12 The Ecology of Human Colonization in Pristine Landscapes

C. Michael Barton, Steven Schmich, and Steven R. James

The peopling of the Western Hemisphere was one of the most significant biogeographic phenomena in modern human history prior to the development of agriculture. Humans spread into two new continents and into the last continental-scale "pristine" ecosystem on the planet. The first colonizers of the Americas were successful arctic hunter-gatherers who were adapted to the rigorous environments of Siberia and Beringia and possibly to the frigid coasts that bordered these areas. As they entered the Americas, they found themselves in a truly new world: a world of forest and woodland instead of steppe and tundra, a world with a new flora and naïve fauna, some of which were similar to the taxa they knew but many of which were unfamiliar.

Such circumstances have happened only two other times for modern humans on a continental scale: the colonization of Sahul (the New Guinea–Australia continent during low Pleistocene sea levels) and the colonization of the land areas exposed by retreating ice sheets at the end of the Pleistocene. These settings provide the only baselines for evaluating the effects of preagricultural humans on pristine ecosystems and the effects of any humans on continental-scale pristine ecosystems. These settings also allow us to view aspects of human behavioral ecology that are not readily apparent in populated landscapes. Certainly the later human expansion to islands of the Pacific Ocean, Indian Ocean, and Mediterranean Sea also provides valuable examples for study. However, the limited geographic size and biological isolation of most of these islands, coupled with the fact that most of the colonizer societies were agriculturalists, make them special cases that are distinct from the initial colonization of the terrestrial ecosystems that characterize continental landmasses.

In the last decade, research into the peopling of the Americas and other landmasses has started to move away from simply documenting the earliest human presence or detailing the activities of single sites and has begun to look more broadly at the processes and effects of colonization behavior from an ecological perspec-

tive. This change in focus is exemplified by many of the chapters in this volume, and Anderson and Gillam (2000) provide an excellent review of such studies elsewhere. One such pioneering work is Kelly and Todd's (1988) article on the peopling of the Americas. Subsequent treatments by Amick (1996), Anderson and Gillam (2000), MacDonald (1999, this volume), Meltzer (2002, this volume), and Steele et al. (1998) build on this work in the New World. Studies by Housely et al. (1997) exemplify similar contributions on Europe, and those by Beaton (1991) and Webb (1998; Webb and Rindos 1997) focus on the colonization of Australia.

These studies model different aspects of the initial colonization of the continental regions and the behaviors of their first inhabitants. Our objective here is not to propose another new model for the first Americans, but to synthesize from these more specific works a general model of initial human colonization of empty landmasses. Several other writers have proposed general first-colonization models, most notably Beaton (1991) and Webb and Rindos (1997).

Beaton proposed two modal strategies for first colonists: "transient explorer" and "estate settler." Transient explorers are highly mobile and constantly on the lookout for landscape patches with a familiar theme, such as a river valley. Estate settlers establish themselves in territories and colonize continents by splitting off into adjacent regions as populations grow. They colonize as small groups essentially drop off along the way. Beaton's two concepts are not mutually exclusive; foraging groups can operate in either mode depending on social and ecological contexts. However, he characterizes the initial colonization of Australia and the Americas as more of a transient explorer phenomenon, whereas the subsequent spread throughout the landscape is better characterized in terms of estate settlers.

Webb and Rindos take a somewhat different perspective. They note that initial colonizers encounter ecosystems that are different from those from which they came and have scant information about resource availability and distribution. This leaves the first colo-

nizers poorly adapted to the new lands. With only a coarse perception of the new landscape and its resources, these colonizers can most readily recognize, and hence make use of, only the most obvious resources. "Skimming the cream" from the top of an ecosystem, they focus primarily on large animals and the most apparent, most easily processed plant foods. However, this strategy gives the new landscape a low effective carrying capacity: resources are quickly exhausted locally, forcing these poorly adapted colonizers to move to new locales. The result is an extremely rapid spread of initial colonizers, all of whom use a similar restricted set of resources throughout their range.

Although simple and appealing, both models leave unanswered questions about initial colonists. For example, rather than moving to new locales, why don't first colonists simply build on their knowledge of their home territory? Isn't movement to yet another unknown place riskier than staying put? What happens when there is no place left to move to? What processes actually drive the switch from transient explorer to estate settler?

Evolutionary Ecology and Colonization Models

The general models described above can be recast in terms of the concepts of evolutionary ecology. By focusing on individual decisions that are ultimately based on cost-benefit analysis, evolutionary ecology can address some of the unanswered questions and make these models more inclusive. Two now classic ecological models for explaining forager behavior with respect to resource availability and distribution are diet breadth and patch choice. These models are described in detail by Bettinger (1991:83–110), Foley (1985), Kelly (1995:65–160), and Smith and Winterhalder (1992; Winterhalder and Smith 2000). Diet breadth models predict that potential resources can be ranked according to caloric returns minus procurement and processing costs. They predict that, when possible, foragers will tend to take higher-ranking resources. As high-ranking resources become unavailable, they will not be replaced by just lower-ranking resources, but by an increasing diversity of lower-ranking resources. Conversely as higher-ranking resources become more available, diet breadth will decrease as diverse lower-ranking resources are replaced by fewer higher-ranking ones.

Patch choice models describe forager spatial responses to variation in resource availability and dis-

tribution. As humans forage in a particular landscape patch, resources become depleted and their procurement costs rise as they become more difficult to find. At some point, procurement costs in one patch exceed the costs of moving to a new patch where resources have not been depleted. Note that foragers are not expected to exhaust resources within a patch; they only deplete them enough to make moving to a new patch less costly than continuing to forage in the current patch.

Both diet breadth and patch choice models make several simplifying assumptions about the environment and the distribution of resources. Furthermore, the actual costs of caloric benefits are difficult to calculate accurately. These and other pragmatic concerns make these models difficult to apply among modern foragers, whose behavior can be observed, and virtually impossible to use in any quantitative sense for archaeological foragers (Kelly 1995:333–334). Nevertheless, the concepts embodied in these models can be usefully applied qualitatively in a heuristic manner to better understand the behavior of prehistoric foragers.

In this chapter, we combine concepts of both diet breadth and patch choice to develop a general model for initial human colonizers of empty landscapes. Arguably these humans fill an empty niche, although there may be some overlap with other animals, primarily large carnivores and scavengers (see Whitney-Smith, this volume) and the few large omnivores. The absence of other human competition and especially the lack of prior human predation increase the effective availability of large herbivores. Access to large prey would be particularly important to the first colonizers of the Americas, who were almost certainly High Arctic foragers. Foragers in high latitudes, by necessity, derive most of their caloric intake from large terrestrial herbivores and marine fauna (Kelly 1995; Speth and Spielmann 1983). These colonizers are thus preadapted to take advantage of large herbivores in the unoccupied human niche. The same would be true of the hunter-gatherers who first recolonized northern Europe as the Scandinavian ice sheet retreated northward at the end of the Pleistocene. Even tropical foragers can rapidly become big-game hunters under the same ecological circumstances (Webb and Rindos 1997). Furthermore, large animals would be easily identified food sources for colonizing foragers who lacked detailed information about the new land, making their procurement costs lower than those of less obvious resources (Kelly and Todd 1988). These characteristics combine with high caloric values to give these taxa a high dietary ranking,

causing humans initially to forego many other potential food sources. Although animal bones (along with stone artifacts) are among the best-preserved residues of the resources used by humans, the same overall pattern of use should apply to other classes of materials. Hence, the most obvious, most easily procured and processed, and highest-quality resources—be they plants, lithic raw materials, or wood—should be the most commonly used resources by initial colonizers.

At any given locale, as humans filled their niche, competition for large herbivores would increase as their numbers declined due to successful hunting. Simultaneously these animals would learn to avoid humans. These factors would decrease the effective availability of large herbivores. Faced with a loss of such high-ranking foods, humans would diversify their diet and include foods that incur higher costs in procurement or processing or that provide fewer calories per unit.

This scenario, however, ignores the possibility of movement as described in patch choice models. Although the depletion of high-ranking resources could lead to increased dietary diversity, patch choice models suggest that foragers will move to a new locality when faced with resource depletion, as long as the costs associated with movement are less than the costs of resource procurement in the original locale. As high-ranking resources become more difficult to procure, foragers would simply move to another locality rather than change their diet. Movement is generally costly, especially movement beyond a group's territory or home range, because the new landscape may be already occupied by other humans. Movement into an area already used by others increases competition for resources, incurs social debts, and may even provoke territorial defense measures, all of which raise the costs of long-distance movement. Movement within a home range is less costly; it incurs only the costs that are directly associated with moving people and their belongings and with building new facilities (e.g., residential structures, nonportable processing equipment, and storage facilities; Kelly 1983, 1995:120–148). In a populated landscape, however, home ranges are generally too small for human movement alone to permit depleted herds of large herbivores to recover.

In an unpopulated landscape, long-distance movement incurs the same physical costs as movement within a home range but does not incur the social costs garnered in a populated landscape. For first colonizers, diet breadth models predict that foragers entering an empty human niche will focus their subsistence on high-ranking large herbivores. Patch choice models predict that when human population growth or herbivore population decline increases procurement costs, foragers will move to new locales where large herbivores are more easily obtained. An important aspect of patch choice models is that they predict foragers will move when procurement costs exceed movement costs, not when resources in a patch are exhausted. For initial colonizers, this threshold would be rapidly crossed because of the lack of other humans in the area. Rather than diversifying their diet by eating more costly foods, humans would move frequently after only modest depletion of herbivore populations.

Expectations and Testing

By applying the ecological models described above, we can propose some general expectations about the nature of settlement systems for the first human colonizers of a landmass. We would expect them initially to focus their subsistence on high-ranking resources, that is, those offering the greatest caloric return for the lowest procurement and processing costs. In terminal-Pleistocene, temperate-latitude, continental environments (and probably subtropical savannahs; Foley 1982), such resources would be best represented by large mammalian herbivores. Although marine mammals offer significant caloric returns, their procurement is generally more costly than that of terrestrial mammals (Bleed 1986; Torrence 1989). If plants contribute to the diet, first colonizers would place the greatest emphasis on those that require the least processing relative to caloric return. This focus would tend to exclude those plants whose processing would require special equipment, such as grinding stones or graters, that would need to be produced, transported, or curated, thus adding to the overall procurement cost. Diet breadth would also be restricted due to the focus on high-ranking resources.

Because mobility costs are generally limited to the physical costs of movement during initial colonization (i.e., there are no social costs as in populated landscapes), declines in availability of high-ranking resources would lead more to settlement shifts than to increased diet diversity. Also, because humans are colonizing a new landmass and moving frequently, landscape knowledge would be almost as limited for the location of a planned move as for an existing settlement. Furthermore, the focus on large, usually wide-ranging, mammalian herbivores and the lack of social or infor-

mational impediments to movement would tend to encourage long-distance moves over shorter ones.

In the archaeological record, manifestations of the first human colonizers would include a predominance of large mammals in faunal remains, a lack of plant-processing equipment, widely spaced settlements, and a rapid spread across large areas. As pointed out by Webb and Rindos (1997), the spread of first colonizers could be so rapid as to appear "instantaneous" within the range of error of radiocarbon dates (see also Fiedel 1999b).

We can also apply foraging models to examine how this pattern might shift over time. As the landscape becomes more populated and the social costs of movement increase, movement rates should slow down. As movement becomes more restricted, large herbivores should become more depleted and, hence, more costly to procure. With increased procurement costs for large herbivores and higher movement costs, human groups would find it cost-effective to collect and process a wider diversity of smaller fauna to assuage subsistence shortfalls. Although large herbivores might become depleted earlier due to their more extensive habitat requirements, other high-ranked resources should suffer similar local depletion and replacement. For example, people may shift to small seed plants that are abundant but costly to process.

Colonizers entering populated landscapes would be more complicated to model, but several general predictions can be made. In some cases, these colonizers may possess a competitive advantage—either technological or organizational—that would permit them to use resources more efficiently (i.e., that would support more people per square kilometer) than extant populations or to access resources that extant populations cannot use. Established farmers moving into areas occupied by foragers represent examples of such colonization and may be seen archaeologically in the Iron Age Bantu expansion in sub-Saharan Africa and in the Neolithic LBK expansion in Europe, although aspects of both cases remain open to discussion (Bogucki and Grygiel 1993; Diamond 1997:376–402; Ehret 1984; Phillipson 1993; Thorpe 1996; Vansina 1995; Whittle 1996). Although such colonization could result in population replacement when profound technological or organizational differences are involved, it is difficult to conceive of sufficient competitive differences between two populations of modern human foragers that would lead to similar replacement (but see Fiedel, this volume).

In the more likely case, extant populations would have considerable advantages over immigrants in terms of accumulated information and organizational strategies adapted to a landscape over the long term. In such circumstances, colonizers would be relegated to marginal habitats and niches that are comparatively costly to occupy and exploit for extant populations. The results and archaeological manifestations of such colonization would vary according to the nature of the marginal niches and the success with which they were occupied. One result simply would be absorption of colonizers into extant populations. Emulation of successful behaviors of extant populations and intermarriage to gain access to less marginal habitats would lead to the disappearance of archaeological evidence for immigrants. Alternatively selection might favor the evolution of specialized technologies and organizations that allow colonizers to exploit a niche that would be marginal for extant populations. This would be the behavioral equivalent of character displacement. In such cases, we might expect to find a specialized technology within a fairly narrow environmental range. Such cases might also show rapid spread within a narrow habitat range as colonizers skip over extant populations to fill the new niche. The initial LBK expansion can also be viewed in perspective, as can the late prehistoric Thule expansion across the High Arctic of North America (see Fiedel, this volume).

Most of Eurasia was populated by humans prior to the late Pleistocene, making these models difficult to test both because of the potential for taphonomic alteration and loss of the archaeological record over such a long period, and because of the unknown degree to which mid-Pleistocene humans differed behaviorally from modern ones. During the late Pleistocene, however, modern humans had several opportunities to colonize large landmasses: Sahul, the Americas, and the regions that had been covered by continental glaciers but were reexposed during deglaciation. In this chapter, we compare the model of first colonizers outlined above to archaeological data in glacial Europe and the Americas, and we refer to the colonization of Sahul/Australia.

Northwestern Europe

Northwestern Europe enjoys several advantages as a locale for testing models of initial human colonization of empty landscapes. Foremost is the certainty that humans were colonizing unoccupied landscapes. Unlike Australia and the Americas, northwestern Europe was undoubtedly unoccupied prior to late Pleistocene colonization; the area had been covered by thousands of

TABLE 12.1 European Sites Used for Age-Distance Analysis

European Site	Region	Uncalibrated Radiocarbon Years B.P.[*]	Calibrated Years B.P. (1 Sigma Range)	Reference
Gönnersdorf	N. Germany	12,828 ± 164	15,721–14,480	Street 1998
Etiolles	Paris Basin	12,634 ± 143	15,526–14,351	Gowlett et al. 1986
Andernach-Martinsberg	N. Germany	12,644 ± 87	15,517–14,377	Street 1998
Slotseng	Denmark	12,520 ± 190	15,471–14,262	Holm 1991
Pincevent	Paris Basin	12,153 ± 109	15,171–13,863	Housley et al. 1997
Køge Bugt Solrød	Denmark	12,140 ± 100	15,154–13,860	AAR-1036 (University of Aarhus Radiocarbon Lab, Denmark)
Poggenwisch	N. Germany	12,500 ± NA	14,759–14,361	Fischer and Tauber 1986
Meiendorf	N. Germany	12,360 ± NA	14,752–14,270	Fischer and Tauber 1986
Stellmoor (Lower)	N. Germany	12,170 ± NA	14,385–14,052	Fischer and Tauber 1986
Klein-Norden	N. Germany	12,035 ± NA	14,106–13,840	Street 1998
Miesenheim II & IV	N. Germany	11,178 ± 104	13,190–13,013	Street 1998
Trollesgave	Denmark	11,100 ± NA	13,158–13,004	Fischer 1989
Fensmark	Denmark	10,810 ± 120	12,983–12,655	Hedges et al. 1993
Kartstein Rockshelter	N. Germany	10,500 ± 113	12,825–12,178	Fischer and Tauber 1986
Lundby Moor	Denmark	9938 ± NA	11,337–11,257	Museum of South Zealand 2002
Lake Fløyrlivatn	SW Norway	9750 ± 80	11,204–11,143	Bang-Andersen 2003
Lake Myrvatn	SW Norway	9610 ± 90	11,166–10,743	Bang-Andersen 1990
Vig	Denmark	9510 ± 115	11,092–10,582	Hedges et al. 1993
Barmose I	Denmark	9176 ± 47	10,401–10,238	Hedges et al. 1992
Lavringe Mose	Denmark	6860 ± NA	7684–7669	Sørensen 1987

[*]Multiple ¹⁴C dates from same stratigraphic context were averaged using Calib 4 (S. Stuiver, University of Washington) prior to calibration.

meters of the Scandinavian ice sheet. The region also has a long history of archaeological study and, hence, a comparatively fine-grained archaeological record, with numerous sites and a well-established chronological framework. However, the dynamics of the retreating ice sheet, rising sea levels in the Baltic and North Seas, and isostatic rebound make characterization of the landscape—and even the extent of available land area—complicated. Furthermore, the retreating ice simply expanded the area of the European subcontinent that was available for human habitation. No physical barrier (such as a seaway, narrow land isthmus, or ice sheet) precluded bidirectional movement between the newly available landmass and the Pleistocene refugia for human populations in Europe. Also, the differences

between the environments of the source region and the colonized area appear to have been minimal. Fauna recolonizing the deglaciated zones would have had a long history of adaptation to (and avoidance of) humans. Colonization processes may have been different than in the continents of Australia and the Americas, which were separated from source populations by oceanic or ice barriers, had flora and fauna that differed from those of the colonists' homelands, and had naïve faunas. With these caveats in mind, we examine the archaeological data for the colonization of northwestern Europe after the Scandinavian ice sheet retreated north of the Baltic Sea by 13,000 B.P.

Figure 12.1 shows the earliest radiocarbon dates for occupation of sites in northwestern Europe (see
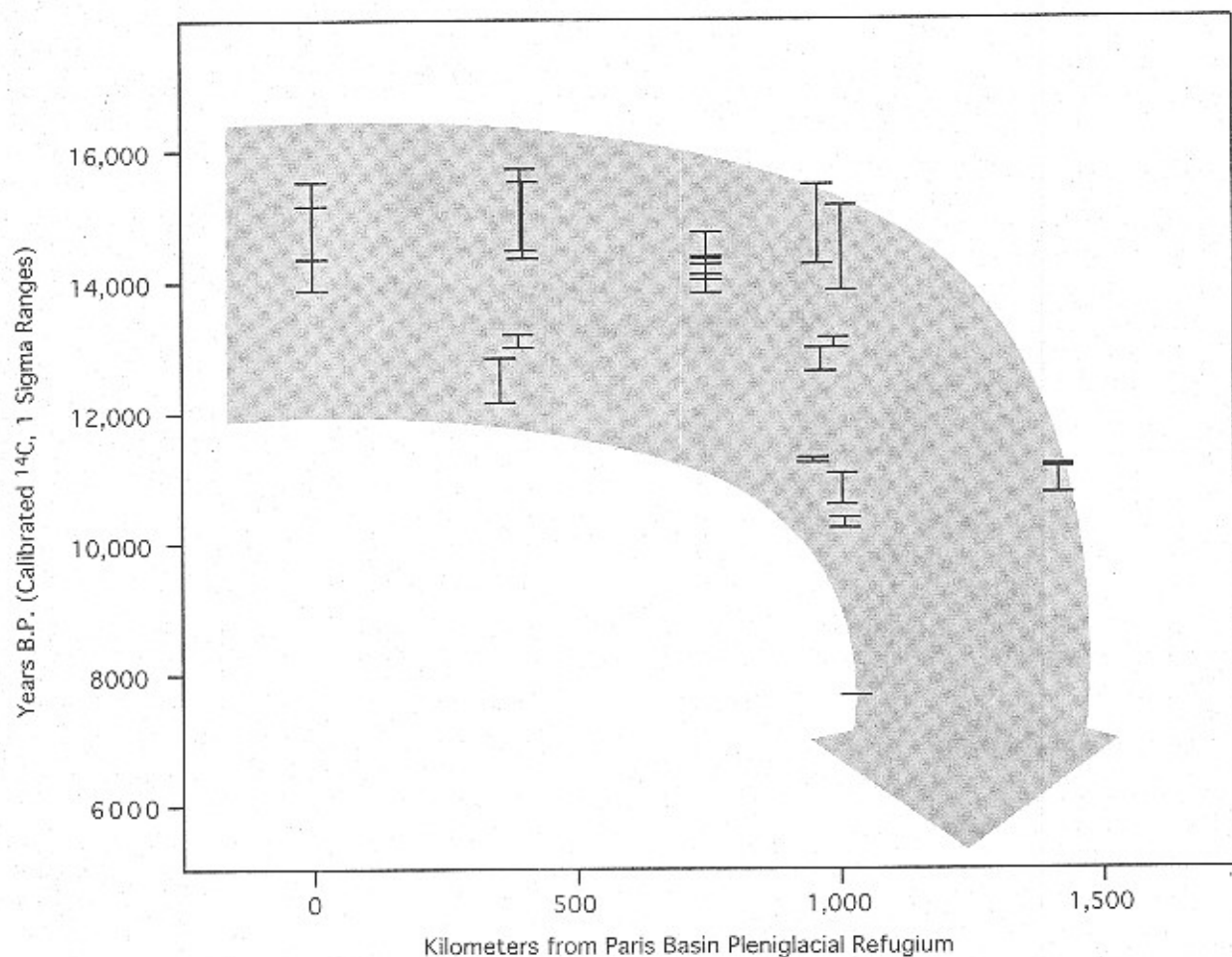
FIGURE 12.1 Calibrated dates (1 sigma ranges) versus distance from Paris Basin pleniglacial refugium for earliest sites in deglaciated northwestern Europe.

table 12.1) and the distance of those sites from one of the Pleistocene refugia in northern France. (We use calibrated dates throughout this paper except as explicitly indicated.) The initial rate of colonization is high at 0.9 km/yr but is considerably lower than the rate of 2–3 km/yr predicted by Webb and Rindos (1997). This is not surprising given the ecological similarities between the source and colonized areas and the smaller region compared with the continent-wide scale mentioned by Webb and Rindos. The rate of colonization, however, slows rapidly as this much smaller area becomes populated by foragers, dropping to 0.3 km/yr by the early Holocene.

Diet diversity (fig. 12.2) also shows patterns that follow those predicted by the behavioral ecology models discussed above (see tables 12.2 and 12.3). The measure of diversity used here is based on the reciprocal of Simpson's index (James 1990; Simpson 1949) and combines values for richness and evenness. In Pleistocene refugia (fig. 12.2A), diet diversity is initially moderate for European foragers in the Early Glacial and drops to low values during the Pleniglacial in the European steppe-tundra. As climate changes at the end of the Pleistocene and the landscape is covered initially by pine-birch woodland and subsequently by deciduous forest, gregarious large herbivores of the steppe-tundra become more difficult to procure; diet diversifies accordingly in these populated areas (Simek and Snyder 1988). Contemporaneously in the recently deglaciated regions (fig. 12.2B), however, movement is a less costly alternative to diet diversification as a means of dealing with increasing risk of scarcity in high-ranking faunal resources. In these areas, diet diversity remains low until
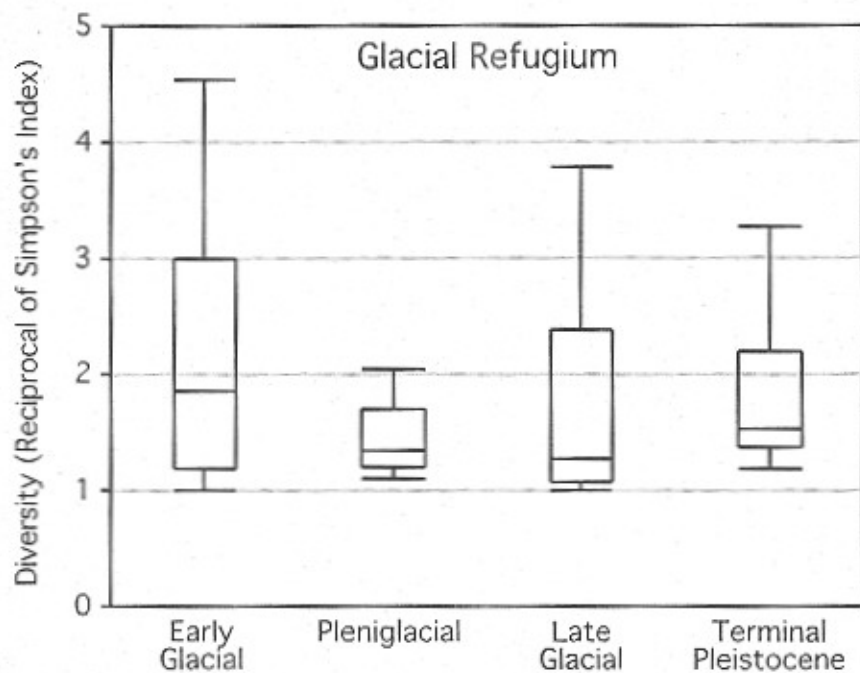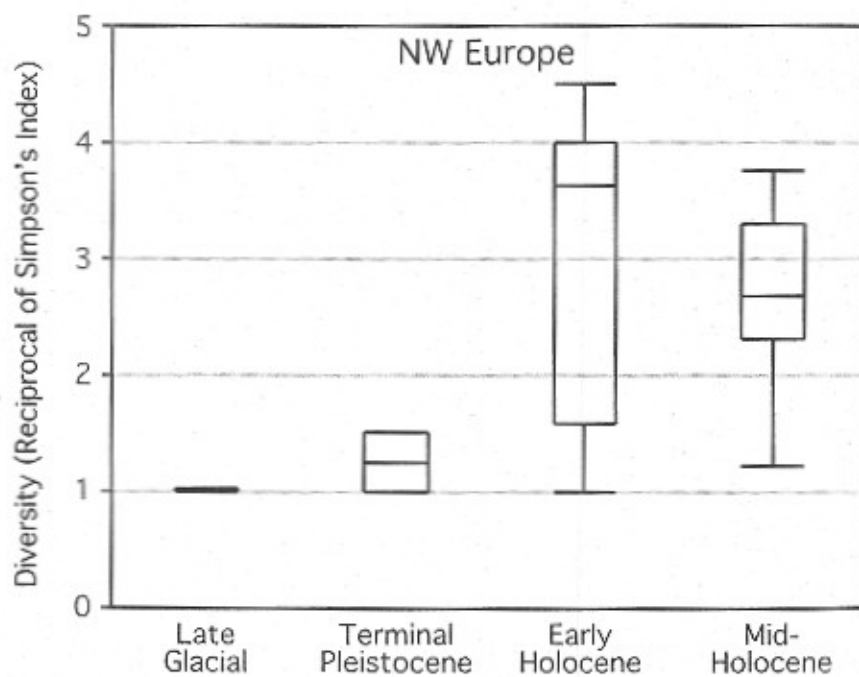
FIGURE 12.2 Diet diversity (reciprocal of Simpson's index of NISP for fauna) for *(A)* pleniglacial refugia and *(B)* deglaciated northwestern Europe.

TABLE 12.2 European Sites Used for Diet Diversity Analysis: Refugia in Southwestern and Central France and Central Germany

Refugia Site	Period	Phase	Diversity Index	Reference
Baerenkeller	Late Glacial	Hamburgian Bromme	1.03	Eriksen 1996
Lausnitz	Late Glacial	Hamburgian Bromme	1.21	Eriksen 1996
Oelknitz	Late Glacial	Hamburgian Bromme	1.19	Eriksen 1996
Teufelsbruecke 3–4	Late Glacial	Hamburgian Bromme	2.81, 1.60	Eriksen 1996
Blassac	Terminal Pleist.	Azilian	3.27	Boyle 1990
Bois Ragot 3–4b	Terminal Pleist.	Azilian	1.35, 1.62	Boyle 1990
Campalou	Terminal Pleist.	Azilian	1.38	Boyle 1990
Grotte du Tai SN SX, C'1, C"1	Terminal Pleist.	Azilian	2.45, 1.95, 1.86	Boyle 1990
La Faurelie II 2–3	Terminal Pleist.	Azilian	1.19, 1.27	Boyle 1990
Pages	Terminal Pleist.	Azilian	1.41	Boyle 1990
Pont d'Ambon 2–4	Terminal Pleist.	Azilian	1.24–3.22	Boyle 1990
Roc d'Abeilles	Terminal Pleist.	Azilian	2.86	Boyle 1990
Bergerie	Late Glacial	Late Magdalenian	1.19	Boyle 1990
Bois Ragot 5b–6	Late Glacial	Late Magdalenian	2.46, 1.70	Boyle 1990
Bruniquel	Late Glacial	Late Magdalenian	1.13	Boyle 1990
Cap Blanc	Late Glacial	Late Magdalenian	3.22	Boyle 1990
Faustin	Late Glacial	Late Magdalenian	3.62	Boyle 1990
Fongaban 2–6	Late Glacial	Late Magdalenian	1.03–2.39	Boyle 1990
Fontarnaud	Late Glacial	Late Magdalenian	2.95	Boyle 1990
Gabillou	Late Glacial	Late Magdalenian	1.34	Boyle 1990
Gare de Couze (B–H)	Late Glacial	Late Magdalenian	1.27	Boyle 1990
Grotte des Fees	Late Glacial	Late Magdalenian	1.12	Boyle 1990
La Madeleine 2–16	Late Glacial	Late Magdalenian	1.00–2.71	Boyle 1990
La Mairie	Late Glacial	Late Magdalenian	2.39	Boyle 1990
La Mege	Late Glacial	Late Magdalenian	2.39	Boyle 1990
Le Flageolet IX	Late Glacial	Late Magdalenian	1.28	Boyle 1990
Le Morin AI–AIV, B1–BII	Late Glacial	Late Magdalenian	1.04–3.63	Boyle 1990
Marcamps	Late Glacial	Late Magdalenian	1.81	Boyle 1990
Montmorillon	Late Glacial	Late Magdalenian	3.70	Boyle 1990
Reignac	Late Glacial	Late Magdalenian	2.14	Boyle 1990
Roc d'Abeilles	Late Glacial	Late Magdalenian	5.43	Boyle 1990
Rond du Barry D–E	Late Glacial	Late Magdalenian	2.24, 3.78	Boyle 1990
Ste. Eulalie I, III	Late Glacial	Late Magdalenian	1.35, 1.35	Boyle 1990
Combe Cullier 4–5, 8–9, 11–16	Pleniglacial	Middle Magdalenian	1.16–1.56	Boyle 1990
Lachaud	Pleniglacial	Middle Magdalenian	1.86	Boyle 1990
Laugerie Haute Est	Pleniglacial	Middle Magdalenian	1.18, 1.19	Boyle 1990

TABLE 12.2 Continued

Refugia Site	Period	Phase	Diversity Index	Reference
Cottier n II–III	Pleniglacial	Early Magdalenian	1.92	Boyle 1990
Fritch 3–6	Pleniglacial	Early Magdalenian	1.32–1.98	Boyle 1990
Laugerie Haute Est	Pleniglacial	Early Magdalenian	1.10, 2.05	Boyle 1990
Abri Pataud 7	Early Glacial	Late Aurignacian	2.01	Boyle 1990
Caminade Est D	Early Glacial	Late Aurignacian	4.41	Boyle 1990
F4–F1 fr. Ga–Ge sag.	Early Glacial	Late Aurignacian	2.22	Boyle 1990
Font de Gaume	Early Glacial	Late Aurignacian	1.92	Boyle 1990
G0 fr. G0 & F sag.	Early Glacial	Late Aurignacian	1.82	Boyle 1990
G1 sag. G1–G3 fr.	Early Glacial	Late Aurignacian	4.23	Boyle 1990
La Chevre	Early Glacial	Late Aurignacian	2.80	Boyle 1990
La Ferrassie J & K1–3, L1–H1	Early Glacial	Late Aurignacian	3.07, 4.54	Boyle 1990
Maldidier 5–6	Early Glacial	Late Aurignacian	3.30–3.89	Boyle 1990
Pair-non-Pair K	Early Glacial	Late Aurignacian	3.22	Boyle 1990
Roc de Combe 5–6	Early Glacial	Late Aurignacian	1.17, 1.42	Boyle 1990
Abri Pataud 11–14	Early Glacial	Early Aurignacian	1.00–1.91	Boyle 1990
Battus 3	Early Glacial	Early Aurignacian	1.97	Boyle 1990
Bourgeois-Delauny	Early Glacial	Early Aurignacian	2.18	Boyle 1990
Fontaury C2–C3	Early Glacial	Early Aurignacian	2.02, 1.81	Boyle 1990
La Chevre	Early Glacial	Early Aurignacian	1.54	Boyle 1990
La Ferrassie	Early Glacial	Early Aurignacian	1.55	Boyle 1990
La Gravette	Early Glacial	Early Aurignacian	1.11	Boyle 1990
Pair-non-Pair KD	Early Glacial	Early Aurignacian	3.34	Boyle 1990
Roc de Combe 7a–7b	Early Glacial	Early Aurignacian	1.13–1.24	Boyle 1990

population packing again limits movement in the early Holocene. At that time, diet diversity in the deglaciated zone rises dramatically. Overall the available archaeological data for deglaciated northwestern Europe at the end of the Pleistocene fit the model of initial colonizers based on the general principles of evolutionary ecology.

The Americas

For almost all archaeologists, the colonization of Western Hemisphere continents was a late Pleistocene phenomenon that involved completely modern humans, although debate remains over whether the initial colonization took place in the middle or near the end of the late Pleistocene. The Americas encompass a much larger land area than northwestern Europe, potentially affecting the total time span of colonization and the rate of change in subsistence and settlement organization. Unlike in northwestern Europe, there were (and still are) much more pronounced physiographic restrictions to human movement between the Americas and source population areas in northeastern Asia, and another bottleneck exists between North and South America. Even though temperate North America and temperate Eurasia share many aspects of a Holarctic flora and fauna, they do differ, especially in the South American taxa that spread northward after the two American continents collided in the late Tertiary. The initial colonizers of the Americas were almost certainly High Arctic foragers, whether they focused on marine resources, terrestrial resources, or some combination of

TABLE 12.3 European Sites Used for Diet Diversity Analysis: Deglaciated Northwestern Europe

NW European Site	Period	Phase	Diversity Index	Reference
Aamølle	M. Holocene	Mesolithic	3.04	Bay-Petersen 1978
Ageröd I (B, D, HC) & V	M. Holocene	Mesolithic	1.63–3.48	Mithen 1990
Bredasten	M. Holocene	Mesolithic	1.81	Mithen 1990
Dyrholmen	M. Holocene	Mesolithic	3.41	Bay-Petersen 1978
Eretebølle	M. Holocene	Mesolithic	2.90	Bay-Petersen 1978
Faareville	M. Holocene	Mesolithic	2.38	Bay-Petersen 1978
Hallebygaard	M. Holocene	Mesolithic	1.23	Bay-Petersen 1978
Havnø	M. Holocene	Mesolithic	3.76	Bay-Petersen 1978
Kildegaard	M. Holocene	Mesolithic	2.13	Bay-Petersen 1978
Klintesø	M. Holocene	Mesolithic	2.52	Bay-Petersen 1978
Lavringe mose	M. Holocene	Maglemose	5.46	Sørensen 1987
Magleø	M. Holocene	Mesolithic	2.57	Bay-Petersen 1978
Segebro	M. Holocene	Mesolithic	2.88	Mithen 1990
Skateholm	M. Holocene	Mesolithic	2.81	Mithen 1990
Tingbjerggaard	M. Holocene	Mesolithic	2.38	Bay-Petersen 1978
Bedburg	E. Holocene	Early Mesolithic	1.59	Street 1998
Hesselbjgaard	E. Holocene	Early Mesolithic	4.50	Bay-Petersen 1978
Holmegaard	E. Holocene	Early Mesolithic	3.63	Bay-Petersen 1978
Øgaarde	E. Holocene	Early Mesolithic	3.43	Bay-Petersen 1978
Stellmoor (Upper)	E. Holocene	Ahrensburgian	1.00	Eriksen 1996
Svaerdborg	E. Holocene	Early Mesolithic	3.65	Bay-Petersen 1978
Vinde Helsinge	E. Holocene	Early Mesolithic	4.00	Bay-Petersen 1978
Bromme	Terminal Pleist.	Bromme	1.52	Street 1998
Klein-Nordende	Terminal Pleist.	Bromme	1.00	Street 1998
Meiendorf	Late Glacial	Hamburgian	1.03	Eriksen 1996
Poggenwisch	Late Glacial	Hamburgian	1.00	Eriksen 1996
Stellmoor (Lower)	Late Glacial	Hamburgian	1.00	Eriksen 1996

the two. America south of the ice sheets, however, was comparatively mesic and vegetated in a heterogeneous open woodland (Barton 1979; Chilton, this volume; Guilday 1984; Guthrie 1984; Meltzer, this volume; Steele et al. 1998), which was a dramatically different landscape from the steppe-tundra of unglaciated Alaska and northeastern Asia. In contrast with the people who recolonized northwestern Europe, the first colonizers of the Americas found themselves largely isolated from their original homelands and in a very different ecosystem from the one to which they were accustomed but also one rich in easily procured resources.

With this background in mind, we compare the archaeological evidence for the earliest occupants of the Americas with the predictions of the behavioral ecology model described above. We have chosen to use Paleoindian data for this comparison for a variety of reasons. The claimed pre-Clovis localities are few and widely dispersed, and their dates are highly variable (see Meltzer, this volume; Schmitz, this volume). These consider-
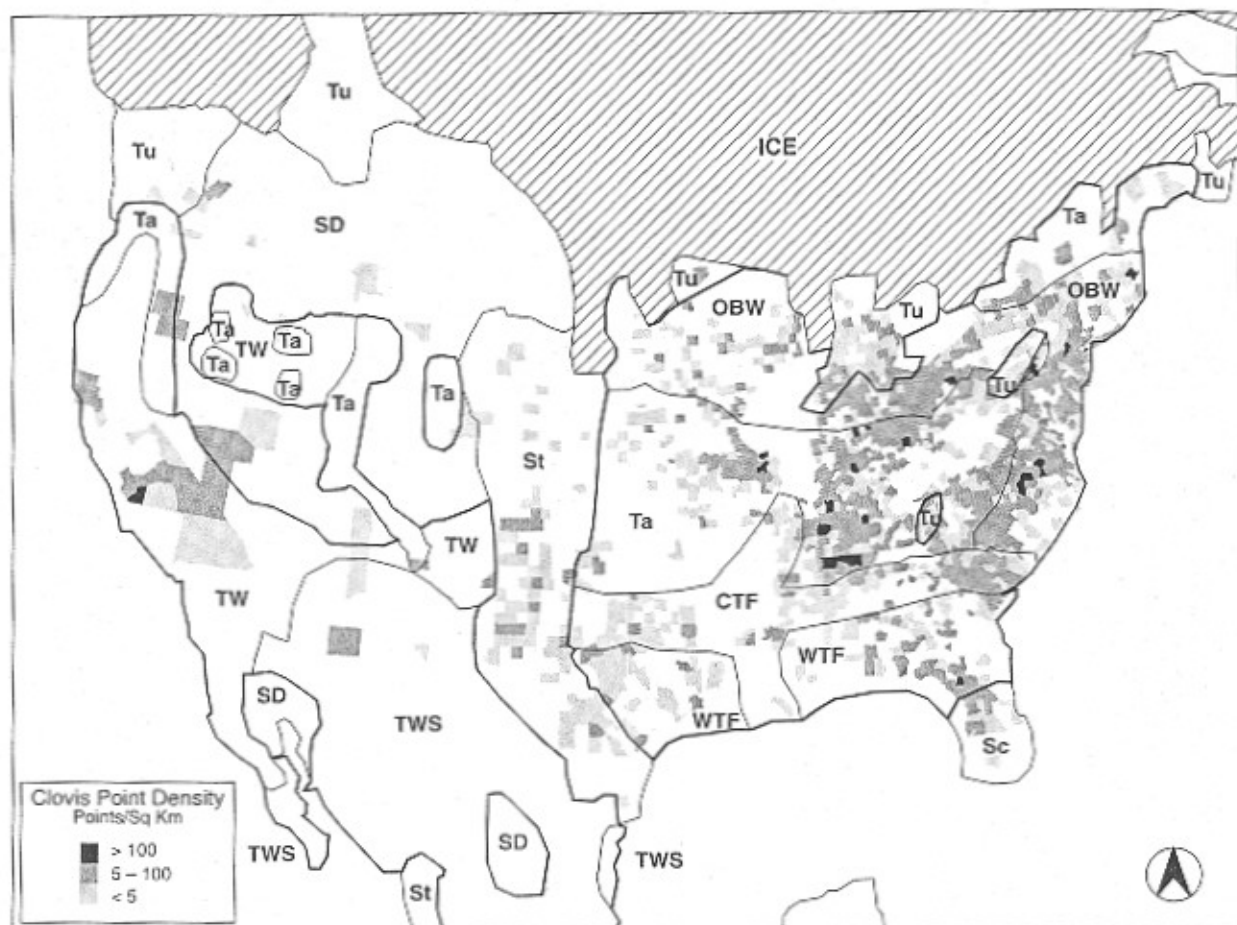
FIGURE 12.3 Distribution of Clovis and morphologically similar points (Anderson and Faught 1998a,b) and North American biomes at 15,600 cal B.P. (13,000 uncal B.P.; Adams and Faure 1998). Heavy line indicates resource-rich woodland and open-forest biomes. CTF = cool temperate forest, OBW = open boreal woodland, Sc = scrub, SD = semidesert, St = steppe, Ta = taiga, Tu = tundra, TW = temperate woodland, TWS = temperate woodland/scrub, WTF = warm temperate forest.

ations, along with the many questions about the reliability of the data from these localities and their interpretation, make it difficult to test the applicability of the ecological model we propose. Furthermore, analysis of the Paleoindian data set from the perspective of this model can shed light on the nature of the Paleoindian colonization, including its relationship to any prior colonization.

Land Use and Mobility

Figure 12.3 shows the distribution of early Paleoindian (i.e., Clovis and morphologically similar) projectile points and reconstructed contemporaneous biomes. Areas of higher densities of discarded projectile points probably indicate zones of more intensive use by these foragers—that is, repeated reoccupation or use by larger social groups than were typical—and, hence, represent major foci of Paleoindian land use. Early Paleoindian points accumulated most densely in the mixed temperate woodlands and open forests of North America. Although the data are much more limited, the same pattern seems to hold true for South America, with the earliest known sites concentrated in late Pleistocene forest-savannah mosaic in northern Brazil, Columbia, and Venezuela and in open forests of the Andean uplands along the western continental margin (Barton et al. 1999). Perhaps the closest modern analog of these communities is the savannah of subtropical Africa
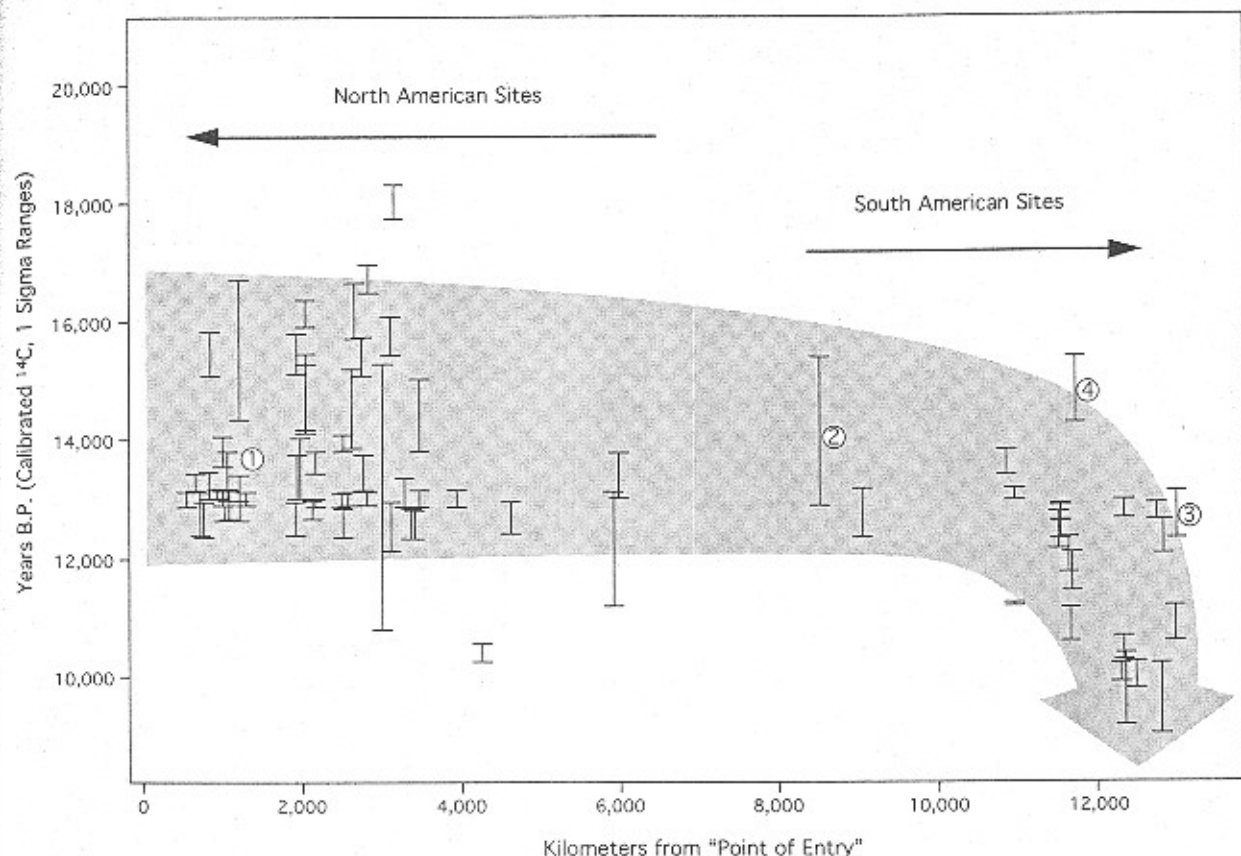
FIGURE 12.4 Calibrated dates (1 sigma ranges) versus distance from entry point for earliest Paleo-indian sites in North and South America. Sites mentioned in text: *(1)* Union Pacific (UP) Mammoth, United States; *(2)* Pachamachay, Peru; *(3)* Fell's Cave, Chile; and *(4)* Monte Verde, Chile.

(Foley 1982; Marean 1997). Like the African savannah, these biomes supported rich and diverse plant communities, many of whose members are no longer found in association with one another. They also seem to have supported an extremely rich array of large gregarious herbivores and the large carnivores and scavengers that preyed upon them (Guilday 1984; Guthrie 1984; Steele et al. 1998). These earliest Paleoindian sites are notably scarcer in completely open steppe and closed dense forest. This pattern suggests an economic emphasis on the most productive biomes, especially those that supported the richest assemblages of large herbivores.

Figure 12.4 shows radiocarbon dates (see tables 12.4 and 12.5) for the earliest Paleoindian sites in the Americas and their linear distances from a hypothetical point of entry at the southern terminus of the late Pleistocene corridor between the Cordilleran and Laurentide ice sheets. (The graph changes very little if an alternate

entry point along the northwestern coast is chosen.) At this bicontinental scale, it is clear that initial movement rates were extremely high, perhaps averaging as much as 10–20 km/yr. This is an order of magnitude greater than the rates discussed above for northwestern Europe and higher than those predicted by Webb and Rindos (1997). In terms of radiocarbon dates, this would appear almost instantaneous (see also Fiedel 1999b). However, it is also apparent that, as in northwestern Europe, movement rates declined over time as the hemisphere became populated; the final colonization of southern South America took nearly as long as the colonization of the rest of the hemisphere. For example, the overall colonization rate from the Union Pacific (UP) Mammoth site in north-central North America to Fell's Cave in the southern tip of South America is about 8 km/yr, whereas the rate from Pachamachay in Peru to Fell's Cave is only 0.4 km/yr (fig. 12.4). Interestingly, when

TABLE 12.4 North American Sites Used for Age-Distance Analysis

N. American Site	Region	Uncalibrated Radiocarbon Years B.P.*	Calibrated Years B.P. (1 Sigma Range)	Reference
Ester Creek	Far NW	12,051 ± 78	15,006–13,841	Dixon 1999; Rainey 1939
Mesa	Far NW	11,660 ± 80	13,824–13,465	Gal 1982; Kunz and Reanier 1996
Tuluaq	Far NW	11,191 ± 87	13,190–13,021	Rasic and Gal 2000
Charlie Lake Cave	Far NW	10,538 ± 82	12,835–12,344	Driver 1988; Driver et al. 1996; Fladmark 1996; Fladmark et al. 1988
Fort Rock Cave	Northwest	13,200 ± 720	16,730–14,367	Bryan and Tuohy 1999; Gilsen 2000; Willig and Aikens 1988
Wasden, Owl Cave	Northwest	12,930 ± 150	15,831–15,086	Bryan and Tuohy 1999
Cooper's Ferry	Northwest	11,370 ± 70	13,457–13,164	Bryan and Tuohy 1999; Davis and Sisson 1998
Connley Cave	Northwest	11,200 ± 200	13,424–12,994	Gilsen 2000; Willig and Aikens 1988
Marmes Rockshelter	Northwest	10,810 ± 300	13,140–12,392	Lyman 2000; Willig and Aikens 1988
Lake Abert	Northwest	10,810 ± 120	12,983–12,655	Gilsen 2000; Pettigrew 1985
Lind Coulee	Northwest	10,680 ± 190	12,951–12,370	Galm and Gough 2000; Lyman 2000
Buhl Burial	Northwest	10,675 ± 95	12,915–12,632	Green et al. 1998; Neves and Blum 2000
Agate Basin	N. Central	11,840 ± 130	14,061–13,565	Haynes et al. 1992; Stanford 1999b
UP Mammoth	N. Central	11,360 ± 350	13,808–13,000	Taylor et al. 1996
Colby	N. Central	11,200 ± 220	13,433–12,987	Frison and Todd 1986; Taylor et al. 1996
Lange/Ferguson	N. Central	11,140 ± 140	13,186–12,992	Hannus 1990; C. V. Haynes Jr. 1991a; Taylor et al. 1996
Casper	N. Central	11,190 ± 50	13,183–13,026	Frison 2000; Stanford 1999b
Jim Pitts	N. Central	11,033 ± 101	13,151–12,904	Stanford 1999b
Hell Gap	N. Central	10,919 ± 206	13,145–12,668	Haynes et al. 1984, 1992
Dent	N. Central	10,980 ± 90	13,136–12,891	Taylor et al. 1996
Anzick	N. Central	10,940 ± 90	13,121–12,882	Taylor et al. 1996
Mud Lake	Midwest	13,440 ± 60	16,381–15,918	Overstreet 1993; Overstreet and Stafford 1997
Hebior	Midwest	12,501 ± 203	15,464–14,184	Overstreet 1993; Overstreet and Stafford 1997
Schaefer Mammoth	Midwest	12,310 ± 60	15,295–14,134	Overstreet 1993; Overstreet and Stafford 1997
Eppley Rockshelter	Midwest	12,185 ± 130	15,207–13,876	Brush 1993; Lepper 1999; Maslowski et al. 1995
Paleo Crossing	Midwest	10,981 ± 95	13,137–12,891	Brose 1994; Fiedel 1999b; Lepper 1999; Maslowski et al. 1995; Tankersley and Holland 1994
Sheriden Cave	Midwest	10,930 ± 89	13,115–12,880	Tankersley 1997; Tankersley and Redmond 1999; Tankersley et al. 1997
Big Eddy	S. Central/SW	12,940 ± 120	15,822–15,134	Hajic et al. 2000; Lopinot et al. 1998, 2000
Johnson	S. Central/SW	11,980 ± 110	14,107–13,825	Broster and Norton 1996; Fiedel 1999b
Domebo	S. Central/SW	11,480 ± 450	14,036–13,007	Haynes 1967; Stafford et al. 1990; Taylor et al. 1996

TABLE 12.4   Continued

N. American Site	Region	Uncalibrated Radiocarbon Years B.P.[*]	Calibrated Years B.P. (1 Sigma Range)	Reference
Aubrey	S. Central/SW	11,570 ± 70	13,802–13,435	Ferring 1995; Taylor et al. 1996
Blackwater Draw	S. Central/SW	11,300 ± 240	13,753–13,014	Taylor et al. 1996
Lehner	S. Central/SW	10,940 ± 40	13,015–12,887	Haynes 1967; Taylor et al. 1996
Murray Springs	S. Central/SW	10,890 ± 50	12,995–12,685	Haynes 1967; Taylor et al. 1996
Rodgers Shelter	S. Central/SW	10,700 ± 200	12,966–12,378	Ray et al. 2002
Dust Cave	S. Central/SW	10,570 ± 60	12,848–12,365	Driskell 1996
Cactus Hill	Central East	15,070 ± 70	18,307–17,753	McAvoy and McAvoy 1997
Saltville	Central East	13,950 ± 70	16,983–16,492	McDonald 2000
Enoch Fork Shelter	Central East	13,480 ± 350	16,656–15,731	Tankersley 1990b
St. Albans	Central East	12,910 ± 60	15,755–15,092	Brashler et al. 1994
Baucom	Central East	11,100 ± 1530	15,307–10,787	Goodyear 1999
Page-Ladson	Southeast	13,130 ± 200	16,107–15,435	Goodyear 1999
Little Salt Springs	Southeast	12,030 ± 200	15,049–13,822	Anderson et al. 1996; Clausen et al. 1979
Warm Mineral Springs	Southeast	10,980 ± 160	13,150–12,880	Tesar 2000
State Road Ripple	Northeast	11,385 ± 140	13,761–13,158	Herbstritt 1988; Lepper 1999
Lamb	Northeast	11,400 ± 100	13,758–13,167	Gramly 1999
Whipple	Northeast	11,050 ± 300	13,363–12,862	Bonnichsen and Will 1999; Curran 1984; Haynes et al. 1984
Debert	Northeast	10,011 ± 90	13,170–12,874	MacDonald 1966, 1968; Stuckenrath 1964; Stuckenrath et al. 1966; Wilmeth 1978
Hiscock	Northeast	11,004 ± 45	13,136–12,902	C. V. Haynes Jr. 1991a; Laub and Haynes 1998; Laub et al. 1988
Shawnee-Minisink	Northeast	10,625 ± 289	12,971–12,132	McNett 1985b
Vail	Northeast	10,530 ± 103	12,837–12,335	Bonnichsen and Will 1999; Gramly 1982; Haynes et al. 1984; Levine 1990
Hedden	Northeast	10,526 ± 81	12,829–12,340	Spiess and Mosher 1994; Spiess et al. 1995
Alvina de Parita	Mesoamerica	11,350 ± 250	13,779–13,030	Crusoe and Felton 1974
Corona Rockshelter	Mesoamerica	10,440 ± 650	13,132–11,197	Cooke and Ranere 1992b; Gruhn and Bryan 1977
Los Tapiales	Mesoamerica	10,710 ± 170	12,958–12,427	Gruhn and Bryan 1977
Los Grifos	Mesoamerica	9233 ± 108	10,559–10,239	Santamaria 1981
Cueva los Vampiros	Mesoamerica	8560 ± 650	10,397–8651	Cooke and Ranere 1992b

[*]Multiple ^{14}C dates from same stratigraphic context were averaged using Calib 4 (S. Stuiver, University of Washington) prior to calibration.

TABLE 12.5 South American Sites Used for Age-Distance Analysis

S. American Site	Region	Uncalibrated Radiocarbon Years B.P.*	Calibrated Years B.P. (1 Sigma Range)	Reference
Pachamachay	Northern	$11,800 \pm 930$	15,413–12,910	Gruhn 1997; Rick 1980
Pedra Pintada	Northern	$10,531 \pm 50$	13,183–12,349	Roosevelt et al. 1996
Monte Verde	Southern	$12,200 \pm NA$	15,419–14,307	Dillehay 1989, 1997b; but see Fiedel 1999b
Quereo	Southern	$11,600 \pm 190$	13,829–13,406	Gruhn 1997; Núñez et al. 1994
Tagua Tagua 1	Southern	$11,115 \pm 146$	13,180–12,979	Núñez et al. 1987, 1994
Tres Arroyos	Southern	$10,523 \pm 84$	13,134–12,338	Borrero 1995
Piedra Museo	Southern	$10,831 \pm 107$	12,988–12,662	Miotti 1995; Miotti and Cattaneo 1997
Cerro la China 2	Southern	$10,735 \pm 97$	12,944–12,644	Flegenheimer and Zarate 1997
Cueva del Medio	Southern	$10,659 \pm 56$	12,919–12,633	Borrero 1995
Cerro la China 1	Southern	$10,654 \pm 66$	12,900–12,631	Flegenheimer and Zarate 1997
Cerro la China 3	Southern	$10,610 \pm 180$	12,899–12,331	Flegenheimer and Zarate 1997
Cerro el Sombrero	Southern	$10,457 \pm 66$	12,795–12,170	Flegenheimer and Zarate 1997
Fell's Cave	Southern	$10,743 \pm 120$	12,642–12,089	Bird 1969; Empéraire et al. 1963; Nami 1985; Schobinger 1972
Paso Otero 5	Southern	$10,305 \pm 87$	12,351–11,774	Martínez 2001
Cueva Tixi	Southern	$10,144 \pm 78$	12,092–11,444	Mazzanti 1997
Tagua Tagua 2	Southern	9844 ± 62	11,256–11,195	Núñez et al. 1987, 1994
Marazzi	Southern	9590 ± 200	11,197–10,581	Borrero 1995
Abrigo los Pinos	Southern	9570 ± 120	11,158–10,601	Mazzanti 1997
Cueva de los Manos	Southern	9310 ± 90	10,668–10,291	Borrero 1995
Los Toldos	Southern	8750 ± 480	10,402–9164	Borrero and McEwan 1997; Roosevelt et al. 2002
Pali Aike	Southern	8639 ± 450	10,224–9033	Bird 1951
El Verano	Southern	8960 ± 140	10,222–9774	Borrero 1995, 1999
Cueva del Arroyo Feo	Southern	8952 ± 72	10,211–9919	Borrero 1995

*Multiple ^{14}C dates from same stratigraphic context were averaged using Calib 4 (S. Stuiver, University of Washington) prior to calibration.

Monte Verde, Chile, is plotted in this way, it appears as only a modest outlier to the overall curve.

Although the graph of figure 12.4 provides a useful overview of the colonization process, it is unlikely that humans actually spread southward across the Americas in a consistent wave, such as the "blitzkrieg" schematically portrayed by Martin (1967, 1973, 1984b; Mosimann and Martin 1975). Although the biomes of unglaciated North and South America probably differed less during the late Pleistocene than in the Holocene, the floral and faunal communities still varied geographically (Chilton, this volume). Some biomes would have been more pro-

ductive for initial colonizers than others. Based on the model we outline here, we would expect initial colonizers to move first into the most productive biomes, that is, those that produced the highest return for foraging effort (see also Steele et al. 1998). Subsequently, as people accumulated more knowledge of the landscape (lowering the procurement costs associated with uncertainty) and the area became more populated (increasing movement costs while making some resources scarcer), the people would begin to occupy less desirable biomes. In effect, the initial colonizers would leapfrog through the richest biomes, and their descendents would back-
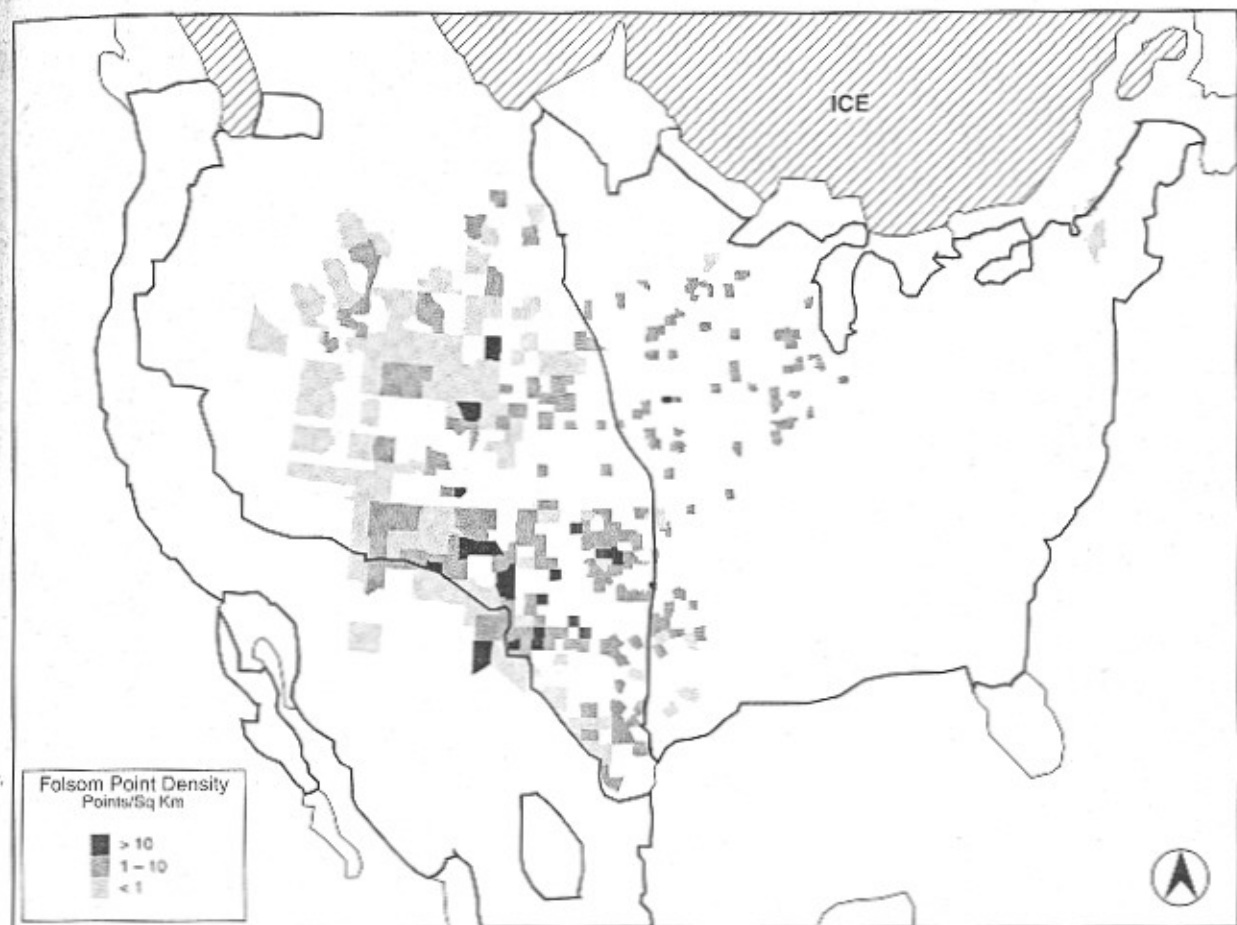
FIGURE 12.5 Distribution of Folsom and morphologically similar points (Anderson and Faught 1998a,b) and North American biomes at 12,000 cal B.P. (11,000 uncal B.P.; Adams and Faure 1998). Heavy line indicates resource-rich woodland and open-forest biomes.

fill the rest of the landscape (see also Meltzer, this volume). The overall distribution of Clovis and Folsom points (Anderson and Faught 1998a,b), as shown in figures 12.3 and 12.5, also supports this model. Although Clovis points are most concentrated in the rich open woodlands (fig. 12.3), Folsom points are found in biomes that people carrying Clovis points seemed to bypass (fig. 12.5).

We model such a process in figure 12.6. We use the earliest Paleoindian sites in each of the potentially richest biomes to represent the initial colonization of highly productive regions and the surrounding Paleoindian sites to represent the backfill effect. Replotting distance versus age using this model offers a different perspective on colonization (fig. 12.7). The "effective colonization distance" to a site is no longer the straight-line distance from an entry point; it is the distance from an entry point to a hypothetical initial colonization "center" in the richest regional biome and then the distance from this "center" to the site. Within each region, "effective colonization distance" correlates well with the age of each site; r^2 values are comparatively high for these chronologically coarse-grained archaeological data. Although the movement rates within any given region are much lower than the overall rates at a continentwide scale (about 2 km/yr), they are much closer to those predicted by Webb and Rindos (1997) for initial colonizers. These patterns lend support to our model of initial colonizers moving extremely rapidly across a landscape at a large scale, as well as the subsequent regional dynamics of peopling the American continents.
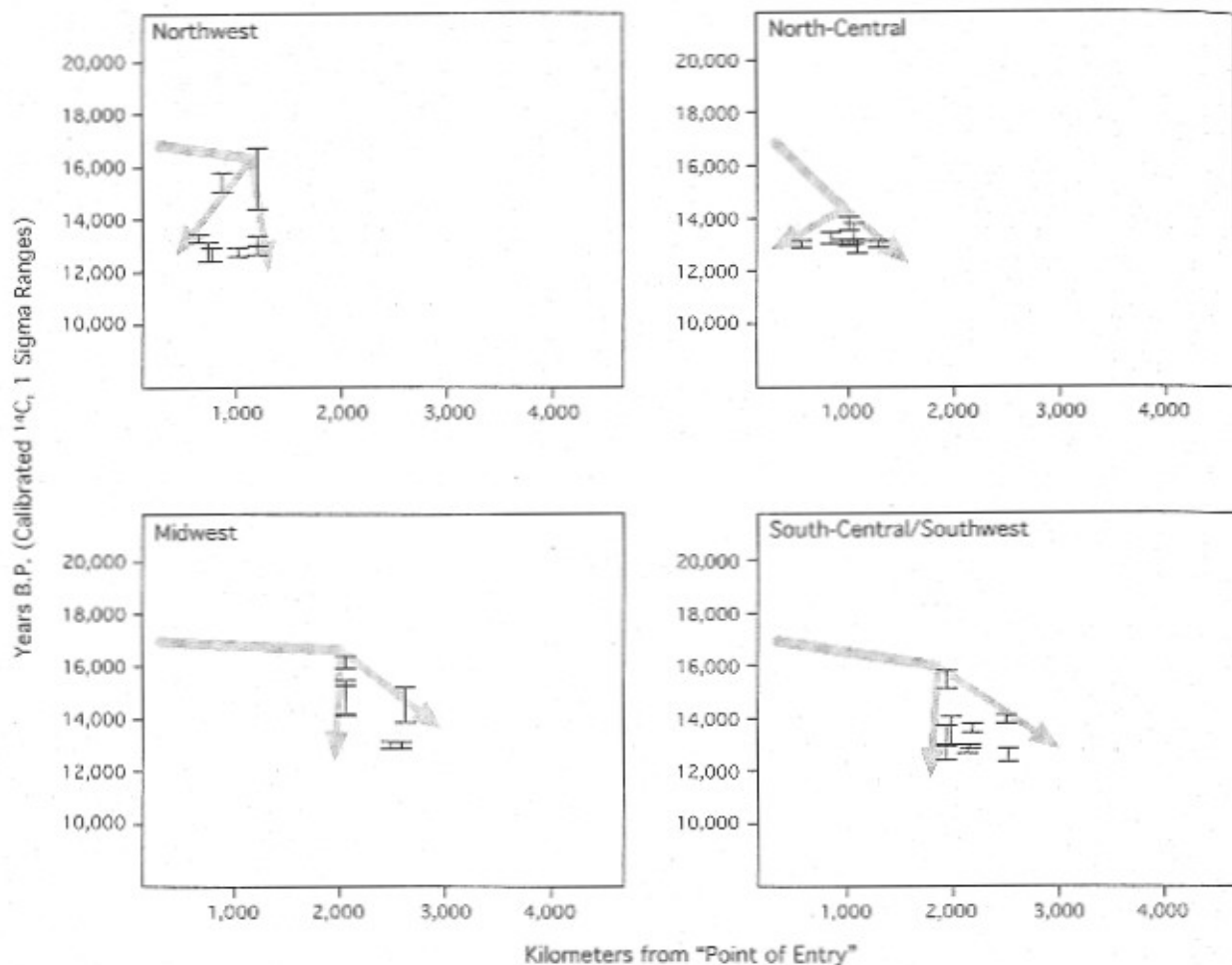
FIGURE 12.6 Modeling initial and regional "backfill" colonization in North America in four regions (see text). Example regions are from the date series shown in figure 12.4.

Demography

The land-use patterns modeled here would lead to low population densities and large use areas or ranges. Such demographic patterns have been suggested for North America on the basis of other evidence, including research by Amick (1996), Anderson and Gillam (2000), Fiedel (this volume), and MacDonald (1999, this volume). Recent population estimates by Amick (1996) and MacDonald (1999, this volume) suggest population densities of 0.002–0.006 persons/sq km for Folsom and regular use areas of 115,000–135,000 sq km per minimal social unit or band. Our modeling suggests that earlier Clovis densities would be even lower. The numbers for Folsom translate into 200–250 bands for the entire unglaciated hemisphere. At around 25 individuals per band, this represents only 5,000–7,000 people.

Furthermore, this population assumes that *all* unglaciated lands were equally occupied, a situation we feel was unlikely (Meltzer, this volume).

These figures seem extremely low for maintaining a viable biological population (MacDonald, this volume; Meltzer, this volume); the actual population of the Americas in the late Pleistocene may have been higher. However, these calculations do offer a baseline for assessing Paleoindian demography and give some idea of the demographic differences between the earliest occupants of the Americas and recent hunter-gatherers. These estimates also underscore the effects of initial colonization on patterning in the archaeological record. Few people are needed to leave lithic debris in South America very shortly after their initial entry into the hemisphere. Because of the rapidity at which humans
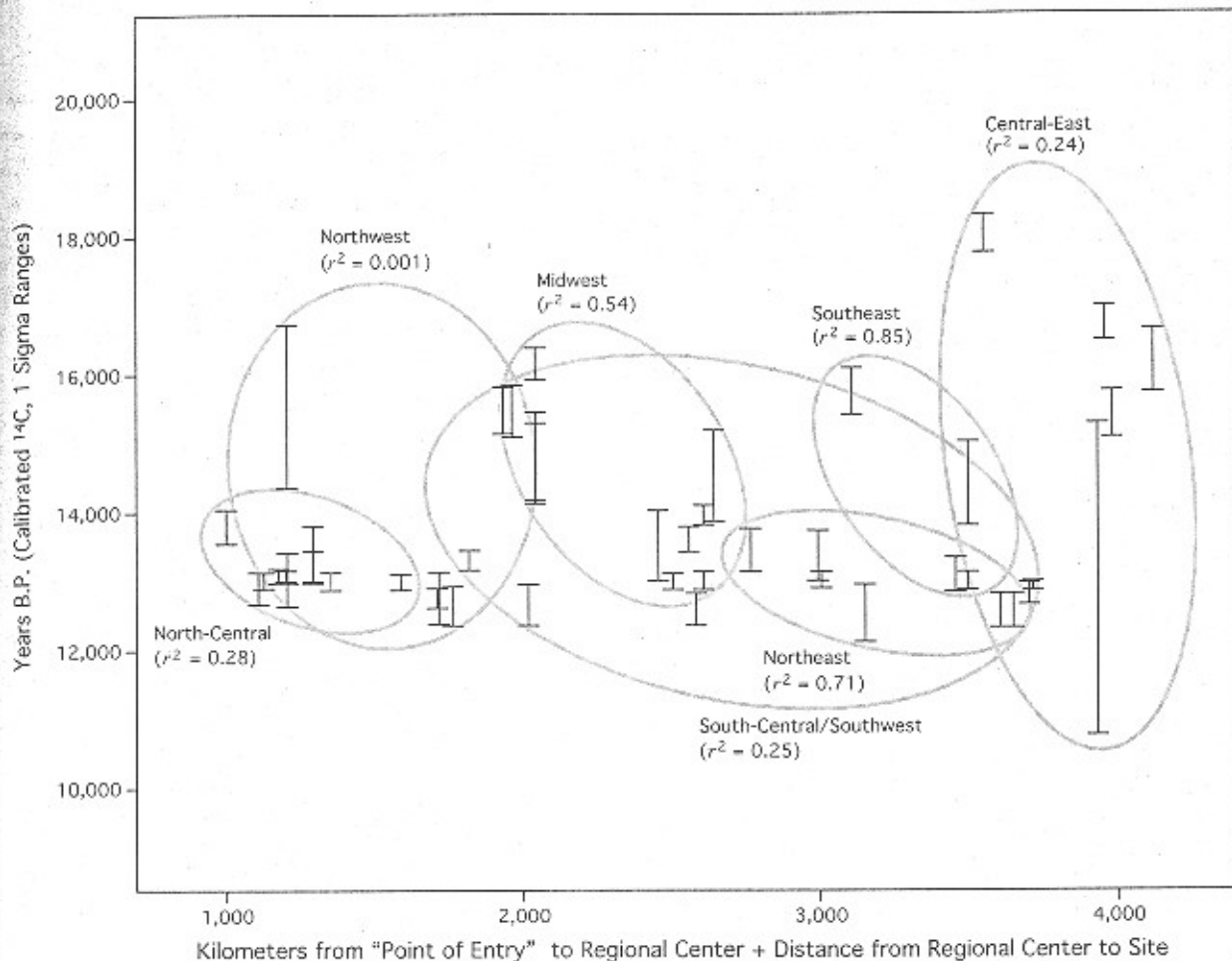
FIGURE 12.7 Modeling initial and regional "backfill" colonization in North America (see text). Correlation values refer to adjusted distances, using calibrated mean ages.

may spread under these circumstances, their wide and patchy dispersal, and the effects of more than 12,000 years of taphonomic processes, early sites could appear virtually anywhere in the hemisphere, including South America (see also Anderson and Gillam 2000). Only by looking at the entire suite of sites can we hope to see even limited evidence of the direction of colonization.

Resource Use

The ecological models discussed here predict low diet diversity for initial colonizers and increasing diet diversity as the landscape becomes populated and high-ranking resources become more costly to procure. Unfortunately many early Paleoindian "sites" are surface accumulations that lack associated faunal remains, and the archaeofauna from many excavated sites have not

been reported in a way that permits quantitative assessment of diversity. Of the sites for which published data are available, however (table 12.6), it appears that diet diversity is very low for Clovis sites (fig. 12.8). In fact, diversity values for the suite of Clovis sites with relevant data are very similar to those for the initial colonizers of northwestern Europe. Also paralleling the northwestern European case study, diet diversity rises after the Clovis period as the landscape becomes more populated (fig. 12.8). This is seen most dramatically in the broad-spectrum foraging that characterizes the late Archaic, as exemplified in a suite of sites from the southwestern United States with relevant published archaeofaunal data (fig. 12.8; table 12.6).

TABLE 12.6 American Sites Used for Diet Diversity Analysis

American Site	Period	Phase	Diversity Index	Reference
Agate Basin	Late Glacial	Clovis	3.77	Frison 1982a; Walker 1982
Colby	Late Glacial	Clovis	1.08	Walker and Frison 1986
Domebo	Late Glacial	Clovis	1.00	Leonhardy 1966
Escapule	Late Glacial	Clovis	1.00	Hemmings and Haynes 1969
Lange-Ferguson	Late Glacial	Clovis	1.00	Hannus 1990b
Lehner	Late Glacial	Clovis	1.27	Haury et al. 1959; Saunders 1977
Mill Iron	Late Glacial	Goshen	1.00	Kreutzer 1996; Todd et al. 1996; Walker and Frison 1986
Monte Verde	Late Glacial		1.09	Casamiquela and Dillehay 1989
Naco	Late Glacial	Clovis	1.00	Haury et al. 1953
Agate Basin	Terminal Pleist.	Folsom	1.58	Frison 1982a; Walker 1982; Zeimens 1982
Bull Brook	Terminal Pleist.	Bull Brook	1.20	Spiess et al. 1985
Hanson	Terminal Pleist.	Folsom	1.00	Ingbar 1992
Horner	Terminal Pleist.	Folsom	1.01	Frison and Todd 1987
Lindenmeier	Terminal Pleist.	Folsom	1.36	Wilmsen and Roberts 1978
Michaud	Terminal Pleist.	Bull Brook	1.00	Spiess and Wilson 1987
Stewart's Cattle Guard	Terminal Pleist.	Folsom	1.00	Jodry and Stanford 1992
Whipple	Terminal Pleist.	Bull Brook	1.00	Spiess et al. 1985
Agate Basin	E. Holocene	Agate Basin	1.01	Frison 1982a; Walker 1982; Zeimens 1982
Agate Basin	E. Holocene	Hell Gap	1.19	Frison 1982a; Walker 1982; Zeimens 1982
Ventana Cave 6–8	E. Holocene	Early Archaic	2.24–2.75	Bayham 1982; James 1990
Coffee Camp	L. Holocene	Late Archaic	2.16	James 1993
Donaldson	L. Holocene	Late Archaic	3.52	Huckell 1995
Tator Hills	L. Holocene	Late Archaic	3.02	James 1993
Ventana Cave 3–5	L. Holocene	Late Archaic	3.86–6.01	Bayham 1982; James 1990

Implications and Discussion

Timing of Initial Colonization

Scholars have argued that the circumstances of late Pleistocene ecosystems and the social and demographic organization of contemporaneous human populations were sufficiently different from those of modern foragers that the latter are poor analogs for understanding the relevant socioecological dynamics in this distant past. In fact, there is no reason to expect inherent behavioral uniformitarianism for any human society, regardless of their mode of subsistence. This is even more the case with modern foragers, who have long

been relegated to the few habitats that are inhospitable to agriculture and who have coexisted (often mutualistically) with agriculturalists for millennia. Evolutionary ecology, however, is not based on uniformitarian ethnographic analogy, except for the fundamental assumption that, due to long-term selection, people act to maximize the returns for their efforts (however they may perceive those maximum benefits) within the constraints of the social and ecological contexts in which they find themselves. Evolutionary ecology also assumes that decisions are ultimately made by individuals. Modern societies, including modern foragers, are often used to test models developed in evolutionary
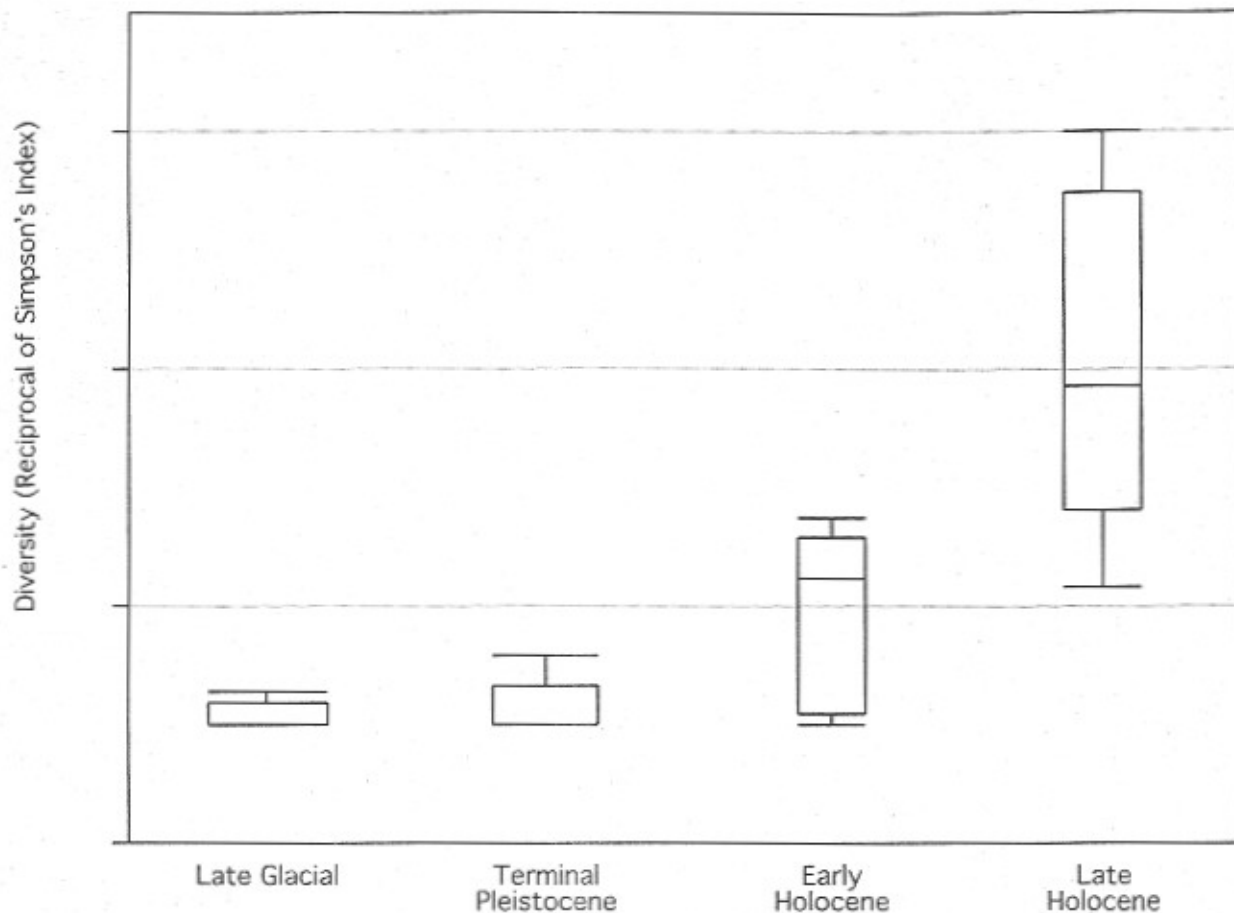
FIGURE 12.8 Diet diversity (reciprocal of Simpson's index of NISP for fauna) for Paleoindian and Archaic sites in North America.

ecology, but analogy with modern peoples is not the source of these models. Hence, we feel that such models are especially relevant for understanding the dynamics of past humans whose socioecological circumstances were much different from any that may be observed today.

In the Americas, the late Pleistocene Paleoindian occupation appears to closely match our proposed model for initial colonizers of empty landscapes. Moreover, critical aspects of the Paleoindian occupation closely parallel the recolonization of northwestern Europe after deglaciation. The late Paleolithic foragers who colonized this part of Europe were clearly entering a landscape devoid of humans. This strongly suggests that the people whose material residues we term "Paleoindian" were behaving *as if* they were initial colonizers of a landscape empty of other humans (see also Fiedel, this volume; Meltzer, this volume). Any prior

colonists also would have had to pass through the Northeast Asian and Alaskan ecological filter before entering the Americas. Successfully living in and passing through this arctic environment would have required sophisticated technological and social skills equal to those of Paleoindian colonizers (see Schmitz, this volume). Furthermore, prior colonists would have had ample opportunity to populate the landscape and accumulate information about the spatial and temporal distribution of resources. Hence, any pre-Paleoindian occupants of the Americas should have been highly effective competitors to subsequent Paleoindian occupants. Note that in the two reasonably well-documented colonizations of the Americas after the late Pleistocene, the immigrants were relegated to narrow niches (the mountain margin zone for the Na-Dene/Athabaskans and the High Arctic coastal zone for the Thule) and have never represented more than a tiny fraction of the

previously established Amerind populations of the Western Hemisphere (see Hill, this volume; Schmitz, this volume).

If humans were present in the Americas prior to the Paleoindian entry, they proved to be such ineffective competitors that Paleoindian colonizers behaved as if they did not exist. This seems highly atypical of humans with generally equivalent technological, economic, and social organizations. It is possible, of course, that one or more pre-Paleoindian colonizations failed, and prior human populations had existed but were extinct by the time of the Paleoindian arrival. Such phenomena probably did happen in the past but are not generally recognized because relevant populations failed to reach a level that would achieve archaeological visibility. Although individual populations may have died out, more general colonization failures—in which humans were successful enough to spread across two continents and leave visible residues at a handful of widely dispersed locales but then decline to extinction—seem largely atypical of the spread of modern humans across the globe. The more parsimonious interpretation of the data currently available is that the Paleoindian entry into the New World was the initial colonization of the continents of the Western Hemisphere. The rapidity of this initial human dispersal, its patchy distribution in the most productive environments, and the taphonomic roulette of the 12,000-year-long archaeological record could account for the handful of sites that seem "out of order" with respect to their age and location (see also Anderson and Gillam 2000; Fiedel 1999b).

Human Impacts on Pleistocene Ecosystems

As stated at the beginning of this chapter, the initial colonization of the Americas was a momentous biogeographical phenomenon, as much for American ecosystems as for the first Americans. It would not be an exaggeration to compare it to the impact of the joining of North and South America in the late Tertiary after the two continents had been separated and had developed their own very different ecologies over tens of millions of years. Most scientific study of the ecological impacts of human entry into the New World has focused on the late Pleistocene extinction of large herbivores (see Martin and Klein 1984 and the references therein). In fact, a cursory reading of our model might lead one to the conclusion that it substantiates the human role in the evolutionary demise of late Pleistocene megafauna. In reality this is not the case. If one looks beyond the simplistic view of humans as predators to their role as members and shapers of ecosystems, it becomes apparent that human impacts were likely more far-reaching and considerably more complex than this, and that hunting of large herbivores may well have been among the lesser impacts on faunal and floral communities.

In another case of continental colonization—Australia (or Sahul)—human predation has also been proposed as the primary cause of extinction of large fauna (Martin 1984b). Webb (1998) takes a more sophisticated look at the ecological dynamics of the introduction of humans into Australia. Webb points out that Australia, prior to human colonization, could support only a few large carnivore taxa. The first and foremost ecological impact of humans was as competitors of these large carnivores. Although paleontological data are difficult to read at the resolution desired, it appears that large carnivores became extinct or very rare before the large herbivores did. Webb suggests that by outcompeting large carnivores and driving them to extinction, humans upset a delicate predator-prey relationship between these carnivores and large herbivores. Because their predation patterns differed considerably from those of large marsupial carnivores, humans did not simply replace them in Australian ecosystems. This left large herbivores without the predator-dependent population controls to which they had become adapted over millions of years, sending their populations into boom-bust cycles. According to Webb, this loss of population control combined with large-scale vegetation changes due to human-caused burning and increasing climatic variability during the late Pleistocene were probable primary causes of large herbivore extinctions, though the new human predation patterns may have contributed.

In other words, the introduction of humans into American ecosystems is not simply a matter of rapacious hunters slaughtering naïve animals. Human social and economic behaviors are complex and have diverse and far-reaching environmental consequences (Redman 1999). It is useful to conceive of the overall effect of human entry into the Americas as one in which the hemisphere was transformed into a socioecosystem in which humans became not just members or exploiters, but also active shapers of the new American ecology. Although it is not possible to explore herein the many ramifications of such a perspective, it is valuable to point out some of the most notable potential impacts as directions for future study.

An important component of Webb's model for the impact of humans on Australian megafauna is the low

carrying capacity of that continent for large fauna and the inherent fragility of the ecosystem to perturbation. To the best of our knowledge, this is *not* the case for American ecosystems. Late Pleistocene vegetation communities were both richer and more diverse than those of contemporaneous Australia. Furthermore, the landmass of the two American continents is much larger than Australia and extends over a tremendous latitudinal range. As a consequence, large animals were also much more numerous and diverse. In contrast to the three large carnivores that Webb lists for Australia, the Americas supported a diversity of large felids, canids, and ursids (Anderson 1984; Mead and Meltzer 1984; Whitney-Smith, this volume). With these differences, can Webb's models apply to the American context as well?

The entry of humans into the Western Hemisphere brought two large carnivores: humans and their dogs, which were descended from Eurasian wolves (Schwartz 1997:15–18). If humans behaved as predicted by the ecological models discussed above, and as supported by at least some of the archaeological evidence, they and their dogs would have been in direct competition with other large American carnivores. Despite the comparative richness of American ecosystems, large carnivores by necessity exist in much lower numbers than their prey species, making them potentially more vulnerable to extinction when faced with competition for resources. (See Klein 1992 for a discussion of humans and carnivore extinction in early Pleistocene Africa.) If the primary impact of human entry into the Americas was overpredation of large herbivores, the extinction of large carnivores should follow on the heels of herbivore extinction (or be contemporaneous with it) as their food sources were eliminated by humans. However, if initial human impact represented a more subtle form of competition with carnivores, they might become extinct before the large herbivores, as Webb has suggested for Australia. A review of the extinction dates for American fauna compiled by Mead and Meltzer (1984) suggests that carnivores may have become extinct before large herbivores. Although several caveats must be raised in determining extinction dates (J. I. Mead, personal communication 1999; Webb 1998), this reference remains the most comprehensive data set available for late Pleistocene American extinctions. An ANOVA indicates that large carnivore extinctions did precede those of large herbivores overall (N of carnivores $= 4$, N of herbivores $= 19$, $F = 3.30$, $p = .08$). Computer modeling of human-carnivore competition by Whitney-Smith (this

volume) has produced results analogous to those suggested by us for the late Pleistocene Americas and by Webb for Pleistocene Australia.

The ecological models outlined above predict comparatively modest direct human impacts on large herbivores (but see Haynes 2002 for sophisticated modeling of an alternative view). Patch choice models suggest that initial colonizers would move to new unpopulated locales long before they eliminated large game in a region. Only when movement became more restricted due to the geographic spread of humans did they increase their procurement efforts within a region. By that time, large intelligent herbivores would have become behaviorally adapted to human predation, further increasing their procurement costs. Diet breadth models predict that, when faced with increased procurement costs for large herbivores, humans diversify their diet rather than intensify their efforts to hunt scarcer large game. Although human predation certainly would have affected large herbivore populations, as would any other new predator, humans would be no more likely to expend the increasing effort to eliminate megafauna than would dirk-toothed felids or dire wolves.

To date, there has been little scientific study of the role of human-caused fire in the late Pleistocene ecosystems of the Americas. However, such research elsewhere (Anderson 2002; Bush 1988; Dods 2002; Kershaw et al. 1997; Pyne 1998; Pyne and Goldammer 1997; Webb 1998) indicates that humans dramatically alter the "natural" fire regimes (including temporal and spatial distribution and intensity) of the landscapes they inhabit, with far-reaching consequences for plant communities at regional or even continental scales. In these studies, pollen cores and other sediment samples in which microcharcoal particles have been counted provide evidence for the frequency and extent of burning. Although fires are also caused by lightning or more rarely by volcanic eruptions (James 1989, 1996), human-related burning tends to produce a distinctive signature. Even if humans do not intentionally burn the landscape (though there is considerable ethnohistoric evidence that they do so regularly, as summarized in the studies mentioned above), they build and maintain fires on a daily basis throughout the year. This alone greatly increases the chances of unintentional landscape burning outside the season of natural fires (Pyne 1998; Pyne and Goldammer 1997).

The available data for landscape fires during the late Pleistocene of the Americas are few but suggestive. Relevant pollen and microcharcoal studies are avail-

able from Lake La Yeguada, Panama (Bush et al. 1992; Kershaw et al. 1997), southern Wisconsin and Massachusetts (Winkler 1997), and the western slopes of the Sierra Nevada in California (Anderson and Smith 1997). There are dramatic spikes in the amount of microcharcoal coincident with the Paleoindian occupation of each of these regions: at 12,000 cal B.P. in Panama, 14,700–14,100 B.P. in southern Wisconsin, 12,000 B.P. in Massachusetts, and 10,200 B.P. (and possibly as early as 11,400 B.P.) in the Sierra Nevada. Notably the dates vary geographically and seem to better fit our model for spreading human populations more than the synchronous, continentwide climatic changes. In this respect, the Sierra Nevada cores, in an initially less-optimal montane area that we predict would have been populated by backfill rather than initial colonization, show a microcharcoal spike more than 2,000–4,000 years later than the spikes in the other regions.

Viewed from the perspective of evolutionary ecology, the initial colonization of the Americas did not loose a "blitzkrieg" of human predation that led to the extinction of numerous large animal taxa during the late Pleistocene. The entry of humans, however, must have had a significant impact on American ecosystems. It is now apparent that the climatic changes that initiated the early Holocene took place extremely rapidly, with major temperature increases within a few decades (Fiedel 1999b; Taylor 1999). These climatic changes interacted with the large-scale alterations in floral communities due to hemisphere-wide anthropogenic burning and produced the much more fragmented habitats that characterize the Holocene. These continentwide changes in vegetation communities, the loss of predator-based population controls due to human competition with large carnivores, and the introduction of two new carnivores (humans and dogs) probably pushed many large animal taxa beyond the point where they could no longer maintain viable breeding populations. The loss of even some of these large herbivores (proboscideans, for example) would have additional effects on vegetation communities, which were adapted to herbivores as much as the animals were adapted to the plants. The resulting cascade of changes dramatically and permanently altered American ecosystems.

Humans, as participants in the new socioecosystems, were equally affected by these long-term changes that they themselves helped to initiate. Habitat fragmentation due to a combination of climatic changes,

anthropogenic burning, and loss of large herbivores encouraged geographic specialization among humans in social, economic, and technological realms. At the same time, the loss of wide-ranging, high-ranking, large fauna encouraged diet diversification and reliance on a variety of local resources. The result is seen in the regionally diverse material residues of Holocene humans that archaeologists term the Archaic (Barton 1979; Meltzer, this volume).

Conclusions

Although many gaps remain in our study, as well as in those of others who have attempted to understand the dynamics of the colonization of the Americas, data alone will not lead to better understanding (see also Meltzer, this volume). We hope we have shown that ecological modeling based on well-developed evolutionary theory and the extant data compiled by decades of dedicated archaeological research can provide insights into the peopling of the Americas and into the general processes of human colonization. This kind of study can also reveal the type of data that can best develop our understanding of the first Americans. Although more and better dated sites would certainly be helpful, other data may be even more useful. For example, we still lack many systematic surveys and geoarchaeological studies that can tell us where the earliest humans were *not* as well as where they were. We also need a better understanding of the environments in which early Americans lived and more comprehensive information about their diet and the resources (both subsistence and other) that they used (see Chilton, this volume). Finally, there is little direct evidence for the role that the first colonizers played in reshaping American ecosystems into the socioecosystems that characterized the rest of the world. We were surprised to find that, despite decades of research on late Pleistocene environments, microcharcoal analysis (a comparatively simple procedure) is lacking in most studies.

Colonization is not an event but a process that varies dynamically across space and time. The human colonization of "pristine" landscapes offers unique opportunities to understand the full extent of the human role on Earth. Until humans colonize other planets, the only way we can study the long-term consequences of human colonization is through archaeology. In this sense, the peopling of the New World is not simply a long-past event; it is also the beginning of an ongoing

process that remains highly relevant to our identity and our future on this planet.

Acknowledgments