the northern distribution of cavid rodents is characterized by markedly disjunct populations which implicate anthropogenic transport and possibly feral status [16-18,21-25].

Two domesticated camelid species are scientifically recognized, the llama (*Lama glama*) and alpaca (*Vicugna pacos*), although indigenous herders distinguish a more complex taxonomy. Independent centers of domestication have been suggested in the high altitude grasslands of Peru some 6,000 years ago and in Argentina a millennium later. Domesticated camelids were subsequently moved northward to southern Colombia and southward to northern Chile and Argentina by the time Europeans arrived. Today's breeds possibly reflect increased uniformity due to extensive hybridization following the breakdown of controlled pre-Columbian breeding and massive destruction of native stock [21,26,27].

3.2. Human Movement of Non-Domesticated Animals on the Neotropical Mainland

Sources written not long after the Conquest describe how large numbers of live birds and other vertebrates were regularly transported over long distances for trade and as tribute or gift to supply the large aviaries and zoos of indigenous nobility [37,39]. Today, unusually isolated relict populations, far removed from their nearest relatives, can be a contemporary footprint of Pre-Columbian transport [38,88]. This might be best seen in extant Neotropical psittacid populations that are often characterized by disjunct distributions [29]. Indeed, the many feral populations of exotic parrot species around the world attest to their exceptional colonizing abilities, which is also why they are prime candidates for conservation-based introductions into new localities regardless of native or invasive origin [28]. Archaeological evidence substantiates the importation of Scarlet (*Ara macao*) and Military

Macaws (*A. militaris*) as far north as southwestern New Mexico early in the second millennium after Christ. Unequivocal archaeological associations clearly demonstrate that tropical macaws were bred prehistorically and extra-limitally in northern Mexico; historic documents indicate that this was also common in southern Arizona [30-32]. Macaw skeletons are found in prehistoric Panamanian burial contexts, where historic documents mention their use in local elite exchange and as sacrificial offerings in human interments. Their archaeological context could argue either for importation of exotic specimens or a wider pre-Columbian range distribution [33-36,89].

Living, dead, intact, and disassembled animals were transported by land and sea over vast areas of the pre-Columbian Neotropics for many reasons [40-42]. Specimens of exotic birds from lowland areas on either side of the Andes have been identified in high elevation contexts of northern Ecuador dating to before the time of Christ. This adds great temporal depth to the bird trade described in historic documents of the area, and implicates the potential importance of human movement for determining Holocene distributions [43]. In the same contexts, other animal remains clearly suggest contact with western and eastern lowland areas [44], particularly identification of the tropical squirrel monkey (*Saimiri* spp.). It had long been speculated that certain disjunct squirrel monkey populations (*S. oerstedii*), today restricted to narrow coastal zones of Costa Rica and Panama and widely separated from more or less continuously distributed sister populations in the Amazon, were the legacies of pre-Columbian human transport by land or sea. This entirely isolated range was believed to parallel that of the bush dog (*Speothos venaticus*), also considered to have been introduced by pre-Columbian humans [45]. However, others have recently challenged the anthropogenic origin of Central American squirrel monkey populations with evidence from a local molecular clock calibrated to fossil evidence which calculates divergence long before the arrival of humans [47].

3.3. Human Movement of Non-Domesticated Animals in Neotropical Islands

Vertebrate populations on the Caribbean islands are naturally disjunct. Continental South America is the assumed source for most endemic Caribbean vertebrates, and both vicariance and natural waif dispersal are considered as possible mechanisms for distributing non-volant faunas, although a significant portion of island biota also may have been introduced prehistorically by humans. Clearest resolution for anthropogenic movement is on the oceanic islands of the Antilles, to which animals were introduced primarily from the South American mainland, and from which animals were transported from island to island. Although trade is often associated with the arrival of ceramic-producing cultures more than 4,000 years ago, it is entirely possible that pre-ceramic populations had practiced long-distance transport. It has also been suggested that the discontinuous distribution of insular resources was an important reason for the exchange of exotic materials and products through direct acquisition with the mainland, as well as local inter-island and long distance trade [48,49]. A South American source for most of the introduced faunas is supported by zoological affinities and by the overall greater richness and abundance of animals, especially mainland forms, on non-pelagic islands closest to the continent. These include mainland mammals as Woolly opossum (*Caluromys philander*), Red Howler Monkey (*Alouatta seniculus*), Southern Tamandua (*Tamandua tetradactyla*), Lowland Agouti (*Cuniculus paca*), Ocelot (*Leopardus pardalis*), and Peccary (*Tayassu* or *Pecari*) [16,50,51].

The origins of some West Indian herpetofaunas are currently uncertain, especially on islands with poorly known fossil records which unfortunately include most Caribbean localities. In particular, the insular distributions of the South American Red-footed Tortoise (*Geochelone carbonaria*), Turniptail Gecko (*Thecadactylus rapicaudus*) and Green Iguana (*Iguana iguana*) have been alternately considered as introductions by pre-Columbian indigenes, Europeans, natural rafting, or as mixtures of all three. Currently, two species of *Geochelone* (*Chelonoidis*) form sympatric populations of tortoises that are important gathered and easily storable food sources throughout large areas of lowland South America. Encountered throughout the Lesser Antilles, *G. carbonaria* was either first introduced into the islands prehistorically by humans or was present in the fossil record and had its range subsequently extended between islands by both native and European inhabitants, [52-58]. The gecko has a wide distribution from southeastern Mexico south through the Amazon basin to northern Bolivia and north through the Lesser Antilles and the Virgin Islands. Some authorities question whether its Caribbean distribution might be at least partly attributed to humans, while others point to late Quaternary fossil evidence from the Lesser Antilles in support of its native status [55,57]. Whereas the West Indian Iguana (*I. delicatissima*) appears to be endemic to the islands, speculation surrounds the insular status of the Green Iguana (*I. iguana*) which is currently common throughout the lowland Neotropics from Mexico south to Pacific Ecuador, Paraguay, Atlantic Brazil, and northward into the Lesser Antilles as far as the Virgin Islands. Some have characterized its variability as that of an endemic population which could have been originally introduced through waif rafting [59,60], while others have questioned whether humans introduced it into island context, or minimally re-distributed it between islands [55,57,61,62]. Other possible herpetofaunal introductions include a fresh water slider (*Trachemys*) whose insular distribution is suggestive of prehistoric intra-island movement [16,17], although various West Indian species are recognized in the genus [53]. Neotropical boids are not considered as Caribbean endemics, rather as snakes that were possibly distributed by humans [61,63].

Psittacids are prominently suspected as possible pre-Columbian introductions into island context. Some ornithologists believe that these introductions may have been substantial [28], and because of the strong possibility of intra-island transport, their natural distributions must remain questionable where pre-human fossil evidence is absent [62]. At least two genera, including Macaws (*Ara*) and Amazons (*Amazonas*) are implicated as important pre-Columbian trade commodities [16,64-67]. An extinct Macaw (*Ara autochthones*) is known only from contexts in St. Croix, to which it may have been introduced, and Puerto Rico where it has recently been described. Although its archaeological presence on St. Croix may be due to human introduction, it is argued that the Caribbean may have sustained indigenous populations of up to 60 species in the absence of humans [67]. However, other authorities cite evidence for only two endemic species, highly doubting that so many endemic species could ever have been supported [66]. The extinct flightless Antillean Cave Rail (*Nesotrochis debooyi*), identified in Puerto Rican fossil context, is also found in archaeological middens from the Virgin Islands where it is believed to have been introduced by humans [65,66,68]. Another possible avian introduction may include the Red-Legged Thrush (*Turdus plumbeus*), which could have been transported to Dominica for its pleasing appearance and song [69], although this has also been disputed by others who attribute its distribution to natural long-distance dispersal [70].

Large and conspicuous rodents provide relatively good evidence for the pre-Columbian movement of vertebrates, both into and between the Caribbean islands. Most authorities attribute the insular presence of Agouti (*Dasyprocta* spp.), a ubiquitous Neotropical dietary staple, to early human introduction. The literature identifies its presence in the West Indies under a variety of different species designations and it is today represented around the Neotropics by almost a dozen poorly described species with more than double the number of subspecies. Currently at least three different forms (*D. leporina*, *mexicana*, *punctata*) are identified as insular introductions. Archaeologically, *Dasyprocta* specimens have been recovered from ceramic-bearing contexts principally in the Lesser Antilles, where some have speculated on its tamed or semi-domesticated status. It has been suggested that their appearance declines in abundance north of St. Kitts and south of the Virgin Islands [16-18,45,46,51,62-64]. Endemic Caribbean hystricognath rodents include two families (Capromyidae, Heptaxodontidae) with as many as two dozen species, almost half of which are extinct. Except for one extinct species (*Amblyrhiza*) all are endemic to the Greater Antilles or Bahamas, particularly Cuba and Hispaniola; their overall insular distribution has been attributed to inter-island movement from original native habitats by humans, possibly in captivity [15-18,45,46,51,65,66,68].

3.4. Human Movement of Synanthropic Faunas

During their pre-Columbian movement around the Neotropics, humans must have relocated many synanthropic vertebrates that were to some degree commensal but not domesticated. Synanthropic taxa tend to share many features associated with invasive species, such as rapid reproduction and maturation, high dispersibility, wide tolerance of different surroundings and food types, and phenotypic plasticity. Commensal faunas are usually similar to those capable of invading disturbed areas as they successfully occupy anthropogenically modified habitats [71]. Large, broadly tolerant populations are favored under conditions where resources fluctuate, especially when they become markedly elevated. These latter conditions can sustain lowered species diversity (in terms of richness and evenness, or equitability) and confer competitive advantages on large populations of r-selected eurytopic faunas, particularly colonizing taxa whose big and productive populations rear larger litters as they harvest the most food [72,73]. Humans actively manipulate their landscapes in order to create or take advantage of the increased productivity characteristic of these unstable conditions [74].

The West Indies were home to as many as three endemic and now extinct Rice Rats, including a small mouse-sized Jamaican species (*Oryzomys antillarum*) and two much larger oryzomyines (*Megalomys desmarestii* and *M. luciae*) reported from Martinique and St. Lucia in the Lesser Antilles. All appear to have been extirpated in the historic era. Whether or not humans were possible vectors implicated in the introduction of continental forms of oryzomyines to the islands certainly awaits additional data as well as more zoological study of this complex rodent group. However, as everywhere else, human settlement was likely an important factor in creating conditions that conferred a competitive advantage for commensal rats and mice, as well as other continental taxa like Agouti, Opossum (*Didelphis*), and Armadillo (*Dasybus*) which are regularly associated with, and exploited in, agricultural clearings. It is interesting to contemplate the restricted Lesser Antillean distribution of these typically human-associated taxa [16-18,45,50,51,63,75], in contrast to the primarily Greater

Antillean distribution of endemic hystricognaths. At the moment, one can only speculate as to whether this distribution maps an incomplete data base, a real biogeographical or cultural barrier, the expanding prehistoric northward incursion of continental forms, or some combination of each.

4. Conclusions

The buried record can be a crude and imprecise source of information for inferring what were likely very complex issues in the Neotropical past. High resolution retrodiction of possible mechanisms underlying earlier species distributions are usually inferred from contextual associations representing areas and times where population disjunctures are most visible. However, interpretive visibility in the buried record is not a straight-forward matter. It relies upon the vagaries of preservation, our ability to interpret partial and time-averaged assemblages with appropriate precision, and the hazardous assumption that our knowledge base is somehow complete. Paleontological assemblages, which can be securely demonstrated to have accumulated before the presence of any known human occupation, provide partial glimpses of native vertebrates in our area of interest. However, most data are preserved in and recovered from archaeological contexts that were accumulated, whether altogether unintentionally or intentionally by humans, in cultural landscapes.

Numerous studies around the world, and especially on islands, have suggested that local rates of extinction accelerate rapidly after the arrival of humans. Corroborating evidence is sought in the buried record from contexts that associate fragmented and charred bone specimens with cultural residue. Even when the mode of assemblage accumulation clearly implicates purposeful human action, supporting evidence usually remains circumstantial and equivocal. Archaeological associations are used to support inferences about cause and effect, yet they rarely offer direct evidence. This is particularly significant for understanding the exact cause of extirpations. Also, the common practice of lumping together the timing of faunal extinctions between the early appearance of humans and the later arrival of Europeans around AD 1500 does not tell us whether it was a pre-or post-Columbian event. Indeed, many species extirpations are attributed to habitat alteration and exotic animal introductions that occurred well into the historic period [15,63,64,76]. Causation remains equivocal, but it could be just as likely that the presence of certain animals in specific contexts may be directly due to pre-Columbian humans. Some animals may no longer be found in certain areas because the humans responsible for their introduction were extirpated. It is equally important to remember that endangered species have also been excluded from conservation plans when their native status has been placed into question [47].

What the buried record reveals, with a requisite degree of fuzziness, is the possibility of a rather substantial degree of vertebrate faunal dispersal by humans throughout the Neotropics. Ethnographic sources are replete with accounts of contemporary people moving animals around the landscape. This is occasionally corroborated for the past in historic documents. Unfortunately, it is in the largest tracts of fluviially interconnected tropical lowland areas that the necessary evidence for pre-Columbian transport does not preserve, is poorly studied, or can not reliably supply the disjunct evidence used to support these inferences. The Caribbean data are particularly interesting in this regard. It is well documented that the islands were inhabited by Arawaks at the time of Columbus' arrival in AD 1492, and archaeology has established that the earliest ceramic-period occupations of the Caribbean can be

attributed to the arrival of ancestral Arawaks from mainland South America. This is particularly significant because before the cataclysm of contact, Arawak speakers were characteristically distributed in vast and contiguous regional Neotropical networks along major riverine systems which they linked through shared language, cosmology, social and political alliances, and trade [77-79]. That Arawaks, in particular, were involved in this West-Indian movement of people, ideas, and commodities, lends credence to the notion of significant vertebrate relocations, not only into the Caribbean, but around the greater Amazon Basin and beyond. Their involvement, along with the comparably large and possibly interconnected blocs of Tupian and other Amazonian language groups, belies the popular depiction of environments like the Amazon as remote remnants of surviving global wildernesses that were relatively insensitive to biotic exchange and little affected by human intervention [9,10].

A related issue of interest is the dearth of animal husbandry in the Neotropical lowlands. The West Indian literature frequently mentions the possibility of prehistoric animal management, or even incipient and proto-domestication. However, with the potential exception of domesticated Muscovy duck, whose origins are unknown, no animals were recognized to have been domesticated in these areas. This may appear to be paradoxical, particularly in highly diverse tropical environments which, contrary to established thought, are not only susceptible to invasives but were also subject to a long history of anthropogenic management. The impediment may have been at least in part of cultural origin. Although contemporary Amazonians are celebrated for their inclination to tame a wide range of pets, it has been pointed out that this is to be seen neither as a form of proto-domestication nor as the creation of a mobile protein reserve. Rather, it was a way in which to resolve a basic dilemma created through the act of hunting. Amazonian systems have been characterized as animic, endowing natural beings with human dispositions, and holding to two modalities for the treatment of nature and others: through the negotiation of peaceable exchange, or through the strict equivalence between humans and animals ([80,81] for an important discussion of extensive Amerindian perspectivism and multinaturalism which recognizes spiritual unity with corporeal diversity). The conflict created between one-sided predation by the hunter's actions on the one hand, and the widespread emphasis of reciprocity on the other, is palliated through assimilation of animals into human society. Although tamed and hunted animals are usually of the same species, the status of the former is changed to become different from the latter, and these traditional modes of relating to pets are considered as major obstacles for animal domestication [82].

It has also been suggested that native Amazonian productive systems were focused less on the domestication of individual animal species than on the domestication of landscapes that provided abundant, storable, and possibly sustainable protein [83,84]. Through integrating agroforestry into its productive functioning, indigenous Neotropical landscape management is particularly adept at maintaining high species richness. Introduced invasive species are usually associated with decreased richness and increased extinction rates when they harm native species. Nonetheless, local richness can be augmented by the introduction of new species when extinction rates remain unchanged through balanced emigration and re-colonization from metapopulations of native species in surrounding habitat patches [5,85]. Two hallmarks of indigenous agroforestry promote increased species richness: intermediate-level disturbance, and the production of landscapes with a mosaic of habitats and edges that can maintain native metapopulations.

Of course, precisely who is to blame for a species' extirpation, or why it is that native Amazonians chose not to domesticate animals, is less important to the aims of restoration ecology than is the knowledge of what was extirpated, what was introduced, and approximately when these events took place. Restoration ecologists see their endeavor as the long-term future of conservation biology because species diversity loss will increase in the next half century, after which a stabilized human population will make room for ecological reversal projects on land once occupied and later abandoned by people [86]. But what should they choose as an appropriate reference point? The decision is inherently arbitrary, especially when the target is transient, dynamic, and historically contingent [6,7,87]. It is difficult to replicate real world conditions when historical contingencies are not taken into account. When they are taken into consideration, it becomes possible to choose from a number of different reference points that do not require the notion of climax or predisturbance states [87], or perhaps it might be better to realign, rather than restore, ecologies to current or anticipated conditions [7]. Whichever decision is taken remains a value judgment. It is a judgment based partially on age and also on desirability, as it accounts for the control of an invasive species not simply because it is considered exotic at a chosen reference point, but also because it is currently unwanted. The Neotropics are inherently interesting in this regard, for it is here that we are preserving, conserving, or restoring in great part what we want, and not necessarily what was or wasn't there, certainly if AD 1500 is consistently chosen as the appropriate benchmark.

References and Notes

1. Diamond, J.M. The present, past, and future of human-caused extinctions. *Phil. Trans. R. Soc. Lond. B* **1989**, *325*, 469-477.
2. Pimentel, D.; Pimentel, M.; Wilson, A. Plant, animal, and microbe invasive species in the United States and the world. In *Biological Invasions*; Nentwig, W., Ed.; Springer-Verlag: Berlin, Germany, 2007; pp. 315-330.
3. Kornaś, J. Plant invasions in Central Europe: historical and ecological aspects. In *Biological Invasions in Europe and the Mediterranean Basin*, 2nd ed.; di Castri, F., Hansen, A.J., Debussche, M., Eds.; Kluwer Academic: Leiden, The Netherlands, 1990; pp. 19-36.
4. Kraus, F. Invasion pathways for terrestrial vertebrates. In *Invasive Species*; Ruiz, G.M., Carlton, J.T., Eds.; Island Press: Washington, DC, USA, 2003; pp. 68-92.
5. Myers, J.H.; Bazely, D. *Ecology and Control of Introduced Plants*; Cambridge University Press: Cambridge, UK, 2003.
6. Baleé, W. The research program of historical ecology. *Ann. Rev. Anth.* **2006**, *35*, 75-98.
7. Miller, C.I.; Brubaker, L.B. Climate change and paleoecology: new contexts for restoration ecology. In *Foundations of Restoration Ecology*; Falk, D.A., Palmer, M.A., Zedler, J.B., Eds.; Island Press: Washington, DC, USA, 2006; pp. 315-340.
8. Nentwig, W. Biological invasions: why it matters. In *Biological Invasions*; Nentwig, W., Ed.; Springer-Verlag: Berlin, Germany, 2007; pp. 1-6.
9. Frank, J.H.; McCoy, E.D. Invasive adventive insects and other organisms in Florida. *Flor. Entom.* **1995**, *78*, 1-15.

10. Simberloff, D. The biology of invasions. In *Strangers in Paradise: Impact and Management of Nonindigenous Species in Florida*; Simberloff, D., Brown, T.C., Eds.; Island Press: Washington, DC, USA, 1997; pp. 3-17.
11. Sala, O.E.; Chapin, F.S., III; Armesto, J.J.; Berlow, E.; Bloomfield, J.; Dirzo, R.; Huber-Sanwald, E.; Huenneke, L.F.; Jackson, R.B.; Kinzig, A.; Leemans, R.; Lodge, D.M.; Mooney, H.A.; Oesterheld, M.; Poff, N.L.; Sykes, M.T.; Walker, B.H.; Walker, M.; Wall, D.H. Global diversity scenarios for the year 2100. *Science* **2000**, *287*, 1770-1774.
12. Sanderson, E.W.; Malanding, J.; Ivey, M.A.; Redford, K.H.; Wannebo, A.V.; Woolmer, G. The human footprint and the last of the wild. *Bioscience* **2002**, *52*, 891-904.
13. Stahl, P.W. Vertebrate analysis. In *Encyclopedia of Archaeology*; Pearsall, D.M., Ed.; Academic Press: New York, NY, USA, 2008; Vol. 3, pp. 2173-2180.
14. Pielou, E.C. *Biogeography*; John Wiley and Sons: New York, NY, USA, 1979; p. 259.
15. Morgan, G.S.; Woods, C.A. Extinction and the zoogeography of West Indian land mammals. *Biol. J. Linn. Soc.* **1986**, *28*, 167-203.
16. Wing, E.S. Native American use of animals in the Caribbean. In *Biogeography of the West Indies: Patterns and Perspectives*, 2nd ed.; Woods, C.A., Sergile, F.E., Eds.; CRC Press: Boca Raton, FL, USA, 2001; pp. 481-518.
17. Wing, E.S. The sustainability of resources used by native Americans on four Caribbean islands. *Int. J. Osteoarch.* **2001**, *11*, 112-126.
18. Wing, E.S. Native pets and camp followers in the West Indies. In *Case Studies in Environmental Archaeology*, 2nd ed.; Reitz, E., Scarry, C.M., Scudder, S.J., Eds.; Springer: New York, NY, USA, 2008; pp. 405-425.
19. Crawford, R.D. Introduction to Europe and diffusion of domesticated turkeys from the America. *Archiv. Zootech.* **1992**, *41*, 307-314.
20. Stahl, P.W.; Muse, M.C.; Delgado-Espinoza, F. New evidence for pre-Columbian muscovy duck *Cairina moschata* from Ecuador. *Ibis* **2006**, *148*, 657-663.
21. Stahl, P.W. Animal domestication in South America. In *Handbook of South American Archaeology*; Silverman, H., Isbell, W.H., Eds.; Springer: New York, NY, USA, 2008; pp. 121-130.
22. Stahl, P.W. Pre-Columbian Andean animal domesticates at the edge of empire. *World Arch.* **2003**, *34*, 470-483.
23. Stahl, P.W.; Norton, P. Precolumbian animal domesticates from Salango, Ecuador. *Am. Ant.* **1987**, *52*, 382-391.
24. Wing, E.S. Prehistoric fishing economies of the Caribbean. *Journal of New World Archaeology* **1982**, *5*, 13-32.
25. Eisenberg, J.F. *Mammals of the Neotropics: The Northern Neotropics*; University of Chicago Press: Chicago, IL, USA, 1989; Vol. 3.
26. Wheeler, J.C.; Russell, A.J.F.; Redden, H.; Llamas and alpacas: pre-conquest breeds and post-conquest hybrids. *J. Arch. Sci.* **1995**, *22*, 833-840.

27. Wing, E.S. Domestication of Andean mammals. In *High Altitude Tropical Biogeography*; Vuilleumier, F., Monasterio, M., Eds.; Oxford University Press: New York, NY, USA, 1986; pp. 246-264.
28. Wiley, J.W.; Snyder, N.F.R.; Gnam, R.S. Reintroduction as a conservation strategy for parrots. In *New World Parrots in Crisis: Solutions from Conservation Biology*; Beissinger, S.R., Snyder, N.F.R., Eds.; Smithsonian Institution Press: Washington, DC, USA, 1992; pp. 165-200.
29. Juniper, T.; Parr, M. *Parrots: A Guide to the Parrots of the World*; Yale University Press: New Haven, CT, USA, 1998.
30. Creel, D.; McKusik, C. Prehistoric macaws and parrots in the Mimbres area, New Mexico. *Am. Ant.* **1994**, *59*, 510-524.
31. Hargrave, L.L. *Mexican Macaws. Comparative Osteology and Survey of Remains from the Southwest*; University of Arizona Press: Tucson, AZ, USA, 1970.
32. Minnis, P.E.; Whalen, M.E.; Kelley, J.C.; Stewart, J.D. Prehistoric macaw breeding in the North American Southwest. *Am. Ant.* **1993**, *58*, 270-276.
33. Cooke, R.G. Birds and men in prehistoric Central Panama. In *Recent Developments in Isthmian Archaeology: Advances in the Prehistory of Lower Central America*; Lange, F.W., Ed.; British Archaeological Reports, International Series 212: Oxford, UK, 1984; pp. 243-281.
34. Cooke, R.G. Archaeozoology, Art, documents, and the life assemblage. In *Case Studies in Environmental Archaeology*, 2nd ed.; Reitz, E., Scarry, C.M., Scudder, S.J., Eds.; Springer: New York, NY, USA, 2008; pp. 95-121.
35. Cooke, R.G.; Ranere, A.J.; Precolumbian influences on the zoogeography of Panama: an update based on archaeofaunal and documentary data. *Tul. Stud. Zool. Bot.* **1992**, *1*, 21-58.
36. Stone, D. *The Talamancan Tribes of Costa Rica*; Papers of the Peabody Museum of Archaeology and Ethnology; Harvard University: Cambridge, MA, USA, 1962; Vol. 43.
37. Haemig, P.D. Aztec emperor Auitzotl and the great-tailed grackle. *Biotrop.* **1978**, *10*, 11-17.
38. Haemig, P.D. Secret of the painted jay. *Biotropica* **1979**, *11*, 81-87.
39. Kisling, V.N., Jr. Ancient collections and menageries. In *Zoo and Aquarium History: Ancient Animal Collections to Zoological Gardens*; Kisling, V.N., Jr., Ed.; CRC Press: Boca Raton, FL, USA, 2000; pp. 1-47.
40. Shimada, I. Evolution of Andean civiversity: regional formations (500 B.C.E.–C.E. 600). In *The Cambridge History of the Native Peoples of the Americas*; Salomon, F., Schwartz, S.B., Eds.; Cambridge University Press: Cambridge, UK, 1999; Vol. 3, pp. 350-517.
41. Stahl, P.W. Selective faunal provisioning in the southern highlands of formative Ecuador. *Lat. Am. Ant.* **2005**, *16*, 313-328.
42. Villamarín, J.; Villamarín, J. Chiefdoms: the prevalence and persistence of “*Se ñor ós Naturales*” 1400 to European conquest. In *The Cambridge History of the Native Peoples of the Americas*; Salomon, F., Schwartz, S.B., Eds.; Cambridge University Press: Cambridge, UK, 1999; Vol. 3, pp. 577-667.
43. Tellkamp, M.P. *Mexican Prehistoric Exploitation and Biogeography of Birds in Coastal and Andean Ecuador*; Ph D. Dissertation, University of Florida, Gainesville, USA, 2005.

44. Stahl, P.W.; Athens, J.S. A high elevation zooarchaeological assemblage from the northern Andes of Ecuador. *J. Field. Arch.* **2001**, *28*, 161-176.
45. Hershkovitz, P. The recent mammals of the neotropical region: a zoogeographic and ecological review. *Quart. Rev. Biol.* **1969**, *44*, 1-70.
46. Hershkovitz, P. Taxonomy of squirrel monkeys genus *Saimiri* (Cebidae, Platyrrhini): a preliminary report with description of a hitherto unnamed form. *Am. J. Primat.* **1984**, *6*, 257-312.
47. Cropp, S.; Boinski, S. The central American squirrel monkey (*Saimiri oerstedii*): introduced hybrid or endemic species? *Mol. Phylogen. Evol.* **2000**, *16*, 350-365.
48. Petersen, J.B. Taino, Island Carib, and prehistoric Amerindian economies in the West Indies: tropical forest adaptations to island environments. In *The Indigenous People of the Caribbean*; Wilson, S.M., Ed.; University Press of Florida: Gainesville, FL, USA, 1997; pp. 118-130.
49. Watters, D.R. Maritime trade in the prehistoric Eastern Caribbean. In *The Indigenous People of the Caribbean*; Wilson, S.M., Ed.; University Press of Florida: Gainesville, FL, USA, 1997; pp. 88-99.
50. Steadman, D.W.; Stokes, A.V. Changing exploitation of terrestrial vertebrates during the past 3000 years. *Hum. Ecol.* **2002**, *30*, 339-367.
51. Wing, E.S.; Reitz, E.J. Prehistoric fishing economies of the Caribbean. *Journal of New World Archaeology* **1982**, *5*, 13-36.
52. Auffenberg, W. Notes on West Indian tortoises. *Herpetologica* **1967**, *23*, 34-44.
53. Bonin, F.; Devaux, B.; Dupré, A. *Turtles of the World*. Johns Hopkins University Press: Baltimore, MD, USA, 2006.
54. Censky, E.J. *Geochelone carbonaria* (Reptilia: Testudines) in the West Indies. *Flor. Scient.* **1988**, *50*, 108-114.
55. Censky, E.J. The Lesser Antillean Fauna. In *Caribbean Amphibians and Reptiles*; Crother, B.I., Ed.; Academic Press: San Diego, CA, USA, 1999; pp. 181-221.
56. Franz, R.; Woods, C.A. A fossil tortoise from Hispaniola. *J. Herpet.* **1983**, *17*, 79-81.
57. Thomas, R. The Puerto Rico area. In *Caribbean Amphibians and Reptiles*; Crother, B.I., Ed.; Academic Press: San Diego, CA, USA, 1999; pp. 169-179.
58. Watters, D.R.; Reitz, E.J.; Steadman, D.W.; Pregill, G.K. Vertebrates from archaeological sites on Barbuda, West Indies. *Annals Carnegie Mus.* **1984**, *53*, 383-412.
59. Censky, E.J.; Hodge, K.; Dudley, J. Over-water dispersal of lizards due to hurricanes. *Nature* **1998**, *395*, 556.
60. Lazell, J.D., Jr. The lizard genus *Iguana* in the Lesser Antilles. *Bull. Mus. Comp. Zool.* **1973**, *145*, 1-28.
61. Crother, B.I. Evolutionary relationships. In *Caribbean Amphibians and Reptiles*; Crother, B.I., Ed.; Academic Press: San Diego, CA, USA, 1999; pp. 269-334.
62. Pregill, G.K.; Steadman, D.W.; Watters, D.R. Late quaternary vertebrate faunas of the Lesser Antilles: historical components of Caribbean biogeography. *Bull. Carnegie Mus. Nat. Hist.* **1994**, *30*, 1-54.
63. Steadman, D.W.; Watters, D.R.; Reitz, E.J.; Pregill, G.K. Vertebrates from archaeological sites on Montserrat, West Indies. *Annals Carnegie Mus.* **1984**, *53*, 1-29.

64. Steadman, D.W.; Pregill, G.K.; Olson, S.L. Fossil vertebrates from Antigua, Lesser Antilles: evidence for Late Holocene human-caused extinctions in the West Indies. *Proc. Nat. Acad. Sci.* **1984**, *81*, 4448-4451.
65. Olson, S.L. Biological archaeology in the West Indies. *Flor. Anth.* **1982**, *35*, 162-168.
66. Olson, S.L.; Maíz López, E.J. New evidence of *Ara autochthones* from an archaeological site in Puerto Rico: a valid species of macaw of unknown geographical origin (Aves: Psittacidae). *Carib. J. Sci.* **2008**, *44*, 215-222.
67. Williams, M.I.; Steadman, D.W. The historic and prehistoric distribution of parrots (psittacidae) in the West Indies. In *Biogeography of the West Indies: Patterns and Perspectives*, 2nd ed.; Woods, C.A., Sergile, F.E., Eds.; CRC Press: Boca Raton, CA, USA, 2001; pp. 176-187.
68. Olson, S.L.; Pregill, G.K. Introduction to the Bahamanian vertebrates. In *Fossil Vertebrates from the Bahamas*; Smithsonian Contributions to Paleontology 48 Series; Olson, S.L., Ed.; Smithsonian Institution Press: Washington, DC, USA, 1982; pp. 1-7.
69. Ricklefs, R.E.; Bermingham, E. Likely human introduction of the red-legged thrush (*Turdus plumbeus*) to Dominica, West Indies. *Auk* **1998**, *125*, 299-303.
70. Ricklefs, R.E.; Olson, S.L. More on the origin of the red-legged thrush (*Turdus plumbeus*) of Dominica, West Indies. *Auk* **1998**, *126*, 449-454.
71. Brown, J.H. Patterns, modes and extents of invasions by vertebrates. In *Biological Invasions: A Global Perspective*; Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., Williams, M., Eds.; Wiley and Sons: New York, NY, USA, 1989; pp. 85-109.
72. MacArthur, R.H.; Wilson, E.O. *The Theory of Island Biogeography*; Princeton University Press: Princeton, NJ, USA, 1967.
73. Valentine, J.W. Resource supply and species diversity patterns. *Lethaia* **1971**, *4*, 51-61.
74. Stahl, P.W. Microvertebrate synecology and anthropogenic footprints in the forested neotropics. In *Time and Complexity in Historical Ecology*; Balée, W., Erickson, C.L., Eds.; Columbia University Press: New York, NY, USA, 2006; pp. 127-149.
75. Jones, A.R. Dietary change and human population at Indian Creek, Antigua. *Am. Ant.* **1985**, *50*, 518-536.
76. Morgan, G.S. Taxonomic status and relationships of the Swan Island hutia, *Geocapromys thoractus* (Mammalia:Rodentia:Capromyidae), and the zoogeography of the Swan Islands vertebrates. *Proc. Biol. Soc. Wash.* **1985**, *98*, 29-46.
77. Heckenberger, M.J. *The Ecology of Power. Culture, Place, and Personhood in the Southern Amazon, A.D. 1000–2000*; Routledge: New York, NY, USA, 2005.
78. Hill, J.D. Introduction. In *Comparative Arawakan Histories. Rethinking Language, Family and Culture Area in Amazonia*; Hill, J.D., Santos-Granero, F., Eds.; University of Illinois Press: Urbana, IL, USA, 2002; pp. 1-22.
79. Hornborg, A. Ethnogenesis, regional integration, and ecology in prehistoric Amazonia. *Curr. Anth.* **2005**, *46*, 589-620.
80. Descola, P. Societies of nature and the nature of societies. In *Conceptualizing Society*; Kuper, A., Ed.; Routledge: London, UK, 1992; pp. 107-126.

81. Viveiros de Castro, E. Cosmological deixis and amerindian perspectivism. *J. Roy. Anthropol. Inst.* **1998**, *4*, 469-488.
82. Erikson, P. The Social significance of pet-keeping among Amazonian Indians. In *Companion Animals and Us. Exploring the Relationships between People and Pets*; Podberscek, A.L., Paul, E.S., Serpell, J.A., Eds.; Cambridge University Press: Cambridge, UK, 2000; pp. 7-26.
83. Erickson, C.L. An artificial landscape-scale fishery in the Bolivian Amazon. *Nature* **2002**, *408*, 190-193.
84. Clement, C. 1492 and the loss of crop genetic resources: 1. crop biogeography at contact. *Econ. Bot.* **1999**, *53*, 203-216.
85. Levins, R. Extinction. In *Some Mathematical Questions in Biology. Lectures on Mathematics in the Life Sciences*; Gerstenhaberr, M., Ed.; American Mathematical Society: Providence, RI, USA, 1970; pp. 77-107.
86. Young, T.P. Restoration ecology and conservation biology. *Biol. Cons.* **2000**, *92*, 73-83.
87. Pickett, S.T.A.; Parker, V.T. Avoiding the old pitfalls: opportunities in a new discipline. *Rest. Ecol.* **1997**, *5*, 338-349.
88. Bonnacorso, E.; Peterson, A.T. A multilocus phylogeny of New World Jay genera. *Mol. Phylogenet. Evol.* **2007**, *42*, 467-476.
89. Cooke, R.G.; Olsen, S.L. An archaeological record for the white-faced whistling-duck (*Dendrocygna viduata*) in Central Panama. *Condor* **1984**, *86*, 493-494.

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