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Do modern hunter-gatherers live in marginal habitats?

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ABSTRACT

Anthropologists often assert that modern hunter-gatherer societies have been relegated to marginal habitats compared to their agricultural neighbors, with the implication that modern social organization and behavior provide little insight into Paleolithic hunter-gatherers. We refer to this idea as the marginal habitat hypothesis (MHH). Despite widespread use of the term 'marginal,' there is little consensus as to what comprises a low quality habitat for humans. Here we reassess the MHH by comparing the net primary productivity (NPP) of habitats occupied by, and the population density (PD) of, a sample of 186 pre-industrial societies (foragers, horticulturalists, intensive agriculturalists, and pastoralists). We found that the nature of the NPP-PD relationship varied by subsistence type, and that foragers did not occupy significantly lower net primary productivity habitats compared to other subsistence types. These results do not support the MHH. We conclude by discussing the limitations of using modern ethnographic datasets to address the MHH and suggest alternative ways in which it may still be relevant.

1. Background

A common view in the anthropological literature is that modern hunter-gatherers occupy 'marginal,' or poor quality habitats, compared to agriculturalists who have displaced them through numerical, political, or military means (Bigelow, 1972; Lee et al., 1968; Marlowe, 2005; Porter and Marlowe, 2007). This view, which we refer to as the marginal habitat hypothesis (MHH), suggests that contemporary foraging populations offer poor ecological models for Pleistocene hunter-gatherers (Porter and Marlowe, 2007). While this claim is commonplace in the anthropological literature, there has been little empirical investigation of the issue (Speth, 2010). Moreover, the term "marginal" has been used imprecisely and variably. Marginality has been used in an absolute sense in referring to habitats with low primary productivity (Marlowe, 2005; Porter and Marlowe, 2007) or those that are arid, cold, or in dense rainforest (Headland, 1987). The term has also been used in a relative sense to contrast the apparently impoverished habitats occupied by mobile foragers to the richer habitats of neighboring agriculturalists (Bigelow, 1972; Wilmsen, 1989).

For some organisms, good or bad (i.e., optimal or marginal) habitats can be relatively straightforward to define using measures such as primary productivity (PP) or net primary productivity (NPP), the latter reflecting the total energy available in a given habitat per year beyond the vegetations' maintenance costs (McNaughton et al., 1989; Van Horne, 1983). Yet annual productivity can produce both food products and non-edible biomass that may not directly reflect available food energy (Kelly, 1995, Porter and Marlowe, 2007). Moreover, humans are biologically dependent on high-quality diets, achieved in part through highly targeted foraging on high-risk, high-reward food items, in addition to the development of complex food acquisition and processing strategies to increase caloric yield and decrease the costs of digestion (Carmody and Wrangham, 2009; Kaplan et al., 2000; Leonard et al., 2007; Wrangham, 2009).

Even with such complications, NPP have been widely and successfully applied in ethnographic studies as a proxy of habitat quality (Binford, 2001; Codding and Jones, 2013; Kelly, 2013), including the one study that has quantitatively tested the MHH, Porter and Marlowe (2007). This study merged data from the Standard Cross Cultural Sample (SCCS) (Murdock and White, 1969) with NASA satellite data on NPP to compare habitats occupied by hunter-gatherers to those occupied by horticulturalists, intensive agriculturalists, and pastoralists. The authors found that, on average, hunter-gatherers did not occupy

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significantly lower NPP habitats compared to other subsistence types. On this basis, Porter and Marlowe rejected the MHH (Porter and Marlowe, 2007).

Our goal in this paper is to revisit the MHH, with additional data and improved methods. To avoid confusion, we choose not to use the terms 'marginal' and 'optimal' when possible, and instead refer to habitat quality as reflected by a standardized measure of environmental productivity, NPP. First, we extend the analyses of Marlowe (2005) and Porter and Marlowe (2007) by incorporating several methodological modifications that account for the possibility that their findings were driven by latitude or by the spatial scale of NPP measurement (*Methods* and *Materials*). Second, we consider another means of assessing NPP as a proxy for habitat quality, population density (PD). To more accurately infer habitat quality for humans, it is important to consider how environmental energy is related to key demographic outcomes, such as PD. In principle, habitat quality should be reflected in both food availability (as indexed by NPP) and population density (Begon et al., 1996; Krebs, 1972). NPP and PD are positively associated among some modern (Chown et al., 2003; Luck, 2007) and pre-historic human populations (Codding and Jones, 2013), although there is also evidence to suggest that PD declines, in areas of high NPP (Balmford et al., 2001). While we expect that terrestrial NPP is useful in predicting general food availability, we also acknowledge that habitat quality is also influenced by non-food factors, including climate, competition, parasites, predators, and seasonality, etc. (Tallavaara et al., 2017).

Currently, we lack an understanding of how humans translate environmental productivity into demographic success in different ecological contexts. While the relationship between environmental productivity and population density has been extensively discussed within archaeological and anthropological discussions of the origin of agriculture (Boserup, 1976; Butzer, 1982; Netting, 1968), it has not been tested at a global scale with quantitative data. Similarly, the association between NPP and PD has not been explored among those human populations that are most relevant to reconstructing the recent ecological history of our species: populations across the globe who engage in pre-industrial subsistence strategies such as horticulture, intensive agriculture, pastoralism, and foraging. Given the capacity for human culture and technology to shape human-environment interactions, we propose that the assessment of habitat quality is improved by including population-specific details such as subsistence type and PD. With this aim, we examined how the relationship between NPP and PD varies by subsistence strategy, which provides a further basis for evaluating the MHH. In particular, if the relationship between NPP and PD varies with subsistence type, then terms such as 'marginal' and 'optimal' would seem to be of limited value when making comparisons across subsistence types (i.e. 'foragers occupy marginal habitats compared to agriculturalists').

Third, we discuss the limitations of using modern ethnographic datasets to address the MHH and suggest alternative ways in which the MHH may still be relevant.

2. Methods

We used ethnographic data from 186 pre-industrial societies of the SCCS (see *Materials* section below) to examine the relationship among NPP, subsistence type, and PD. First, we used environmental data from NASA on the average mean (NPP_{mean}) and max (NPP_{max}) of occupied habitats (based upon SCCS latitude and longitude) to test the MHH, which states that foragers tend to occupy less productive habitats than farming populations (*Objective 1*). Second, we modified this analysis to include latitude, thus accounting for global variation in biome distributions (*Objective 2*). Finally, reflecting the positive relationship between habitat productivity and carrying capacity noted elsewhere, we explore how NPP_{max} and PD are related for each subsistence type (*Objective 3*). We estimate the probability of societies having low, medium, or high PD as a function of NPP, testing NPP as a predictor of habitat quality for societies of each subsistence type, and incorporating PD as a marker of demographic success. To test the reliability of NPP measures, we used NPP_{max} in addition to NPP_{mean}. We also A) included a number of additional environmental and behavioral factors as model covariates, B) used a circular projection of foraging radius (rather than grid), C) sampled habitats based on both a 15 km and 120 km radius (testing NPP_{mean} and NPP_{max} over areas more representative of logistical and residential scales), and D) expanded NASA Moderate Resolution Imaging Spectroradiometer (MODIS) NPP data from 5 to 15 years to reduce error associated with annual variation).

2.1. Materials

We used data from four publicly available primary sources to determine how NPP is related to population density across four pre-industrial subsistence types. The SCCS (Murdock and White, 1969) was created as a means of addressing problems of autocorrelation in cross-cultural research (i.e. Galton's Problem), selecting a subset of pre-industrial societies from the *Ethnographic Atlas* (Murdock, 1967). SCCS societies are representative of cultural, geographic, linguistic, and regional variation, and are thus a collection of independent data points with good ethnographic coverage. From the SCCS we sourced fishing contribution to diet, latitude, longitude, population density, societal mobility, and study year,[1] and the. We obtained mean annual precipitation (mm, MAP) and effective temperature (ET) from Porter and Marlowe (2007). We additionally followed their subsistence classifications, which were derived from SCCS measures as follows (the prefix 'v' followed by numbers refer to variable columns in the SCCS):

Foragers: local diet < 10% agriculture (v3 < 4), < 10% animal husbandry (v5 < 4), and trade < 50% and ≤ any single local source (v1 < 6); excludes equestrian hunters (v858 ≠ 5 [Mounted Hunting]).

Pastoralism: (v858 = 5 [Mounted Hunting] or 6 [Pastoralism > 33%]).

Horticulture: (v858 = 7–10 [7 = Shifting Cultivation with digging sticks or wooden hoes, 8 = Shifting Cultivation with metal hoes, 9 = Horticultural Gardens or Tree Fruits, 10 = Advanced Horticulture with metal hoes]; and foragers reliant upon trade for > 50% of diet [v1 ≥ 4]).

Intensive agriculture: (v858 = 11 [Intensive Agriculture with no plow] or 12 [Intensive Agriculture with plow]).

Subsistence strategies reflect differential efficiency of energy extraction from the environment based on differences in resource abundance and distribution, technology, and degree of agricultural intensification, all of which may lead to variation in carrying capacity (Ellen, 1982, 1994; Redding, 1988; Rindos, 1984). We adopted the subsistence definitions used by Porter and Marlowe (2007). Forager (hunter-gatherer) populations are those primarily dependent on energy extracted directly from the natural environment, and thus not reliant upon plant cultivation, animal husbandry, or products acquired via trade. Following the definition used by both the SCCS and Porter and Marlowe (2007), our 'forager' designation does not preclude food storage behaviors. Horticulture is classified as either the practice of shifting cultivation or the keeping of gardens and/or fruit trees, or as populations of foragers who are themselves reliant upon trade for > 50% of their subsistence (Porter and Marlowe, 2007). This definition varies slightly from the more common definition of horticulture as a mixed strategy of hunting-and-gathering and gardening characterized by sustained fallow periods (Keegan, 1986). Intensive agriculturalists

[1] Murdock and White (1969) reported the approximate year of modern ethnographic study in *Appendix A*, which is included here in Table 1. We note that "modern" is a relative term. Many of the societies in the SCCS were studied in the mid-nineteenth to mid-twentieth centuries. However, data for some SCCS societies were drawn from observations conducted centuries ago (e.g. Aztec, Babylonian, Hebrew, Inca, Khmer, Roman).

may irrigate, use plows, and tend to exercise direct control over the reproduction of domesticated plants (Murdock and White, 1969; Porter and Marlowe, 2007). Finally, pastoralists consume domesticated animal byproducts such as meat, milk, and blood, and frequently also trade for starch-rich plant products (Murdock and White, 1969; Porter and Marlowe, 2007).

For information on biome classifications, we sourced data sets on world ecoregions from The Nature Conservancy, including the Marine Ecoregions Of the World (MEOW) (Conservancy, 2012; Spalding et al., 2007), and the Terrestrial Ecoregions Of the World (TEOW) (The Nature Conservancy, 2009). NPP data (MOD17A3 algorithm) from NASA's MODIS Satellite (Running et al., 2015) were obtained from Numerical Terra Dynamic Simulation Group at the University of Montana (http://www.ntsg.umt.edu/project/mod17).

2.2. Derived variable calculations

We calculated average maximum (NPP_{max}) and mean (NPP_{mean}) NPP within 15 km and 120 km radii of each society's latitude and longitude coordinates, using NPP data averaged over a 15 year period (2000–2014). As NASA reports NPP as the g C/m^2/year for 1km^2 areas, NPP_{max} and NPP_{mean} represent two different ways of summarizing annual productivity over a populations' habitat. We sampled NPP using radii rather than square grids, as radii provide a better approximation than grids to the central-place foraging patterns of pre-industrial human societies (Binford, 1980; Kelly, 2013; Orians and Pearson, 1979). Shortest Euclidean distance from each society to a marine ecoregion (DME) was calculated from GIS shapefiles of MEOW.

The SCCS "Population Density" variable (v64) is reported in an ordinal, discretized form on a statute mile basis, though the denominator at low density is not constant, and several PD levels are potentially overlapping. This inconsistency led us to reduce the original population density categories from seven to three levels, representing a more easily comparable ordinal ranking: low ($<$ 1 person/sq. mile), medium ($\geq$ 1 & $<$ 25 people/sq. mile), or high ($\geq$ 25 people/sq. mile). We opted for three levels in part because it was not feasible to fit a model with 186 observations to a categorical response variable with seven levels. Furthermore, population densities of low, medium, and high are much more intuitive, particularly when comparing across four subsistence types and habitat productivity gradients.

The SCCS societal mobility variable "Fixity of Settlement" (v61) was re-coded into a binary "permanent" (which retained the SCCS "Permanent" bin, n = 102) versus "impermanent" (collapsing the additional five SCCS non-"Permanent" levels, n = 84) indicator variable (MOBILE). The SCCS "Principal Subsistence Category" variable (v820) was used to generate a binary "fishing" versus "non-fishing" indicator variable (FISH). We singled out fishing as the sole subsistence indicator variable because our primary environmental quality indicator, terrestrial NPP, is inherently blind to non-terrestrial sources of food production such as fish. We also adjusted latitude and/or longitude for 28 societies, correcting erroneous values from the SCCS. Four separate issues necessitated these adjustments: 1) some societies were reported with only approximate spatial locations; 2) for island or coastal dwelling societies small errors in spatial location placed society centroids in a marine environment; 3) obvious erroneous entries (i.e., Kenuzi Nubians); and 4) historical factors causing dramatic alteration of habitat (such as the Aswan Dam Project for Egyptians). The SCCS data and revised coordinates, as well as all variables and societies used in our analyses, are available in a Zenodo repository (Worthington and Cunningham, 2018). Revised Latitude and Longitude coordinates are denoted by an asterisk ("*") in the Summary Table 1. The original values as used by Porter and Marlowe (2007) are available in the Zenodo repository.

2.3. Data analysis

Data analyses were conducted for both a combined (warm and cold) sample of all SCCS societies and a warm subsample, delineated using the effective temperature (ET) variable. Porter and Marlowe (Porter and Marlowe, 2007) used a cutoff of ET $\geq$ 14 for the warm subsample, which corresponds to approximately 40–45° degrees absolute latitude. This is suggested to correspond to a difference between higher and lower densities of underground plant storage organs (such as tubers and corms) eaten by human foragers: warm areas are expected to have higher densities (Marlowe, 2005). All analyses and results presented in the main text use the combined (warm and cold) sample. Contrasts between the combined and warm subsamples are presented in the Supplementary Information (Fig. SI 2a and 2b).

2.3.1. Objective 1

To evaluate the MHH, we tested whether subsistence types differ based on the average mean and max NPP of the habitats they occupy. We used general linear models (GLMs) to predict average NPP_{max} and NPP_{mean} for each subsistence type (Fig. 2). NPP_{max} is our primary focus, though comparisons of NPP_{max} and NPP_{mean} are presented in Fig. 2 and Fig. SI 2b. All NPP values are reported in units of grams Carbon/m^2/year (g C/m^2/year). Six environmental variables were used as explanatory variables in models: mean annual precipitation (MAP), effective temperature (ET), absolute latitude (AbLat), distance to marine ecoregion (DME), binary degree of mobility (MOBILE), and binary reliance on fished resources for protein in diet (FISH). In addition, we used GLMs to estimate average NPP_{max} and NPP_{mean} values across subsistence types for both a combined sample of warm and cold climate societies (on the basis of ET) and separately for warm climate societies. In the models, we controlled for MAP, AbLat, DME, MOBILE, and FISH. Pairwise comparisons of average NPP between subsistence types were adjusted for family-wise error using the sequential Bonferroni method (Holm, 1979).

2.3.2. Objective 2

To further explore the relationship between average NPP_{max} and latitude across subsistence types, we used GLMs to predict average NPP_{max} as a function of AbLat (Fig. 3). Absolute latitude was used due to the general decline in solar radiation with increasing distance from the equator, and the associated expected decline in NPP with increasing latitude. Given the SCCS bias towards populations in the Northern Hemisphere (Marlowe, 2005), AbLat allowed for the comparison of populations based on distance from the equator, and proximity to the poles independent of North or South. As with Objective 1a, control variables were excluded from models in a block if statistically non-significant (SI Text).

2.3.3. Objective 3

We used ordinal logistic regression models to estimate the probability of societies having low, medium, or high PD as a function of NPP_{max} and NPP_{mean} and subsistence type, while controlling for ET, MAP, AbLat, DME, MOBILE, and FISH. The assumption of proportional odds was checked graphically by plotting the mean of each predictor variable versus levels of the response variable and comparing this to the expected value of the predictor variable for each response value under the proportional odds assumption.

3. Results

Fig. 1 shows the worldwide distribution of the 186 societies classified according to occupied biome, subsistence type, and climate. The distribution of subsistence types within the SCCS is shown in the inset of Fig. 1. Horticulturalists are the most prevalent (38.7%), followed by intensive agriculturalists (29.6%), foragers (19.4%), and pastoralists (12.4%).

Table 1
Summary data table.

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	Absolute Latitude	NPP Mean (15 km)	NPP Max (15 km)	NPP Mean (120 km)	NPP Max (120 km)	NPP (P &M, 2007)	Population Density	Climate	ET	MAP (mm)	Fishing Binary	Mobility Binary	Biome Simple
1	Nama Hottentot	1860	Pastoralism	17	−27.5	27.5	122.2	198	161.5	958.2	204	Low	Warm	16.18	133	Non-Fishing	Impermanent	Desert
2	Kung Bushmen	1950	Foraging	20.58	−19.833 *	19.833	291.2	415.5	349.8	505.5	472	Low	Warm	16.67	470	Non-Fishing	Impermanent	Savanna/Grassland
3	Thonga	1895	Horticulture	32.333 *	−25.833 *	25.833	850.1	1063	882.5	1794.2	667	High	Warm	18.5	570	Non-Fishing	Impermanent	Forest
4	Lozi	1900	Intensive agriculture	23.5	−16	16	635.7	739.9	609.6	1149.1	756	Medium	Warm	18	954	Non-Fishing	Impermanent	Wetland
5	Mbundu	1890	Horticulture	16.5	−12.25	12.25	780.1	1267	818	1496	1041	Medium	Warm	17.2	1354	Non-Fishing	Permanent	Savanna/Grassland
6	Suku	1920	Horticulture	18	−6	6	863.1	1290	916.9	1304.8	865	Medium	Warm	NA	NA	Non-Fishing	Impermanent	Savanna/Grassland
7	Bemba	1897	Horticulture	30.5	−10.5	10.5	811.8	1234.5	770.3	1289.7	1039	Medium	Warm	17.43	1310	Non-Fishing	Impermanent	Savanna/Grassland
8	Nyakyusa	1934	Intensive agriculture	34	−9.5	9.5	945.8	1384.2	793.4	1405	1106	High	Warm	15.71	884	Non-Fishing	Impermanent	Wetland
9	Hadza	1930	Foraging	35.18	−3.75	3.75	511.1	810.8	651.5	1629.1	607	Low	Warm	20.91	1214	Non-Fishing	Impermanent	Savanna/Grassland
10	Luguru	1925	Horticulture	37.667 *	−6.833 *	6.833	854.6	1486.3	878	1688.2	912	High	Warm	22	1110	Non-Fishing	Permanent	Savanna/Grassland
11	Kikuyu	1920	Pastoralism	37.167 *	−0.667 *	0.667	785	1282	675.2	1504.8	1150	High	Warm	15.82	899	Non-Fishing	Permanent	Savanna/Grassland
12	Ganda	1875	Horticulture	32.5	0.333 *	0.333	1393.7	1807.5	1387.7	2066.9	1341	High	Warm	18.8	1201	Non-Fishing	Permanent	Savanna/Grassland
13	Mbuti	1950	Foraging	28.333 *	1.5	1.5	1318.2	1358.5	1299.1	1489.7	1445	Low	Warm	19.45	1293	Non-Fishing	Impermanent	Forest
14	Nkundo Mongo	1930	Horticulture	19.167 *	−0.75	0.75	1067.9	1162.7	1062.6	1231.5	1570	Medium	Warm	19.6	2440	Non-Fishing	Permanent	Forest
15	Banen	1935	Horticulture	10.8	4.667 *	4.667	894.2	1024	849.7	1071.7	1136	Medium	Warm	18.73	2172	Non-Fishing	Permanent	Forest
16	Tiv	1920	Horticulture	9	7.25	7.25	434.9	659.1	500.1	922.5	624	High	Warm	21.43	1377	Non-Fishing	Permanent	Savanna/Grassland
17	Ibo	1935	Horticulture	7.333 *	5.5	5.5	573.8	812.2	583.1	860.1	718	High	Warm	22.67	1231	Non-Fishing	Permanent	Forest
18	Fon	1890	Horticulture	1.91	7.2	7.2	411.8	586.7	442.7	720.6	698	High	Warm	22	859	Non-Fishing	Permanent	Savanna/Grassland
19	Ashanti	1895	Horticulture	−1.5	7	7	606.4	738.8	590.9	849.2	931	High	Warm	21.33	1481	Non-Fishing	Permanent	Forest
20	Mende	1945	Horticulture	−12	7.833 *	7.833	548	711.6	523.4	934.5	702	High	Warm	21.64	2354	Non-Fishing	Permanent	Forest
21	Wolof	1950	Horticulture	−15.333 *	13.75	13.75	157	243.3	182.1	962.4	420	High	Cold	19.14	516	Non-Fishing	Permanent	Savanna/Grassland
22	Bambara	1902	Intensive agriculture	−7	12.5	12.5	126.5	218	126.5	303.2	312	Medium	Warm	22	1053	Non-Fishing	Permanent	Savanna/Grassland
23	Tallensi	1934	Intensive agriculture	−0.567 *	10.66	10.66	233.7	297.8	223.6	409.5	432	High	Warm	NA	NA	Non-Fishing	Permanent	Savanna/Grassland
24	Songhai	1940	Intensive agriculture	−0.03 *	16.26 *	16.26	0.6	19	4.4	59	44	Medium	Warm	19.14	285	Non-Fishing	Permanent	Tundra
25	Pastoral Fulani	1951	Pastoralism	7.5	15	15	43.4	73.3	41.9	100.1	104	Medium	Warm	19.33	770	Non-Fishing	Impermanent	Savanna/Grassland
26	Hausa	1900	Intensive agriculture	7.5	10.5	10.5	309	381.6	291.6	523.1	546	High	Warm	21.08	1297	Non-Fishing	Permanent	Savanna/Grassland

(continued on next page)

Table 1 (*continued*)

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	Absolute Latitude	NPP Mean (15 km)	NPP Max (15 km)	NPP Mean (120 km)	NPP Max (120 km)	NPP (P &M, 2007)	Population Density	Climate	ET	MAP (mm)	Fishing Binary	Mobility Binary	Biome Simple
27	Massa (Masa)	1910	Intensive agriculture	15.5	10.5	10.5	105.6	198.9	112	291.4	332	High	Warm	22.27	850	Non-Fishing	Permanent	Savanna/Grassland
28	Azande	1905	Horticulture	28.25	5.083 *	5.083	584.7	819.3	609.6	968.5	831	Medium	Warm	20.67	1467	Non-Fishing	Permanent	Savanna/Grassland
29	Fur (Darfur)	1880	Intensive agriculture	24.9 *	12 *	12	135.7	200.6	151.4	313.5	116	Medium	Warm	19.41	817	Non-Fishing	Permanent	Savanna/Grassland
30	Otoro Nuba	1930	Intensive agriculture	30.667 *	11.333 *	11.333	130.5	193.1	121.1	258.9	465	Medium	Warm	22.31	743	Non-Fishing	Permanent	Savanna/Grassland
31	Shilluk	1910	Horticulture	32.1 *	9.89 *	9.89	200.4	289.9	212.8	431.2	559	High	Warm	22.67	817	Non-Fishing	Permanent	Savanna/Grassland
32	Mao	1939	Horticulture	34.667 *	9.267 *	9.267	687	995.2	621.8	1304.6	1102	Medium	Warm	23.33	1241	Non-Fishing	Permanent	Savanna/Grassland
33	Kaffa (Kafa)	1905	Intensive agriculture	36.5	7.267 *	7.267	1287.4	1502.1	1132.9	1754.5	1465	High	Warm	22.31	1241	Non-Fishing	Permanent	Savanna/Grassland
34	Masai	1900	Pastoralism	36.75	−3.5	3.5	535.6	1609.8	595.2	1666.3	878	Medium	Warm	13.56	677	Non-Fishing	Impermanent	Savanna/Grassland
35	Konso	1935	Intensive agriculture	37.5	5.25	5.25	498.7	879.7	588.8	1616.3	656	High	Warm	23.33	1241	Non-Fishing	Permanent	Savanna/Grassland
36	Somali	1900	Pastoralism	47.25	9	9	39.2	60.9	50.2	92.1	184	Medium	Warm	19.23	119	Non-Fishing	Impermanent	Savanna/Grassland
37	Amhara	1953	Intensive agriculture	37.75	12.5	12.5	421.3	686.9	440.3	1311.9	840	High	Warm	20.67	894	Non-Fishing	Permanent	Savanna/Grassland
38	Bogo	1855	Pastoralism	38.75	15.75	15.75	157.2	345.5	85.4	507.9	312	Medium	Warm	18	474	Non-Fishing	Impermanent	Forest
39	Kenuzi Nubians	1900	Intensive agriculture	30.52 *	19.15 *	19.15	39.4	133.1	27.7	133.1	27	NA	Warm	17.08	3	Non-Fishing	Permanent	Desert
40	Teda	1950	Pastoralism	17.5	20.5	20.5	0	0	34.4	59.8	0	Low	Warm	18.7	14	Non-Fishing	Impermanent	Desert
41	Tuareg	1900	Pastoralism	6.5	23	23	17.2	19.6	18.5	37.5	0	Low	Warm	16.08	45	Non-Fishing	Impermanent	Desert
42	Riffians	1926	Intensive agriculture	−3.25	34.917 *	34.917	369.6	720.8	366.8	1485.3	222	High	Warm	15.6	389	Non-Fishing	Permanent	Forest
43	Egyptians	1950	Intensive agriculture	32.65 *	25.7 *	25.7	50.6	197.8	51.5	197.8	196	High	Warm	16.52	1	Non-Fishing	Permanent	Wetland
44	Hebrews	621 BCEE.	Intensive agriculture	35.2 *	31.76 *	31.76	316.1	809.7	342.6	1476	147	High	Warm	16.1	551	Non-Fishing	Permanent	Forest
45	Babylonians	1750 BCEE.	Intensive agriculture	44.43 *	32.47 *	32.47	16	91.9	22.9	112.6	159	High	Warm	15.94	107	Non-Fishing	Permanent	Desert
46	Rwala Bedouin	1913	Pastoralism	38.5	33.25	33.25	47.8	57.9	43.6	115.6	68	Low	Warm	15.23	203	Non-Fishing	Impermanent	Desert
47	Turks	1950	Intensive agriculture	34.25	39.333 *	39.333	242.1	450.4	236.3	723.4	238	High	Warm	13.73	434	Non-Fishing	Permanent	Forest
48	Gheg Albanians	1910	Intensive agriculture	20.167 *	42	42	648	934	655.9	1771.8	443	High	Warm	14.15	1450	Non-Fishing	Impermanent	Forest
49	Romans	110	Intensive agriculture	13.5	41.667 *	41.667	1026.5	1815.6	893.9	1915.2	503	High	Warm	17.43	712	Non-Fishing	Permanent	Forest
50	Basques	1934	Intensive agriculture	−1.667 *	43.25	43.25	839	1445.5	761.9	1670.8	590	Medium	Warm	13.48	708	Non-Fishing	Permanent	Forest
51	Irish	1932	Intensive agriculture	−10	53.5	53.5	749.4	1346.7	859.4	1403.8	672	High	Cold	11.88	886	Non-Fishing	Permanent	Forest
52	Lapps	1950	Pastoralism	21.5	68.7	68.7	208.5	404.6	221.5	595.7	111	Medium	Cold	10.48	467	Non-Fishing	Impermanent	Forest

(*continued on next page*)

Table 1 (*continued*)

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	Absolute Latitude	NPP Mean (15 km)	NPP Max (15 km)	NPP Mean (120 km)	NPP Max (120 km)	NPP (P &M, 2007)	Population Density	Climate	ET	MAP (mm)	Fishing Binary	Mobility Binary	Biome Simple
53	Yurak Samoyed	1894	Pastoralism	51.5 *	68	68	219.5	234.4	202.2	512.9	77	Low	Cold	10.19	214	Non-Fishing	Impermanent	Tundra
54	Russians	1955	Intensive agriculture	41.333 *	52.667 *	52.667	379.5	621.8	392.8	862.6	256	Medium	Cold	10.93	703	Non-Fishing	Permanent	Forest
55	Abkhaz	1880	Pastoralism	40.77	43.125 *	43.125	988.7	1461.2	664.7	1635.1	740	High	Cold	NA	NA	Non-Fishing	Permanent	Forest
56	Armenians	1843	Intensive agriculture	44.5	40	40	407.8	743.1	352.5	1117	288	High	Cold	12.06	513	Non-Fishing	Permanent	Savanna/ Grassland
57	Kurd	1951	Intensive agriculture	44.5	36.5	36.5	184	283.8	161.7	421.5	172	High	Warm	16.19	56	Non-Fishing	Permanent	Forest
58	Basseri	1958	Pastoralism	53	29	29	36.5	94.4	39	143	69	Medium	Warm	14.87	26	Non-Fishing	Impermanent	Forest
59	Punjabi (West)	1950	Intensive agriculture	74	32.5	32.5	443.1	541.5	419.5	1408.7	399	High	Warm	16.34	307	Non-Fishing	Permanent	Desert
60	Gond	1938	Horticulture	80.917 *	19.625 *	19.625	160	361.1	210.6	450.6	453	Medium	Warm	18.73	1253	Non-Fishing	Impermanent	Forest
61	Toda	1900	Pastoralism	76.5	11.5	11.5	655	860.6	616.9	1234.1	1102	High	Warm	19.85	791	Non-Fishing	Impermanent	Forest
62	Santal	1940	Intensive agriculture	87.167 *	23.5	23.5	284.6	355.2	320.1	829	419	High	Warm	17.27	1466	Non-Fishing	Permanent	Forest
63	Uttar Pradesh	1945	Intensive agriculture	83	25.917 *	25.917	355.2	411.4	395.2	727.8	428	High	Warm	17.04	1040	Non-Fishing	Permanent	Forest
64	Burusho	1934	Intensive agriculture	74.583 *	36.433 *	36.433	26.4	131.4	58.3	370.7	90	Medium	Warm	15.33	3452	Non-Fishing	Permanent	Tundra
65	Kazak	1885	Pastoralism	75.5	42.5	42.5	305.2	874.8	273	874.8	209	Medium	Cold	12.79	107	Non-Fishing	Impermanent	Savanna/ Grassland
66	Khalka Mongols	1920	Pastoralism	96.083 *	47.167 *	47.167	76.2	274.8	94.8	431.7	127	Medium	Cold	10.78	337	Non-Fishing	Impermanent	Desert
67	Lolo	1910	Intensive agriculture	103.5	27.5	27.5	642.7	1366.3	684.7	1736.6	484	Medium	Cold	10.57	736	Non-Fishing	Permanent	Forest
68	Lepcha	1937	Intensive agriculture	89	27.5	27.5	482.9	869	648.8	1816	883	High	Cold	12.67	364	Non-Fishing	Permanent	Savanna/ Grassland
69	Garo	1955	Horticulture	91	26	26	887.7	1630.1	1018.4	1796.4	819	High	Warm	17.58	1615	Non-Fishing	Permanent	Forest
70	Lakher	1930	Horticulture	93	22.333 *	22.333	887.7	992	836.5	1071.3	974	Medium	Warm	18.57	2720	Non-Fishing	Permanent	Forest
71	Burmese	1965	Intensive agriculture	95.667 *	22	22	444.6	728.5	541.3	1111.6	411	High	Warm	18.89	886	Non-Fishing	Permanent	Forest
72	Lamet	1940	Horticulture	100.667 *	20	20	1162.3	1275.6	1095.9	1354.7	1106	Low	Warm	15.65	1542	Non-Fishing	Impermanent	Forest
73	Vietnamese	1930	Intensive agriculture	106.25	20.5	20.5	556.4	1034.5	683.8	1316.4	598	High	Warm	18.47	2539	Non-Fishing	Permanent	Forest
74	Rhade	1962	Horticulture	108	13	13	674.4	957.5	733.1	1076	1081	High	Warm	22	1350	Non-Fishing	Impermanent	Forest
75	Khmer	1292	Intensive agriculture	103.833 *	13	13	304.4	893.2	587.5	988.7	648	High	Warm	NA	NA	Non-Fishing	Permanent	Forest
76	Siamese	1955	Intensive agriculture	100.85	14	14	536.7	940.6	532.2	1031.2	657	High	Warm	16.33	1222	Non-Fishing	Permanent	Forest
77	Semang	1925	Foraging	101.25	5	5	747.8	808.4	728.4	1001.8	1334	Low	Warm	17.11	2644	Non-Fishing	Impermanent	Forest
78	Nicobarese	1870	Horticulture	93.75	7	7	707.6	875.1	633.6	1013.1	1545	High	Warm	24.4	2509	Non-Fishing	Permanent	Forest
79	Andamanese	1860	Foraging	92.67 *	12 *	12	840.5	1191.7	828.3	1220.1	1545	Medium	Warm	23.6	3131	Fishing	Impermanent	Forest

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Table 1 (*continued*)

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	Absolute Latitude	NPP Mean (15 km)	NPP Max (15 km)	NPP Mean (120 km)	NPP Max (120 km)	NPP (P &M, 2007)	Population Density	Climate	ET	MAP (mm)	Fishing Binary	Mobility Binary	Biome Simple
80	Vedda	1860	Foraging	81.25	7.75	7.75	569.8	904.7	588.1	1076.2	741	Low	Warm	22.67	1641	Non-Fishing	Impermanent	Forest
81	Tanala	1925	Intensive agriculture	48	−22	22	1420.9	1843.1	1475.9	1950.4	1199	Medium	Warm	19.71	435	Non-Fishing	Impermanent	Forest
82	Negri Sembilan	1958	Intensive agriculture	102.25	2.583 *	2.583	735.6	909.1	723.2	1046	986	High	Warm	18	1313	Non-Fishing	Permanent	Forest
83	Javanese	1954	Intensive agriculture	112.22	−7.7	7.7	844.8	1403.6	825.4	1512.6	865	High	Warm	21.64	2889	Non-Fishing	Permanent	Forest
84	Balinese	1958	Intensive agriculture	115.333 *	−8.5	8.5	1290.9	1519.9	1130.4	1539.2	1723	High	Warm	23.6	1930	Non-Fishing	Permanent	Forest
85	Iban	1950	Horticulture	113	2	2	886.8	980.1	881.5	1014	1074	Medium	Warm	25.11	3968	Non-Fishing	Impermanent	Forest
86	Badjau	1963	Foraging	120	5.2 *	5.2	973.4	1339.8	956.1	1372.9	1727	Low	Warm	25.11	2002	Fishing	Impermanent	Forest
87	Toradja	1910	Horticulture	121	−2	2	883	1051.7	910.2	1185	1051	Medium	Warm	24.22	2844	Non-Fishing	Permanent	Forest
88	Tobelorese	1900	Horticulture	127.85 *	2	2	943	1247.3	936.3	1263.7	1592	Medium	Warm	25.11	3576	Non-Fishing	Permanent	Forest
89	Alorese	1938	Horticulture	124.667 *	−8.333 *	8.333	1090.5	1381.8	896.3	1421	1380	High	Warm	24.4	818	Non-Fishing	Permanent	Forest
90	Tiwi	1929	Foraging	131	−11.375 *	11.375	764.3	1174.3	696.4	1328.6	1307	Low	Warm	22.67	1538	Non-Fishing	Impermanent	Savanna/ Grassland
91	Aranda	1896	Foraging	133.5	−24.25	24.25	100.3	141.6	98.3	310.7	189	Low	Warm	16	275	Non-Fishing	Impermanent	Desert
92	Orokaiva	1925	Horticulture	148	−8.5	8.5	1257.4	1376.1	1312.2	1589.6	1374	Medium	Warm	22.36	1015	Non-Fishing	Permanent	Forest
93	Kimam	1960	Intensive agriculture	138.5	−7.5	7.5	1065.3	1497.2	1286.3	1605.4	941	Low	Warm	20.67	2097	Non-Fishing	Permanent	Forest
94	Kapauku	1955	Horticulture	136	−4	4	1260.8	1425.3	1217	1510.1	1108	High	Warm	24.22	2491	Non-Fishing	Permanent	Forest
95	Kwoma	1937	Horticulture	142.667 *	−4.167 *	4.167	1406.1	1564.1	1391	1634.7	946	High	Warm	27	2482	Non-Fishing	Permanent	Forest
96	Manus	1929	Horticulture	147.167 *	−2.167 *	2.167	765.6	1105.6	697.2	1136.7	1520	High	Warm	26	3912	Non-Fishing	Permanent	Forest
97	New Ireland	1930	Horticulture	152.885 *	−4.33 *	4.33	1115.9	1260.3	1064.7	1357.1	1552	Medium	Warm	25.2	2281	Non-Fishing	Permanent	Forest
98	Trobrianders	1914	Horticulture	151.07	−8.489 *	8.489	995.3	1377.5	980.3	1470.3	1382	High	Warm	24.4	3907	Non-Fishing	Permanent	Forest
99	Siuai	1939	Horticulture	155.55 *	−6.5 *	6.5	1182.2	1284.5	1127.8	1419.6	1283	High	Warm	26	3035	Non-Fishing	Permanent	Forest
100	Tikopia	1930	Horticulture	168.821 *	−12.302 *	12.302	398.3	931.9	398.3	931.9	338	High	Warm	21.33	NA	Non-Fishing	Permanent	Savanna/ Grassland
101	Pentecost	1953	Horticulture	168.2 *	−15.8 *	15.8	978.3	1349.7	1038.8	1426.3	1405	Medium	Warm	21.33	NA	Non-Fishing	Permanent	Forest
102	Mbau Fijians	1840	Horticulture	178.583 *	−18	18	1012.3	1412	1142.3	1472.8	1392	High	Warm	NA	NA	Fishing	Permanent	Forest
103	Ajie	1845	Intensive agriculture	165.667 *	−21.333 *	21.333	1151.5	1545.5	1180.9	1613.7	1092	Medium	Warm	19.85	1064	Non-Fishing	Permanent	Forest
104	Maori	1820	Horticulture	174.2 *	−35.35 *	35.35	1542.4	1830.9	1566.1	1871.3	1482	Low	Warm	14	1607	Non-Fishing	Permanent	Forest
105	Marquesans	1800	Horticulture	−140.167 *	−8.917 *	8.917	1017.4	1514.3	893.1	1519.7	1062	High	Warm	26	1412	Non-Fishing	Permanent	Forest
106	Western Samoans	1829	Horticulture	−172.43 *	−13.75	13.75	942.9	1211.8	889.1	1292.2	1204	High	Warm	20.4	4819	Non-Fishing	Permanent	Forest

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Table 1 (*continued*)

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	Absolute Latitude	NPP Mean (15 km)	NPP Max (15 km)	NPP Mean (120 km)	NPP Max (120 km)	NPP (P &M, 2007)	Population Density	Climate	ET	MAP (mm)	Fishing Binary	Mobility Binary	Biome Simple
107	Gilbertese	1890	Horticulture	172.983 *	3.373 *	3.373	503.7	1121.4	424.7	1164.5	295	High	Warm	28	2238	Non-Fishing	Permanent	Forest
108	Marshallese	1900	Horticulture	171.033 *	7.146 *	7.146	129.8	203.1	265.1	460.5	1293	High	Warm	26	4000	Fishing	Permanent	Forest
109	Trukese	1947	Horticulture	151.615 *	7.356	7.356	359.9	946.6	424.4	1046.1	1527	High	Warm	26	3351	Non-Fishing	Permanent	Forest
110	Yapese	1910	Horticulture	138.09 *	9.5	9.5	703.2	1269.6	699.3	1269.6	1685	High	Warm	26	3103	Non-Fishing	Permanent	Forest
111	Palauans	1947	Horticulture	134.57 *	7.5	7.5	632	1104.8	550.6	1122.3	1613	High	Warm	26	NA	Non-Fishing	Permanent	Forest
112	Ifugao	1910	Intensive agriculture	121.167 *	16.833 *	16.833	1115.2	1386.5	1019	1492.7	868	High	Warm	22.67	1995	Non-Fishing	Permanent	Forest
113	Atayal	1930	Horticulture	120.75	24.333 *	24.333	933.8	1271.8	830.4	1283.2	895	Medium	Warm	17.56	2200	Non-Fishing	Impermanent	Forest
114	Chinese	1936	Intensive agriculture	120.083 *	31	31	540.4	883.5	581.2	1377.9	537	High	Cold	NA	NA	Non-Fishing	Permanent	Forest
115	Manchu	1915	Intensive agriculture	125.5	50	50	327	480.8	318.9	678.4	357	High	Cold	12.29	707	Non-Fishing	Permanent	Forest
116	Koreans	1947	Intensive agriculture	126.417 *	37.6	37.6	665.5	1080.7	649.1	1207.3	399	High	Cold	10.78	288	Non-Fishing	Permanent	Forest
117	Japanese	1950	Intensive agriculture	133.667 *	34.667 *	34.667	837.5	1560.1	878	1740.4	634	High	Warm	14.14	1600	Non-Fishing	Permanent	Forest
118	Ainu	1880	Foraging	143	42.833 *	42.833	641	943	737.4	1288.7	496	Low	Cold	12.25	845	Fishing	Impermanent	Forest
119	Gilyak	1890	Foraging	142.8 *	54.06 *	54.06	455.8	640.9	420.5	828	299	Low	Cold	10.84	325	Fishing	Impermanent	Forest
120	Yukaghir	1850	Foraging	153.5	64.75	64.75	288.2	445.3	273.4	578.8	179	Low	Cold	9.64	151	Fishing	Impermanent	Forest
121	Chukchee	1900	Pastoralism	180	66.5	66.5	71.1	167.2	129.7	313.8	78	Low	Cold	10.19	163	Non-Fishing	Impermanent	Forest
122	Ingalik	1885	Foraging	−159.5	62.5	62.5	360.3	537.3	363.7	706.6	200	Low	Cold	10.38	388	Fishing	Impermanent	Forest
123	Aleut	1800	Foraging	−163.75 *	54.9 *	54.9	388.8	967	348.7	982.4	364	Medium	Cold	10.38	388	Fishing	Impermanent	Tundra
124	Copper Eskimo	1915	Foraging	−112 *	67.5 *	67.5	110.5	202.6	108.9	202.6	85	Low	Cold	8.77	182	Fishing	Impermanent	Tundra
125	Montagnais	1910	Foraging	−74	50	50	469.7	655.7	464	727.2	344	Low	Cold	11.76	874	Non-Fishing	Impermanent	Forest
126	Micmac	1650	Foraging	−63.02 *	46.22 *	46.22	622.8	934.9	763	1362.2	378	Low	Cold	12.53	928	Non-Fishing	Impermanent	Forest
127	Saulteaux	1930	Foraging	−95.5	52	52	484	609.7	497	828.4	591	Low	Cold	11.39	490	Fishing	Impermanent	Forest
128	Slave	1940	Foraging	−122	62	62	422.9	551.3	382.7	730.7	483	Low	Cold	10.74	414	Non-Fishing	Impermanent	Forest
129	Kaska	1900	Foraging	−131	60	60	268.3	373.1	256.3	433.8	214	Low	Cold	10.74	424	Fishing	Impermanent	Forest
130	Eyak	1890	Foraging	−145.5 *	60.5	60.5	388.8	650	238.9	783.3	202	Low	Cold	10.96	1752	Fishing	Impermanent	Forest
131	Haida	1875	Foraging	−132.5	54	54	660.7	803.9	645.4	1184.8	516	Low	Cold	11.28	2360	Fishing	Impermanent	Forest
132	Bellacoola	1880	Foraging	−126.5	52.333 *	52.333	345.5	883.5	365.8	1114.5	217	Medium	Cold	11.85	1518	Fishing	Permanent	Forest
133	Twana	1860	Foraging	−123.25	47.433 *	47.433	781.8	1386.7	824.6	1574.9	726	High	Warm	13.05	864	Fishing	Impermanent	Forest
134	Yurok	1850	Foraging	−124	41.5	41.5	1151.6	1792.7	924.3	1973.7	907	Medium	Cold	12.86	1110	Fishing	Permanent	Forest
135	Pomo (Eastern)	1850	Foraging	−123	39	39	1163.1	1566	992	2345.5	847	Medium	Warm	14.19	1171	Non-Fishing	Impermanent	Forest
136	Yokuts (Lake)	1850	Foraging	−119.5	35	35	292.1	729.8	548.1	2154.3	452	Medium	Warm	14.92	231	Fishing	Impermanent	Forest
137	Paiute (North.)	1870	Foraging	−119	43.5	43.5	221.1	661	212.7	826.1	226	Low	Cold	12.67	366	Non-Fishing	Impermanent	Desert
138	Klamath	1860	Foraging	−121.667 *	42.625 *	42.625	550.9	690.8	491.9	1392.5	449	Low	Cold	11.6	1072	Fishing	Impermanent	Forest
139	Kutenai	1890	Foraging	−116.667 *	49	49	534.3	679.4	523.6	992.6	333	Low	Cold	12.32	722	Fishing	Impermanent	Forest
140	Gros Ventre	1880	Pastoralism	−108	48	48	245.4	417.5	250.9	780.9	285	Low	Cold	11.78	340	Non-Fishing	Impermanent	Savanna/Grassland
141	Hidatsa	1836	Intensive agriculture	−101	47	47	392.8	456.4	371.3	663.9	300	Low	Cold	12.46	391	Non-Fishing	Impermanent	Savanna/Grassland

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Table 1 (*continued*)

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	Absolute Latitude	NPP Mean (15 km)	NPP Max (15 km)	NPP Mean (120 km)	NPP Max (120 km)	NPP (P &M, 2007)	Population Density	Climate	ET	MAP (mm)	Fishing Binary	Mobility Binary	Biome Simple
142	Pawnee	1867	Horticulture	−100	42	42	307.1	500.5	341.3	627.5	332	Low	Cold	12.74	468	Non-Fishing	Impermanent	Savanna/Grassland
143	Omaha	1860	Horticulture	−96.5	41.433 *	41.433	328.4	487.2	357.2	552	388	Medium	Warm	13.11	704	Non-Fishing	Impermanent	Savanna/Grassland
144	Huron	1634	Horticulture	−79	44.5	44.5	561.4	697.1	561.4	1130	301	High	Cold	12.67	782	Non-Fishing	Impermanent	Forest
145	Creek	1800	Horticulture	−86	32.933 *	32.933	778.3	1430.9	800.8	1458.6	503	Medium	Warm	14.74	1269	Non-Fishing	Impermanent	Forest
146	Natchez	1718	Horticulture	−91.417 *	31.5	31.5	540.4	1182	649.6	1508	577	Medium	Warm	15.76	1417	Non-Fishing	Permanent	Forest
147	Comanche	1870	Pastoralism	−101.5	34	34	213.1	328.5	226.4	455.5	320	Low	Warm	14.74	622	Non-Fishing	Impermanent	Savanna/Grassland
148	Chiricahua	1870	Pastoralism	−109.5	32	32	132.9	348.9	124	429.7	280	Low	Warm	14.8	382	Non-Fishing	Impermanent	Desert
149	Zuni	1880	Intensive agriculture	−108.75	35.667 *	35.667	113.1	195	149.2	525.8	200	Medium	Warm	13.35	234	Non-Fishing	Permanent	Forest
150	Havasupai	1918	Intensive agriculture	−112.167 *	35.833 *	35.833	171.6	415.3	167.5	507.3	195	Low	Cold	12.67	556	Non-Fishing	Impermanent	Desert
151	Papago	1910	Intensive agriculture	−112	32	32	85.5	147.3	80.2	270.8	146	High	Warm	15.93	364	Non-Fishing	Impermanent	Desert
152	Huichol	1890	Horticulture	−105	22	22	914.5	1247.2	701.7	1493.6	696	Medium	Warm	13.2	365	Non-Fishing	Permanent	Forest
153	Aztec	1520	Intensive agriculture	−99.167 *	19	19	1068.3	1824.8	859	1954.2	1193	High	Warm	16.77	868	Non-Fishing	Permanent	Forest
154	Popoluca	1940	Horticulture	−94.833 *	18.25	18.25	852.5	1155.7	804.5	1532.3	724	High	Warm	21.08	3085	Non-Fishing	Permanent	Forest
155	Quiche	1930	Horticulture	−91	15	15	781.6	1449.2	942.1	1599.9	1299	High	Warm	19.23	765	Non-Fishing	Permanent	Forest
156	Miskito	1921	Horticulture	−83.25 *	15	15	1261.8	1533.5	1006.4	1657.4	1217	Medium	Warm	23.6	3293	Non-Fishing	Permanent	Wetland
157	Bribri	1917	Horticulture	−83.25	9	9	814	957.8	842.1	1245.8	847	NA	Warm	21.2	3047	Non-Fishing	Permanent	Forest
158	Cuna (Tule)	1927	Horticulture	−78.5	9.25	9.25	842.3	1095.6	852.4	1195.5	713	High	Warm	26	3305	Non-Fishing	Permanent	Forest
159	Goajiro	1947	Pastoralism	−71.75	11.917 *	11.917	312.8	807.7	517.3	1585.8	542	Low	Warm	26	456	Non-Fishing	Impermanent	Desert
160	Haitians	1935	Intensive agriculture	−72.167 *	18.833 *	18.833	879.4	1258.6	912.2	1765.1	812	High	Warm	22.67	1242	Non-Fishing	Permanent	Forest
161	Callinago	1650	Intensive agriculture	−61.35 *	15.45 *	15.45	1402.9	1591.9	1246.4	1654	1821	Medium	Warm	22.36	1678	Non-Fishing	Impermanent	Forest
162	Warrau	1935	Foraging	−62	9.078 *	9.078	1154.4	1323.3	1115	1590.8	908	Low	Warm	14.8	2441	Fishing	Impermanent	Forest
163	Yanomamo	1965	Horticulture	−65	2.417 *	2.417	1058.4	1119.1	1051.1	1200.8	1118	Low	Warm	27.14	3148	Non-Fishing	Impermanent	Forest
164	Carib (Barama)	1932	Horticulture	−60.167 *	7.417 *	7.417	1237.8	1286.9	1237.1	1461.9	966	Low	Warm	25.2	1486	Fishing	Impermanent	Forest
165	Saramacca	1928	Horticulture	−55.75	3.5	3.5	1017.2	1068.2	1016.8	1085.6	1032	Medium	Warm	25.2	2180	Non-Fishing	Permanent	Forest
166	Mundurucu	1850	Horticulture	−56.5	−6.5	6.5	916.3	964.3	910.4	1042.2	1231	Low	Warm	22.8	2770	Non-Fishing	Permanent	Forest
167	Cubeo (Tucano)	1939	Horticulture	−70.5	1.25	1.25	839.7	993.3	845.4	1076.3	1055	Low	Warm	27.14	3148	Non-Fishing	Permanent	Forest
168	Cayapa	1908	Horticulture	−79	1	1	1120.8	1219.9	927.5	1385.1	1049	Medium	Warm	27.14	3148	Non-Fishing	Permanent	Forest

(*continued on next page*)

Table 1 (*continued*)

SCCS ID	Society Name	Study Year	Subsistence	Longitude	Latitude	Absolute Latitude	NPP Mean (15 km)	NPP Max (15 km)	NPP Mean (120 km)	NPP Max (120 km)	NPP (P &M, 2007)	Population Density	Climate	ET	MAP (mm)	Fishing Binary	Mobility Binary	Biome Simple
169	Jivaro	1920	Horticulture	−78	−3	3	1675.7	1763.2	1495.4	1892.5	1541	Low	Warm	22.36	2623	Non-Fishing	Impermanent	Forest
170	Amahuaca	1960	Horticulture	−72.25	−10.333 *	10.333	1916.2	1991.3	1904.4	2260	959	Low	Warm	20.91	1880	Non-Fishing	Impermanent	Forest
171	Inca	1530	Intensive agriculture	−72	−13.5	13.5	521.9	1179.9	878.9	2383.7	485	Medium	Cold	11.45	804	Non-Fishing	Permanent	Savanna/ Grassland
172	Aymara	1940	Horticulture	−65.75	−16	16	2048.9	2088.7	1917.3	2250.7	1131	High	Cold	10	963	Non-Fishing	Permanent	Forest
173	Siriono	1942	Foraging	−63.5	−14.5	14.5	1144.5	1282.5	1130.6	1676.9	459	Low	Warm	19.33	1141	Non-Fishing	Impermanent	Forest
174	Nambicuara	1940	Horticulture	−58.75	−13	13	835.9	1109.8	877	1152	821	Low	Warm	21.08	1388	Non-Fishing	Impermanent	Savanna/ Grassland
175	Trumai	1938	Horticulture	−53.667 *	−11.833 *	11.833	785.6	960.3	766.4	1007.8	584	Low	Warm	21.33	1411	Non-Fishing	Permanent	Forest
176	Timbira	1915	Horticulture	−46	−6.5	6.5	491.8	756.2	509.1	841.2	498	Medium	Warm	22.36	940	Non-Fishing	Impermanent	Savanna/ Grassland
177	Tupinamba	1550	Horticulture	−44.5	−22.792 *	22.792	1705.6	1847.2	1342.3	1852	942	Low	Warm	24.4	1653	Non-Fishing	Impermanent	Forest
178	Botocudo	1884	Foraging	−42.5	−19	19	1145.5	1633.2	1076.2	1735.1	790	Low	Warm	18	1291	Non-Fishing	Impermanent	Forest
179	Shavante	1958	Foraging	−51.5	−13.5	13.5	711.1	1037.8	675	1103.7	340	Low	Warm	21.33	1411	Non-Fishing	Impermanent	Savanna/ Grassland
180	Aweikoma	1932	Foraging	−50	−28	28	1316.8	1815.4	1490.3	1855.4	1060	Low	Warm	14.44	1806	Non-Fishing	Impermanent	Forest
181	Cayua	1890	Horticulture	−55	−23.5	23.5	874.1	1370.9	920.1	1515.9	611	Low	Warm	18	1325	Non-Fishing	Impermanent	Forest
182	Lengua	1889	Horticulture	−58.5	−23	23	465	691.3	458.4	919.5	579	Low	Warm	18.94	1205	Non-Fishing	Impermanent	Savanna/ Grassland
183	Abipon	1750	Pastoralism	−59.5	−28	28	366	582.1	394	825	715	Low	Warm	16.4	1175	Non-Fishing	Impermanent	Savanna/ Grassland
184	Mapuche	1950	Intensive agriculture	−72.583 *	−38.5	38.5	1037.3	1656	1158.4	2023.9	765	High	Warm	14	162	Non-Fishing	Permanent	Forest
185	Tehuelche	1870	Pastoralism	−68	−40.5	40.5	133.2	191.8	134.8	499.1	287	Low	Warm	14.39	135	Non-Fishing	Impermanent	Savanna/ Grassland
186	Yahgan	1865	Foraging	−69.4 *	−55.5	55.5	383.5	991.5	448.6	1050	178	Low	Cold	9.47	622	Fishing	Impermanent	Forest

Primary data used to test the MHH are shown in Table 1. We have also included the NPP score used by Porter and Marlowe (2007) in their test of hunter-gatherer habitat marginality. Latitude and longitude coordinates marked with an asterisk (*) have been modified from the original values listed in the SCCS and used by Porter and Marlowe in their determination of NPP. Certain variables listed here (such as Absolute Latitude, Population Density, Fishing Binary, and Mobility Binary) are original derived variables, based upon SCCS variables (as described in the Methods section; see the *Derived variable calculations* sub-section).
These data are sourced from:
1) The Standard Cross Cultural Sample (SCCS), Columns: [A, B, C, E, F, M, Q, and R].
2) Porter and Marlowe, 2007), Columns: [D, L, N, O, and P].
3) NASA Moderate Resolution Imaging Spectroradiometer (MODIS) NPP data (MOD17A3 algorithm) from Numerical Terra Dynamic Simulation Group at the University of Montana, Columns: [H, I, J, and K].
4) Marine Ecoregions Of the World (MEOW): http://maps.tnc.org/files/metadata/MEOW.xml, Column: [S].
5) Terrestrial Ecoregions Of the World (TEOW): http://maps.tnc.org/files/metadata/TerrEcos.xml, Column: [S].

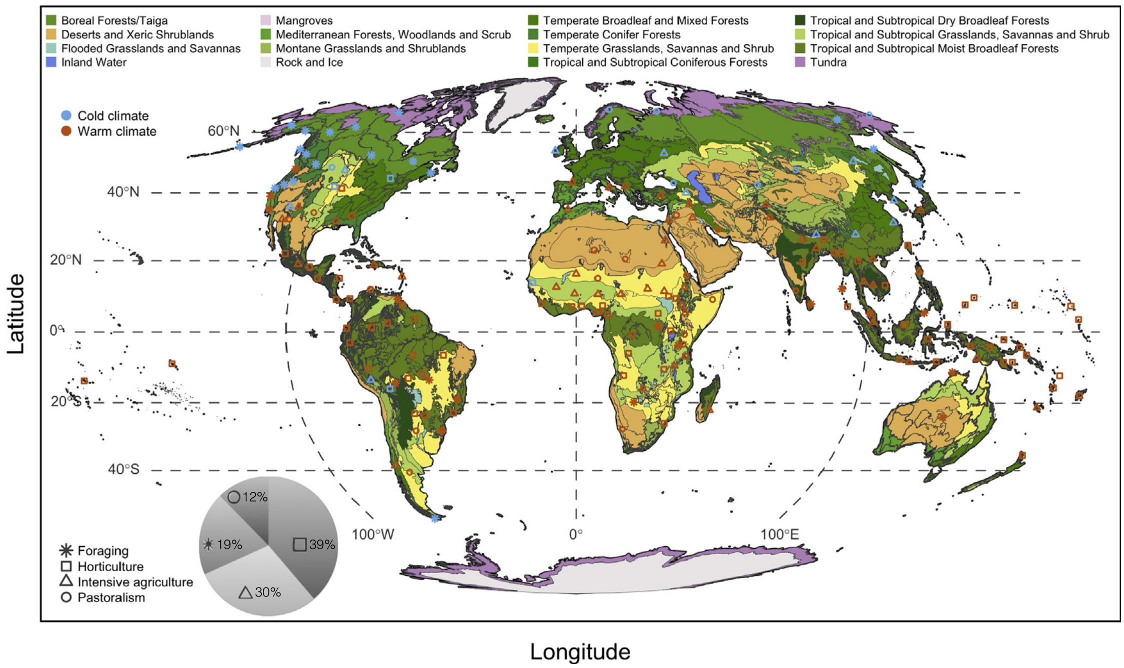

Fig. 1. Pre-industrial societies of the SCCS coded by terrestrial ecosystem.
World map showing terrestrial biotic ecosystems and locations of 186 societies from the SCCS in a Mollweide equal area projection. Societies are grouped by climate (Warm (ET > 13) and Cold (ET < 13)) and subsistence type (Foraging, Horticulture, Intensive Agriculture, and Pastoralism). Inset pie chart indicates the representation (%) of societies in each subsistence type. Map polygons sourced from NASA shape files (https://github.com/nasa/World-Wind-Java/tree/master/WorldWind/testData/shapefiles) with terrestrial biotic ecosystem polygons from The Nature Conservancy shape files (http://maps.tnc.org/gis_data.html).

3.1. Objective 1 — variation in NPP (by subsistence type)

In a final GLM accounting for environmental variables (SI text), with subsistence modes in four separate categories, we found that pastoralists occupied habitats of significantly lower average NPP_{max} than any other subsistence type (mean difference ≥ 354 g C/m^2/year, 95% CI: 85–624, $p \leq 0.0022$; Fig. 2). We found no evidence that average NPP_{max} differed among foragers, intensive agriculturalists, and horticulturalists (mean difference ≤ 138, 95% CI: −70, 346, $p \geq 0.24$; Fig. 2B). Neither of these results changed substantively when we lumped farming types into combinations of two or three types (Fig. 2C), when we used NPP_{mean} rather than NPP_{max}, when we used a 120 km

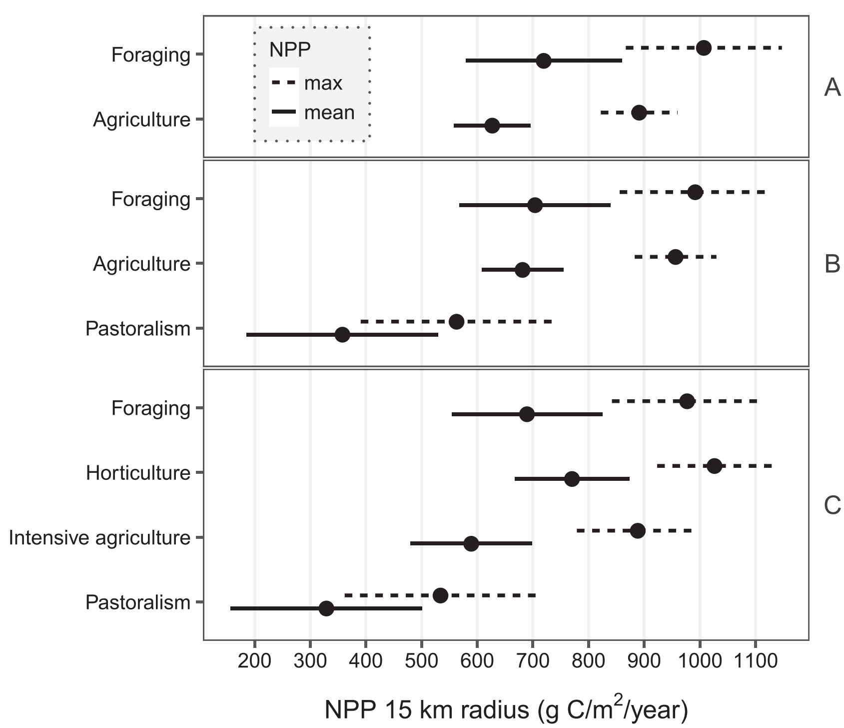

Fig. 2. Predicted NPP_{max} and NPP_{mean} by subsistence type. 15 km radius. Warm and cold climate societies are combined. Error bars represent 95% confidence intervals. Panels represent: (A) binary, (B) ternary, and (C) quaternary subsistence classifications.

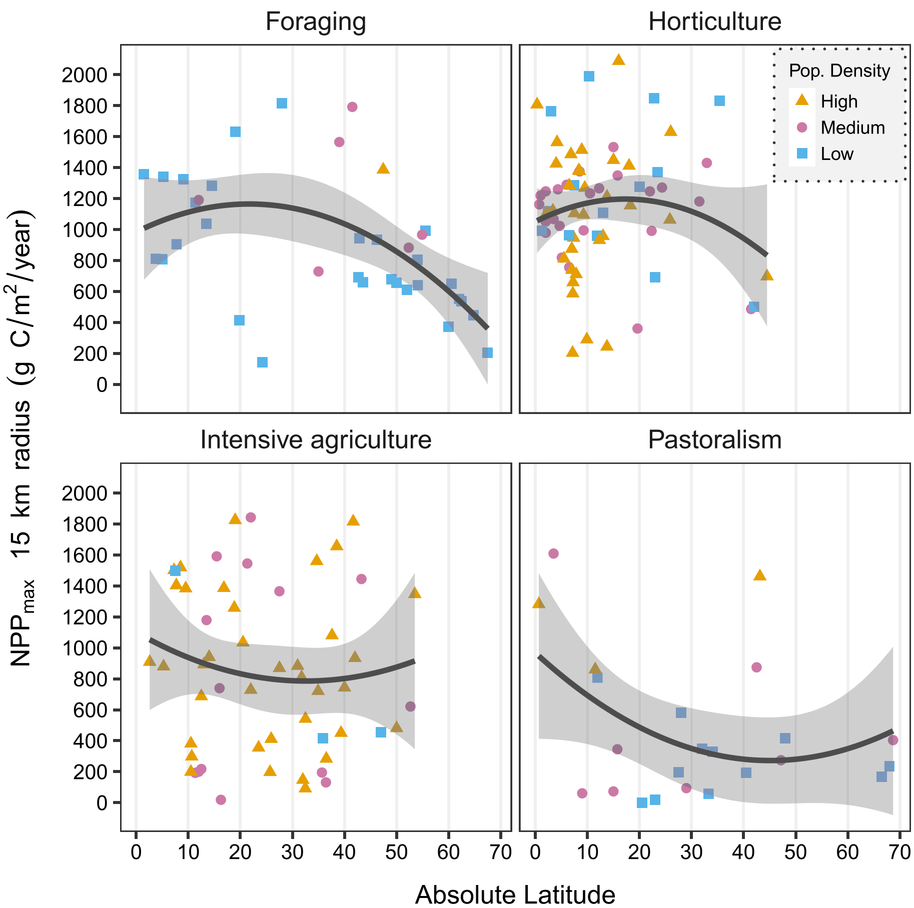

Fig. 3. Predicted NPP_{max} versus absolute latitude by subsistence type. 15 km radius. Lines and error ribbons represent point and 95% confidence interval predictions from a general linear model, respectively. Points correspond to observed NPP_{max} and PD as reported in the SCCS and are colored by PD. Latitudinal distribution covers only the observed range of each subsistence type.

radius rather than a 15 km radius (SI Text, Fig. S1), or when we divided societies by warm only and combined climates (Figs. S2a–S2b).

3.2. *Objective 2 — variation in NPP (by subsistence type) across latitude*

To assess the relationship between average NPP_{max} and latitude, we used GLMs to predict average NPP_{max} as a function of AbLat (Fig. 3). Foragers and pastoralists have latitudinal ranges extending up to almost |70°|, while horticulturalists and intensive agriculturalists have abbreviated ranges not extending much beyond |50°| latitude (Fig. 3). In our final model accounting for environmental variables, NPP_{max} had a positive relationship with MAP ($p = 0.014$), with a 10-centimeter increase in precipitation increasing NPP_{max} by 11.2 g C/m^2/year on average. Subsistence modes had different curvilinear relationships between NPP_{max} and AbLat (test of linear and quadratic AbLat interactions with subsistence mode, $F_{(3,\ 160)} = 3.4$, $p = 0.020$). Foragers and pastoralists exhibited contrasting concave and convex associations, respectively ($t_{(162)} = 2.5$, $p = 0.012$), with foragers displaying a (concave) trend towards increased NPP_{max} at mid latitudes, and lower relative NPP_{max} at relatively low and especially high latitudes. Pastoralists, by contrast showed a convex trend, in which they were more likely to occupy habitats with relatively higher NPP_{max} habitats at low equatorial latitudes. Horticulturalists also differed from pastoralists ($t_{(162)} = 2.4$, $p = 0.019$) in having a slightly concave relationship. We did not find evidence that intensive agriculturalists differed from the other three subsistence modes. There was very high variation in NPP at most latitudes, though the exception to this variation was for high latitude foragers, who had relatively predictable NPP. None of these results changed when we used a 120 km radius rather than a 15 km radius (SI Text, Fig. S3).

3.3. *Objective 3 — probability of subsistence strategies achieving low, medium, and high PD across NPP_{max} gradients*

Finally, we sought to explain how population densities for each subsistence type were related to NPP_{max}. We used an ordinal logistic regression model to estimate the probability of societies having low ($<$ 1 person/sq. mile), medium ($\geq$1 & $<$ 25 people/sq. mile), or high ($\geq$25 people/sq. mile) population density as a function of NPP_{max} and subsistence type, while controlling for all environmental variables. We found that the relationship between NPP_{max} and PD differed among subsistence modes (test of interaction between NPP_{max} and subsistence mode, likelihood ratio $\chi^2_{(3)} = 8.6$, $p = 0.035$). With each 500 g C/m^2/year unit increase in NPP_{max} the odds of population density becoming larger by one unit (from low to medium or from medium to high) changed by 193% (95% CI: 91%, 349%) for foragers, −36% (95% CI: −6%, −56%) for horticulturalists, 40% (95% CI: −6%, 111%) for intensive agriculturalists, and 156% (95% CI: 33%, 393%) for pastoralists. Horticulturalists (Fig. 4, second row from top) were the only subsistence type to exhibit a decreased probability of achieving high PD at high NPP_{max}, though they also had a low probability of having low PD at low NPP_{max}. Results were not markedly affected by our using a 120 km radius rather than a 15 km radius (SI Text, Fig. S4). In summary of Objective 3, we found that as NPP_{max} increased, the probability that population density would increase varied among subsistence types. Foragers and pastoralists had the most predictably positive relationship between population density and NPP. The NPP-PD relationships for horticulturalists and intensive agriculturalists were much less dramatic, as evidenced by their more modest odds ratios.

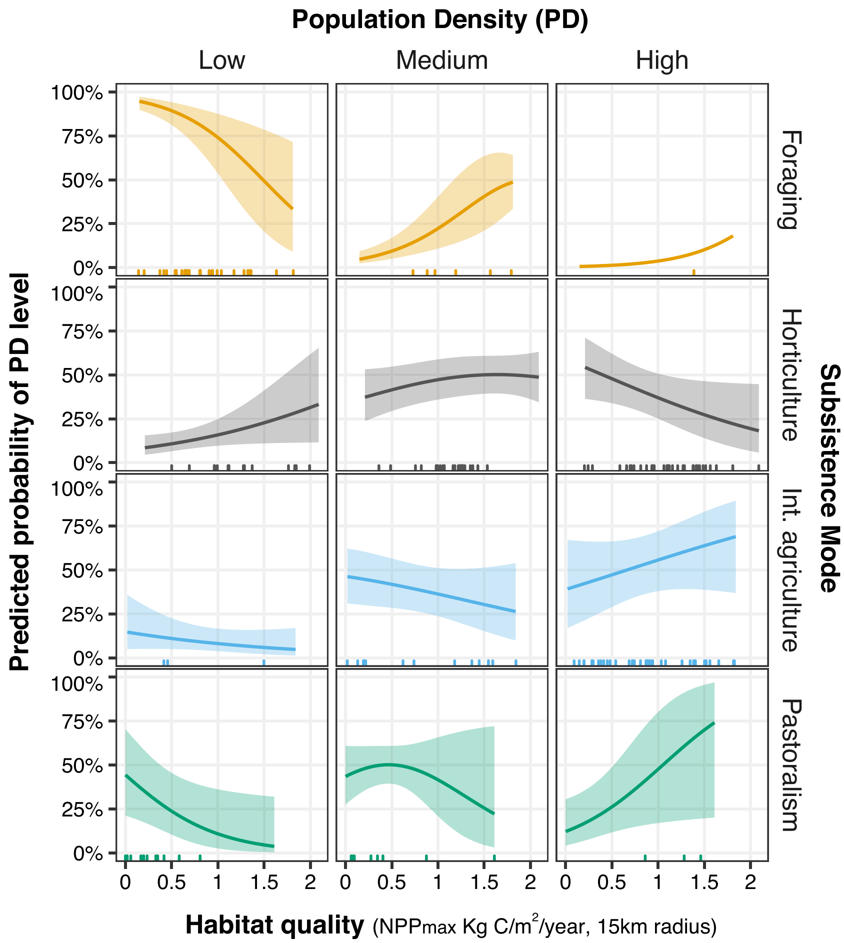

Fig. 4. Probability of population density level as predicted by NPP_{max}, by subsistence type. 15 km radius. Rows correspond to subsistence type. Columns correspond to levels of PD.

4. Discussion

We sought to understand how the association between habitat net primary productivity (NPP) and population density (PD) varied for four subsistence types practiced by pre-industrial human societies. Our first goal (Objective 1) was to thoroughly assess the marginal habitat hypothesis (MHH). The MHH suggests that ethnographic foragers occupied low productivity habitats because agriculturalists would have possessed the social power and technology to exclude foragers from high productivity habitats (Marlowe, 2005; Porter and Marlowe, 2007). Contrary to the predictions of the MHH, Porter and Marlowe (2007) found that the foraging populations (n = 36, Mean NPP = 600 ± 431) represented in the SCCS did not live in significantly worse habitats than agriculturalists (n = 150, Mean NPP = 737 ± 455), based on their comparison of Mean NPP. They concluded by rejecting the MHH and stating that the ethnographic record, while not perfect, does not provide a biased picture of forager subsistence and social organization based on a history of interaction with agriculturalists.

The necessary caveats to our updated and more detailed analysis are the same as in Porter and Marlowe's (2007). The modern environmental data are not contemporaneous with ethnographic data, and subsequent changes in land use practices may have radically altered landscapes between these periods of data collection. Nevertheless, this point is not likely to introduce any systematic bias given that shifts in land usage patterns are no more likely for populations of one subsistence type than another (Porter and Marlowe, 2007). Furthermore, our use of both NPP_{max} and larger 120 km radius projections allowed for an estimation of maximal regional productivity (relative to NPP_{mean} and 15 km radii). Yet, these parameters failed to produce significantly different results than the smaller average models. These points suggest that there is no evidence of systematic bias between subsistence types with regards to changing land use patterns.

We also sought to check Porter and Marlowe's (2007) conclusions by considering a wider variety of variables in our analyses. We adopted more realistic circular projections of habitat use (representing both logistical and residential geographic areas at 15 km and 120 km radii), increased MODIS NPP data from 5 to 15 years, and conducted analyses based on both NPP_{mean} and NPP_{max}. Despite these methodological modifications which were intended to account for the ability of human populations to bias their subsistence activities to the most productive areas of their habitat and range, our findings are similar to those of Porter and Marlowe (2007). Foragers, intensive agriculturalists, and horticulturalists did not occupy habitats of significantly different quality, whereas pastoralists occupied the lowest quality habitats. This analysis appears to confirm that the available evidence does not support the MHH.

Porter and Marlowe (2007) suggested that the MHH may derive in part from the prominence in the literature of deserts occupied by societies such as the!Kung in southern Africa (in a hot desert) or the Inuit in the Arctic (a cold desert), populations inhabiting both productivity and latitudinal extremes. It is worth noting that the SCCS is biased towards populations in the Northern Hemisphere (Marlowe, 2005), with 132 Northern SCCS societies compared to only 54 in the South (although 57 societies are situated within 10° North or South of the equator). Previous work attempted to control for latitudinal effects using effective temperature (ET) (Marlowe, 2005; Porter and Marlowe, 2007).

To improve upon these efforts, our second goal (Objective 2) was to assess human population distribution using explanatory models that account for the effects of latitude and other key covariates on the global pattern of subsistence occupation. In particular, we sought to model the distribution of pre-industrial human settlement as a function of NPP_{max} and absolute latitude. The results for Objective 2 were similar to those of Objective 1. Our results accordingly lend credence to the claim of Porter and Marlowe (2007) that the prominence of certain societies in the anthropological literature may have contributed to a false impression of typical hunter-gatherer habitats. For example, the!Kung (for whom NPP_{max} was measured at 415.5 g C/m^2/year) are often cited as an example of a hunter-gatherer society occupying low quality habitat. In our model, the NPP_{max} value for the!Kung was roughly one third of the predicted value for a forager at AbLat ~20°, falling as an extreme outlier to the 95% confidence interval (Fig. 3, upper left panel at 20° latitude). The!Kung society's occupation of a low productivity habitat at low latitude is thus unusual compared to other foragers in the SCCS.

Our third goal (Objective 3) was to assess and quantify the NPP-PD relationship across subsistence types in order to test our hypothesis that subsistence type moderates the NPP-PD relationship. We hypothesized that variation in PD derives from differences in the extractive efficiency of technologies and domesticates across subsistence types; therefore, including data on PD with environmental variables would provide a more complete picture of 'habitat quality' for pre-industrial humans than would either NPP_{mean} or NPP_{max} alone. We acknowledge that the inter-relationships among environment, technology, and population density are complex (Boserup, 1976), and that numerous mechanisms may be involved in translating environmental energy to PD. For example, disparities in fecundity, mortality, food production and security among subsistence types may all contribute to the divergent population demographic trends. Regardless of the exact mechanism, subsistence types represent cohesive cultural packages with respect to modes of food acquisition, processing, and storage (Ellen, 1982).

To test our hypothesis we modeled the probability of achieving low, medium, or high PD for each subsistence type, across the full range of the observed NPP_{max} gradient (Fig. 4). We assessed the within-subsistence type ordinal PD shift from low to medium, and medium to high, as a function of NPP_{max}. In particular, we address historical claims of marginality. If the NPP-PD relationship varies with subsistence type, this would indicate that 'marginality' is not a useful comparative term. As our findings below indicate, subsistence modes do in fact show unique NPP-PD relationships. We now briefly address the findings regarding each subsistence type.

4.1. Foragers

As we expected, NPP was a reasonably good predictor of habitat quality for ethnographic foragers, as PD in foraging societies appeared to be environmentally constrained (Fig. 4, top row). The positive association between NPP and PD suggests that habitat quality (as indicated by NPP) may indeed be a meaningful tool to assess the merits of the MHH, at least for foragers. Foragers at low NPP_{max} had a high probability of having low PD. In fact, foragers in habitats with $NPP_{max} \leq 1000$ (g C/m^2/year) had a ~75% chance of having low PD (Fig. 4, top left panel). At this productivity threshold ($NPP_{max} = 1000$ g C/m^2/year) foragers had a ~20% probability of having medium PD (Fig. 4, top middle panel). In the most productive habitats, foragers still only had a 50% probability of having medium PD, and a > 25% probability of still only having low PD. Though foragers maintained a relatively low probability of achieving even medium PD even in habitats with medium to high productivity, they did display a strong positive relationship between NPP and PD overall, across their entire range of NPP habitats. Unlike the other three subsistence types, foragers did not appear capable of achieving medium or high PD at low NPP_{max}.

High PD was achieved only among the Twana of the Pacific NW, who occupied the fifth most productive foraging habitat on the basis of NPP_{max}. These complex hunter-gatherers were able to achieve greater PD than other foragers due to their specialization on aquatic resources (anadromous fish) (Ames, 1994; Schalk, 1977). While the Twana were classified as high PD in our ordinal rankings, it should be noted that their PD as reported in the SCCS (26–100 persons/sq. mile) was much less than the PD (101–500 persons/sq. mile; > 500 persons/sq. mile) achieved by some non-foraging societies, though all three population density levels were binned as high PD within our model. Exploitation of abundant marine resources is the main hunting and gathering strategy in high-latitude low-NPP regions, as shown by the SCCS. Thus 13 foraging societies live at a latitude > 50°, of which 11 relied on fished resources. The two exceptions – the Slave and Montagnais foragers – were heavily dependent on seasonally abundant large game such as moose in the seasonal boreal and taiga forests of Canada.

4.2. Non-foragers

Unlike foragers, farmers in low productivity environments were capable of supporting medium and high PD. If farmers and foragers can maintain different PD in the same habitat, and PD is in fact an adequate measure of demographic success, then the concept of 'marginality' requires further context to explain this pattern. Intensive agriculturalists (Fig. 4, third row from top) and pastoralists (Fig. 4, bottom row) demonstrated an overall positive NPP-PD association, like that of foragers. However, unlike foragers, these subsistence types were capable of maintaining medium and high PD even in habitats with low productivity. For intensive agriculturalists, the probability of a society having low PD never exceeded 25%, despite the fact that these populations frequently occupied low NPP_{max} habitats, indicating that low NPP_{max} habitats can be successfully inhabited with technological intensification. Pastoralists had a relatively high probability (~50%) of supporting low PD in low NPP_{max} compared to intensive agriculturalists, whereas foragers maintained a probability of 75% or higher of supporting low PD in such habitats. This is because pastoralists were much more likely than foragers to have medium PD even in low productivity habitats, at a rate approaching that of intensive agriculturalists.

Horticulturalists (Fig. 4, second row from top) appeared to face fundamental geographic constraints, occupying the narrowest latitudinal range of all subsistence types (from 0 to 45° absolute latitude). In high NPP_{max} habitats horticulturalists demonstrated a negative NPP-PD relationship, the only instance of a negative trend across all subsistence types. Tropical environments with short and predictable dry seasons are best suited for swidden agriculture, and swiddening techniques are implausible in temperate environments and grasslands (Ellen, 1982). Swiddening in humid rainforests generates high rates of nutrient draining that increase the fallow period and group dispersion (Ellen, 1982), thus limiting PD. Horticulturalists thus exhibit indirect support for the idea that rainforest habitats may actually be food-limited human habitats, despite their uniquely high levels of productivity (Bailey and Headland, 1991; Hart and Hart, 1986; Headland and Bailey, 1991).

4.3. Revisiting the MHH

The fundamental question surrounding the MHH is whether modern foragers bias our picture of the hunting and gathering lifeway during the Pleistocene, because, as Porter and Marlowe (2007) suggested, "pre-Holocene foragers living in more productive habitats may have had a considerably higher population density, resulting in different social organization" (p. 59).

In light of our findings, we can revisit what we mean by low-quality habitats for foragers. It is clear that tundra/taiga/polar habitats at high latitudes represent low-quality environments, and these habitats were exclusively occupied and exploited by foragers and pastoralists. Arid deserts also represent a low productivity environment, and yet non-foragers in these habitats were still capable of achieving relatively high PD. To a lesser extent, tropical rainforests (occupied principally by horticulturalists and foragers) may also represent low quality (on the basis of NPP-PD dynamics) habitats. While foragers do occupy these habitats, there is also no doubt that they would have occupied other habitats in the past. High-productivity riverine, lacustrine, deltaic, and flood plain aquatic habitats (i.e., Amazon, Ganges, Mississippi, Nile, and Yangtze Rivers) remain underrepresented in any analysis based on societies of the SCCS because these habitats have long been occupied by post-industrial societies. Foragers are similarly absent from South Africa's Cape Floral Region in the SCCS, a productive marine habitat proposed to have played a significant role as a refugia during a critical climatic period in the evolution of *Homo sapiens* (Marean, 2010, 2011).

Could Pleistocene African foragers have frequently achieved higher PD in higher quality habitats?

Among ethnographic foragers, achieving high PD is associated with an exceptional circumstance owing to geography: reliance on marine food sources. Foragers only achieved medium or high PD on seven occasions (out of a total 36 foraging societies), and six of these seven populations relied upon fished resources (the Eastern Pomo the lone exception). In tropical Pleistocene Africa, such high PD would have been unlikely, as marine productivity (unlike terrestrial NPP) increases with latitude (Huston and Wolverton, 2009), and African hunter-gatherers living in intact terrestrial ecosystems did not achieve higher PD levels. Furthermore, foragers at low and mid latitudes were largely absent from low NPP_{max} habitats. Thus, if high PD was achieved among Pleistocene foragers, it may have been achieved in a fundamentally different manner from modern foragers.

5. Conclusion

Consistent with a previous study (Porter and Marlowe, 2007), we did not find quantitative support for the MHH, as the habitats of ethnographic foragers did not evince consistently low NPP. The limitations of the ethnographic record, including the possibility that some non-foraging pre-industrial societies were also forced out of higher quality habitats, precludes a more definitive test of the MHH. Even by the earliest days of ethnographic observation, post-industrialized societies had left their mark on the distribution of smaller scale societies. Yet one distinctive ecological feature of foragers is that their population densities were better predicted by NPP than were non-foragers, especially within low productivity habitats. We suggest the tendency of foragers living in low-NPP habitats to have low PD may have contributed to the widespread perception that forager habitats are marginal.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2019.05.028.

Declaration of Competing Interest

We have no competing interests.

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Author's contributions

AJC conceived of and coordinated the study, participated in the design of the study and in data analysis, and drafted the manuscript; SW participated in the design of the study, carried out the statistical analyses, participated in data analysis, and helped draft the manuscript; VVV participated in data analysis, and helped draft the manuscript; RWW participated in the design of the study, and helped draft the manuscript. All authors gave final approval for publication.

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