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How marginal are forager habitats?

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Abstract

It is frequently suggested that human foragers occupy 'marginal' habitats that are poor for human subsistence because the more productive habitats they used to occupy have been taken over by more powerful agriculturalists. This would make ethnographically described foragers a biased sample of the foragers who existed before agriculture and thus poor analogs of earlier foragers. Here, we test that assertion using global remote sensing data to estimate habitat productivity for a representative sample of societies worldwide, as well as a warm-climate subsample more relevant for earlier periods of human evolution. Our results show that foraging societies worldwide do not inhabit significantly more marginal habitats than agriculturalists. In addition, when the warm-climate subsample is used, foragers occupy habitats that are slightly, though not significantly, more productive than agriculturalists. Our results call into question the marginal habitat criticism so often made about foragers in the ethnographic record.

Keywords: Foragers; Habitat productivity; Hunter-gatherers; Standard cross-cultural sample

1. Introduction

Many anthropologists assume that foragers who have been described by ethnographers (ethnographic foragers) live in marginal (unproductive) habitats [1,7,8,11,20]. This is because agricultural societies, by virtue of their larger populations and greater military strength, sometimes displace foragers from more productive habitats, eliminate them altogether, or incorporate them into their own societies [7,11,15]. If this process has been happening long enough and often enough worldwide, then ethnographic foragers should occupy habitats less productive than the habitats occupied by most foragers prior to the advent of agriculture. Ethnographic foragers would be a biased sample from which to draw inferences about pre-Holocene societies. For example, pre-Holocene foragers living in more productive habitats may have had a considerably higher population density, resulting in different social organization. Larger groups in smaller areas could have favored greater territorial defense [24] and perhaps resulted in more warfare. Bigelow [7,8] suggested that domination by agriculturalists might account for the relatively peaceful nature of so many ethnographic foragers and may explain their egalitarianism as well. It is, therefore, an important question whether foragers live in more marginal habitats. But the impression that they do may derive from the prominence in the more recent literature of certain foragers like the !Kung and Central Australians in very arid deserts, or the Inuit in icy tundra.

While it is often assumed ethnographic foragers occupy marginal habitats, the assumption has never been tested. If agriculturalists have largely displaced foragers from more productive habitats, the ethnographic record should show that the mean productivity of habitats occupied by agriculturalists is significantly higher than the mean productivity of forager habitats. Here we test that prediction using satellite data to estimate the productivity of habitats occupied by foragers and agriculturalists in the Standard Cross Cultural Sample (SCCS) [27].

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1.1. Habitat quality

Habitat quality is best measured with phenological studies in which the actual number of plants of a certain size and species are counted to estimate the quantity of available foods. Because these type of data do not exist in a comprehensive form for habitats across the world, we must use other measures. One proxy for habitat quality is the amount of solar energy that is available for plant growth in a given habitat, the level of precipitation, and temperature variation. Terrestrial habitats are sustained by plant productivity, which is the ultimate source of all food available for human consumption. Aquatic foods available are more difficult to assess but, fortunately, should not affect foragers or agriculturalists in different ways, and so should not produce any systematic bias in this analysis.

Habitat quality can be quickly assessed using effective temperature (ET), a concept introduced by Bailey [4]. It is calculated from mean temperature of the warmest and coldest months and reflects the variability of the local climate. It provides a simple comparative measure of sunlight, warmth, and the length of the growing season [10]. More recently, Binford [9] used equations developed by Thornthwaite and Mather [35,36] and Rosenzweig [31] to evaluate primary production and primary biomass for many forager habitats. Primary biomass is defined as the amount of standing plant matter in a given area. Primary production discards the old plant matter, such as tree trunks, to leave only new production, usually reproductive parts and new growth. Archeologists have previously used measures of primary biomass and primary production based on data from weather stations to examine relationships between habitat quality and foraging [9,16]. However, today we can use remote sensing technology and a more refined algorithm to estimate the habitat quality of any square kilometer of land on earth.

2. Methods

2.1. Measures of habitat quality

Here, we employ methods recently developed by NASA's Earth Observation System (EOS), which use spectral imagery in conjunction with ecological calculations originally proposed by Monteith [25,26] to estimate plant production. Solar radiation data are collected using the Moderate Resolution Imaging Spectrometer (MODIS) sensor on a NASA satellite. The MODIS algorithm combines these data with information provided by the NASA Data Assimilation Office [3] on land cover, leaf area, and biome specific parameters. The algorithm calculates two types of primary productivity: gross primary productivity (GPP), which estimates total production costs, and net primary productivity (NPP), which represents only the non-metabolic plant production. The algorithm calculates GPP over an 8-day period and subtracts the metabolic costs of transpiration to obtain NPP for that same period. Then it sums these daily NPP measurements over 365 days, subtracts extra metabolic costs for yearly upkeep, and calculates an estimate of annual NPP [14,32,33]. NPP thus represents the total energy that is available in a given habitat per year beyond the vegetation's maintenance costs. While both primary biomass and net primary productivity are important, as Kelly notes [16], primary biomass overestimates the quality of forests for humans because they have a lower amount of human food per kilogram of plant biomass than other habitats. Because humans and many of their prey generally subsist on the reproductive parts of plants (i.e. fruits, leaves, and underground storage organs), primary production best represents habitat quality for humans. Therefore, here we use NPP.

Reliable worldwide estimates of NPP began to be produced in 2000 [14]. A recent comparison of MODIS data to estimates calculated from weather stations on the ground indicates that these estimates approximate daily GPP and NPP within a small margin of error across a wide variety of climates [32,33]. Knapp and Smith [17] found that in a given area, NPP can vary 20–30% from year to year. We used an average of five different years (2000–2004) to minimize the noise in our sample.

2.2. The sample

To compare the habitats of foragers and agriculturalists we used the Standard Cross-Cultural Sample (SCCS) [27]. The SCCS is a subset of societies represented in a larger dataset, the Ethnographic Atlas, which includes 1267 mostly traditional societies. The SCCS was created to avoid Galton's Problem in comparative analysis. It includes 186 societies with good ethnographic coverage, chosen to create an unbiased sample of the world's societies with respect to geographic region, language family, and cultural area, so that they represent independent data points.

Foragers were defined as those with less than 10% direct dependence on plant cultivation or animal husbandry, with trade accounting for less than 50% of the diet and less than any single food source. We also excluded horse-mounted hunters. We refer to all other societies here as agriculturalists, though they can be further divided into horticulturalists, pastoralists, and intensive agriculturalists (see Appendix A).

It is often assumed that habitats good for agriculture would also be good for foraging and vice versa. To the extent that is true, then both should be vying for the same habitats. However, some habitats that are poor for plant cultivation may be fine for foraging, or for some other type of agriculture such as pastoralism. Likewise, intensive agriculture may be practical in habitats where horticulture would be difficult. For these reasons, we look at NPP across the three different types of agriculture. The codes for all variables used are explained in Appendix A.

We also created a subsample, which we call the warm-climate subsample. This was defined as those societies where ET $\geq$ 13. This excludes most societies at latitudes higher than approximately 40–45 degrees north and south (see Fig. 1). This area is roughly co-terminus with that within which tubers, or underground storage organs are exploited and which has been occupied by earlier representatives of the genus *Homo* [28]. The warm-climate subsample is therefore more useful

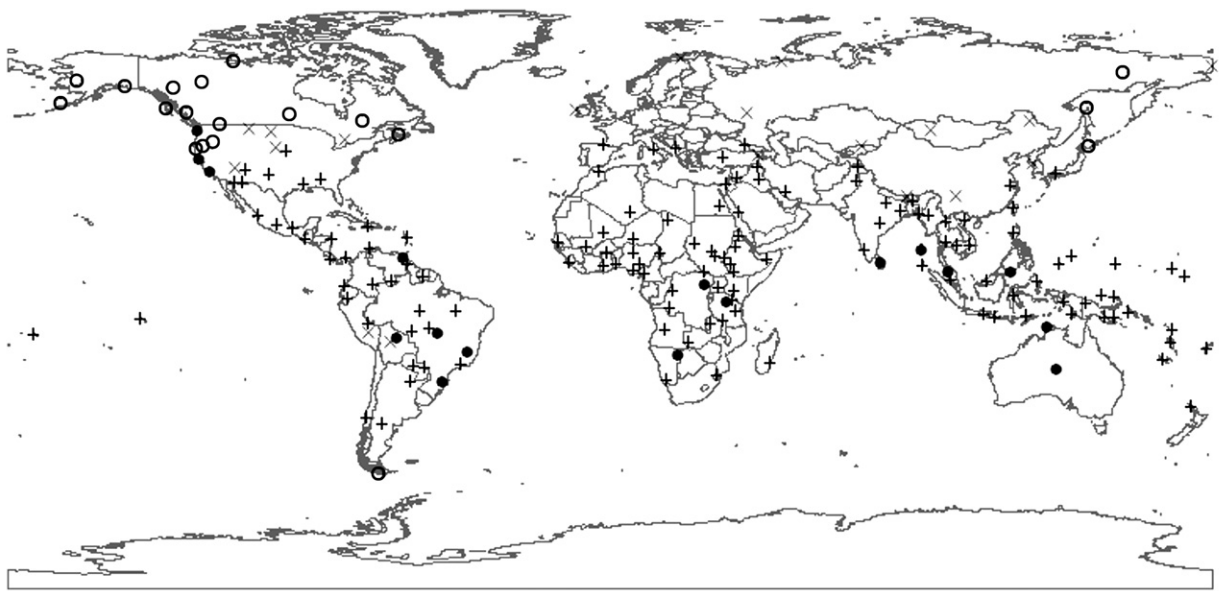

Fig. 1. Geographical location of SCCS: ●, warm-climate foragers; ○, cold-climate foragers; +, warm-climate agriculturalists; ×, cold-climate agriculturalists.

for evaluating habitats which human ancestors have occupied for longer periods. For that purpose, the ET $\geq$ 13 cutoff was used in previous analyses of all foragers vs. warm-climate foragers [21–23], and we chose to apply the same criteria here to be consistent.

The MODIS sensor has collected data on every landmass across the earth's surface at a resolution of one square kilometer. This resolution was reduced to 25 km by 25 km in order to approximate the region where a group lived. We used latitude and longitude coordinates in the SCCS to determine MODIS estimates of NPP except where those coordinates placed the group offshore. In those six cases the coordinates were changed to the nearest land value. Bilinear interpolation was further used to calculate an average NPP of each group's area.

3. Results

Table 1 shows the Standard Cross Cultural Sample and the habitat variables used in this analysis. The mean NPP of foragers is lower than that of agriculturalists (Table 2), but the difference is not statistically significant (Table 3 and Fig. 2a). In the warm-climate subsample the mean NPP of foragers is slightly higher than the mean of agriculturalists, but again the two are not significantly different (Tables 2 and 3 and Fig. 2b).

While NPP does not differ between foragers and agriculturalists, it does differ among the various types of agriculture. This is true whether we consider the total sample or just the warm-climate subsample (Fig. 3a,b). When agriculturalists are divided into the three categories of pastoralists, horticulturalists, and intensive agriculturalists, there are clear differences between them. Pastoralist habitats have the lowest NPP (341 g/m^2 per year) and horticulturalists have the highest (990 g/m^2 year). Intensive agriculturalists occupy intermediate habitats in terms of NPP (573 g/m^2 year). Differences between the three types of agriculture are similar in the warm-climate subsample and the total sample (Table 3). Note that foragers are widely distributed across the full range of NPP values because they are flexible, exploiting whatever niche exists in terms of naturally occurring foods across all latitudes, even the coldest habitats (Table 2 and Fig. 3a).

The MODIS data have been criticized for not being comparable to local measurements of above-ground plant productivity in certain biomes. Turner et al. [37] report that MODIS overestimates production in dry areas. The article also makes suggestions for altering the MODIS algorithm to compensate for the lack of agreement in certain zones. While mean annual precipitation (v189) is lower for foragers than agriculturalists the difference is not statistically significant in the whole sample (forager = 1097, $n = 36$, SD = 758; agriculturalist = 1356, $n = 141$, SD = 1063; $t = 1.68$, df = 74, $p = 0.098$, equal variances not assumed). The same is true of the warm-climate subsample, (forager = 1445, $n = 17$, SD = 797; agriculturalist = 1488, $n = 122$, SD = 108; $t = 0.156$, df = 137, $p = 0.876$, equal variances assumed). Therefore, the data avoid systematic bias because any overestimation of dry habitats will affect foragers and agriculturalists equally.

In addition, SCCS variables evaluating agricultural potentials (v921, v926, v928) all correlate strongly with NPP, suggesting that NPP is a good measurement of habitat quality. Although future analyses with a more precise measure than the current MODIS NPP might produce different results, we do not think they would substantially alter the overall conclusions.

4. Discussion and conclusion

Our results show that foragers do live in slightly (though not significantly) more marginal habitats than agriculturalists worldwide. However, this is due mainly to the large number

Table 1
List of SCCS societies and relevant variables

SCCS no.	Society name	Lat	Long	Subsistence	Mean annual precipitation (mm)	Mean temp. (°C) warmest month	Mean temp. (°C) coldest month	ET	NPP (g/m^2 per year)
1	Nama Hottentot*	−27.50	17.00	Pastoralism	133	27	13	16.18	204
2	Kung Bushmen*	−19.83	20.58	Foraging	470	25	15	16.67	472
3	Thonga*	−25.83	32.33	Horticulture	570	27	19	18.50	667
4	Lozi*	−16.00	23.50	Intensive agriculture	954	25	18	18.00	756
5	Mbundu*	−12.25	16.50	Horticulture	1354	19	17	17.20	1041
6	Suku*	−6.00	18.00	Horticulture					865
7	Bemba*	−10.50	30.50	Horticulture	1310	23	17	17.43	1039
8	Nyakyusa*	−9.50	34.00	Intensive agriculture	884	20	14	15.71	1106
9	Hadza*	−3.75	35.18	Foraging	1214	25	22	20.91	607
10	Luguru*	−6.83	37.67	Horticulture	1110	28	24	22.00	912
11	Kikuyu*	−0.67	37.17	Pastoralism	899	18	15	15.82	1150
12	Ganda*	0.33	32.50	Horticulture	1201	21	19	18.80	1341
13	Mbuti*	1.50	28.33	Foraging	1293	23	20	19.45	1445
14	Nkundo Mongo*	−0.75	19.17	Horticulture	2440	46	24	19.60	1570
15	Banen*	4.67	10.80	Horticulture	2172	22	19	18.73	1136
16	Tiv*	7.25	9.00	Horticulture	1377	30	24	21.43	624
17	lbo*	5.50	7.33	Horticulture	1231	29	25	22.67	718
18	Fon*	7.20	1.91	Horticulture	859	28	24	22.00	698
19	Ashanti*	7.00	−1.50	Horticulture	1481	27	23	21.33	931
20	Mende*	7.83	−12.00	Horticulture	2354	26	23	21.64	702
21	Wolof	13.75	−15.33	Horticulture	516	26	20	19.14	420
22	Bambara*	12.50	−7.00	Intensive agriculture	1053	31	25	22.00	312
23	Tallensi*	10.66	−0.57	Intensive agriculture					432
24	Songhai*	16.58	−1.67	Intensive agriculture	285	34	21	19.14	44
25	Pastoral Fulani*	15.00	7.50	Pastoralism	770	31	21	19.33	104
26	Hausa*	10.50	7.50	Intensive agriculture	1297	28	23	21.08	546
27	Massa (Masa)*	10.50	15.50	Intensive agriculture	850	33	26	22.27	332
28	Azande*	5.08	28.25	Horticulture	1467	26	22	20.67	831
29	Fur (Darfur)*	13.50	25.50	Intensive agriculture	817	30	21	19.41	116
30	Otoro Nuba*	11.33	30.67	Intensive agriculture	743	30	25	22.31	465
31	Shilluk*	9.75	31.50	Horticulture	817	29	25	22.67	559
32	Mao*	9.27	34.67	Horticulture	1241	30	26	23.33	1102
33	Kaffa (Kafa)*	7.27	36.50	Intensive agriculture	1241	30	25	22.31	1465
34	Masai*	−3.50	36.75	Pastoralism	677	18	8	13.56	878
35	Konso*	5.25	37.50	Intensive agriculture	1241	30	26	23.33	656
36	Somali*	9.00	47.25	Pastoralism	119	25	20	19.23	184
37	Amhara*	12.50	37.75	Intensive agriculture	894	30	23	20.67	840
38	Bogo*	15.75	38.75	Pastoralism	474	24	18	18.00	312
39	Kenuzi Nubians*	23.00	38.75	Intensive agriculture	3	33	15	17.08	27
40	Teda*	20.50	17.50	Pastoralism	14	35	20	18.70	0
41	Tuareg*	23.00	6.50	Pastoralism	45	29	12	16.08	0
42	Riffians*	34.92	−3.25	Intensive agriculture	389	24	12	15.60	222
43	Egyptians*	24.75	33.00	Intensive agriculture	1	32	13	16.52	196
44	Hebrews*	31.18	34.92	Intensive agriculture	551	26	13	16.10	147
45	Babylonians*	32.58	44.75	Intensive agriculture	107	33	10	15.94	159
46	Rwala Bedouin*	33.25	38.50	Pastoralism	203	27	9	15.23	68
47	Turks*	39.33	34.25	Intensive agriculture	434	24	2	13.73	238
48	Gheg Albanians*	42.00	20.17	Intensive agriculture	1450	24	5	14.15	443
49	Romans*	41.67	13.50	Intensive agriculture	712	23	17	17.43	503
50	Basques*	43.25	−1.67	Intensive agriculture	708	20	5	13.48	590
51	Irish	53.50	−10.00	Intensive agriculture	886	14	5	11.88	672
52	Lapps	68.70	21.50	Pastoralism	467	12	−13	10.48	111
53	Yurak Samoyed	68.00	51.50	Pastoralism	214	11	−24	10.19	77
54	Russians	52.67	41.33	Intensive agriculture	703	15	−20	10.93	256
55	Abkhaz	43.13	40.77	Pastoralism					740
56	Armenians	40.00	44.50	Intensive agriculture	513	19	−8	12.06	288
57	Kurd*	36.50	44.50	Intensive agriculture	56	34	11	16.19	172
58	Basseri*	29.00	53.00	Pastoralism	26	24	9	14.87	69
59	Punjabi (West)*	32.50	74.00	Intensive agriculture	307	33	12	16.34	399
60	Gond*	19.63	80.92	Horticulture	1253	34	20	18.73	453
61	Toda*	11.50	76.50	Pastoralism	791	26	21	19.85	1102
62	Santal*	23.50	87.17	Intensive agriculture	1466	30	16	17.27	419

Table 1 (*continued*)

SCCS no.	Society name	Lat	Long	Subsistence	Mean annual precipitation (mm)	Mean temp. (°C) warmest month	Mean temp. (°C) coldest month	ET	NPP (g/m^2 per year)
63	Uttar Pradesh*	25.92	83.00	Intensive agriculture	1040	32	15	17.04	428
64	Burusho*	36.43	74.58	Intensive agriculture	3452	28	9	15.33	90
65	Kazak	42.50	75.50	Pastoralism	107	25	−10	12.79	209
66	Khalka Mongols	47.17	96.08	Pastoralism	337	15	−28	10.78	127
67	Lolo	27.50	103.50	Intensive agriculture	736	12	−8	10.57	484
68	Lepcha	27.50	89.00	Intensive agriculture	364	28	−18	12.67	883
69	Garo*	26.00	91.00	Horticulture	1615	28	17	17.58	819
70	Lakher*	22.33	93.00	Horticulture	2720	25	19	18.57	974
71	Burmese*	22.00	95.67	Intensive agriculture	886	30	20	18.89	411
72	Lamet*	20.00	100.67	Horticulture	1542	22	13	15.65	1106
73	Vietnamese*	20.50	106.25	Intensive agriculture	2539	28	19	18.47	598
74	Rhade*	13.00	108.00	Horticulture	1350	28	24	22.00	1081
75	Khmer*	13.00	103.83	Intensive agriculture					648
76	Siamese*	14.00	100.85	Intensive agriculture	1222	29	13	16.33	657
77	Semang*	5.00	101.25	Foraging	2644	18	17	17.11	1334
78	Nicobarese*	7.00	93.75	Horticulture	2509	28	26	24.40	1545
79	Andamanese*	11.75	93.08	Foraging	3131	27	25	23.60	1545
80	Vedda*	7.75	81.25	Foraging	1641	29	25	22.67	741
81	Tanala*	−22.00	48.00	Intensive agriculture	435	27	21	19.71	1199
82	Negri Sembilan*	2.58	102.25	Intensive agriculture	1313	25	18	18.00	986
83	Javanese*	−7.70	112.22	Intensive agriculture	2889	26	23	21.64	865
84	Balinese*	−8.50	115.33	Intensive agriculture	1930	27	25	23.60	1723
85	Iban*	2.00	113.00	Horticulture	3968	27	26	25.11	1074
86	Badjau*	5.00	120.00	Foraging	2002	27	26	25.11	1727
87	Toradja*	−2.00	121.00	Horticulture	2844	26	25	24.22	1051
88	Tobelorese*	2.00	128.00	Horticulture	3576	27	26	25.11	1592
89	Alorese*	−8.33	124.67	Horticulture	818	28	26	24.40	1380
90	Tiwi*	−11.38	131.00	Foraging	1538	29	25	22.67	1307
91	Aranda*	−24.25	133.50	Foraging	275	28	12	16.00	189
92	Orokaiva*	−8.50	148.00	Horticulture	1015	27	24	22.36	1374
93	Kimam*	−7.50	138.50	Intensive agriculture	2097	30	23	20.67	941
94	Kapauku*	−4.00	136.00	Horticulture	2491	26	25	24.22	1108
95	Kwoma*	−4.17	142.67	Horticulture	2482	27	27	27.00	946
96	Manus*	−2.17	147.17	Horticulture	3912	28	27	26.00	1520
97	New Ireland*	−2.50	151.00	Horticulture	2281	29	27	25.20	1552
98	Trobrianders*	−8.64	151.01	Horticulture	3907	28	26	24.40	1382
99	Siuai*	−7.00	155.33	Horticulture	3035	28	27	26.00	1283
100	Tikopia*	−12.50	168.50	Horticulture		27	23	21.33	338
101	Pentecost*	−16.00	168.00	Horticulture		27	23	21.33	1405
102	Mbau Fijians*	−18.00	178.58	Horticulture					1392
103	Ajie*	−21.33	165.67	Intensive agriculture	1064	26	21	19.85	1092
104	Maori*	−35.33	174.17	Horticulture	1607	18	10	14.00	1482
105	Marquesans*	−8.92	−140.17	Horticulture	1412	28	27	26.00	1062
106	Western Samoans*	−13.75	−172.00	Horticulture	4819	23	21	20.40	1204
107	Gilbertese*	3.50	172.33	Horticulture	2238	28	28	28.00	295
108	Marshallese*	6.00	168.50	Horticulture	4000	28	27	26.00	1293
109	Trukese*	7.40	151.67	Horticulture	3351	28	27	26.00	1527
110	Yapese*	9.50	138.17	Horticulture	3103	28	27	26.00	1685
111	Palauans*	7.50	134.50	Horticulture		28	27	26.00	1613
112	Ifugao*	16.83	121.17	Intensive agriculture	1995	29	25	22.67	868
113	Atayal*	24.33	120.75	Horticulture	2200	27	17	17.56	895
114	Chinese	31.00	120.08	Intensive agriculture					537
115	Manchu	50.00	125.50	Intensive agriculture	707	24	−17	12.29	357
116	Koreans	37.60	126.42	Intensive agriculture	288	14	−19	10.78	399
117	Japanese*	34.67	133.67	Intensive agriculture	1600	25	4	14.14	634
118	Ainu	42.83	143.00	Foraging	845	19	−5	12.25	496
119	Gilyak	54.00	142.50	Foraging	325	14	−16	10.84	299
120	Yukaghir	64.75	153.50	Foraging	151	8	−28	9.64	179
121	Chukchee	66.50	180.00	Pastoralism	163	11	−23	10.19	78
122	Ingalik	62.50	−159.50	Foraging	388	12	−22	10.38	200
123	Aleut	55.25	−164.00	Foraging	388	12	−22	10.38	364
124	Copper Eskimo	68.00	−112.50	Foraging	182	4	−27	8.77	85

(*continued on next page*)

Table 1 (*continued*)

SCCS no.	Society name	Lat	Long	Subsistence	Mean annual precipitation (mm)	Mean temp. (°C) warmest month	Mean temp. (°C) coldest month	ET	NPP (g/m^2 per year)
125	Montagnais	50.00	−74.00	Foraging	874	19	−14	11.76	344
126	Micmac	46.00	−63.00	Foraging	928	22	−8	12.53	378
127	Saulteaux	52.00	−95.50	Foraging	490	18	−20	11.39	591
128	Slave	62.00	−122.00	Foraging	414	14	−21	10.74	483
129	Kaska	60.00	−131.00	Foraging	424	14	−21	10.74	214
130	Eyak	60.50	−145.00	Foraging	1752	13	−4	10.96	202
131	Haida	54.00	−132.50	Foraging	2360	14	−3	11.28	516
132	Bellacoola	52.33	−126.50	Foraging	1518	16	−2	11.85	217
133	Twana*	47.43	−123.25	Foraging	864	18	5	13.05	726
134	Yurok	41.50	−124.00	Foraging	1110	15	9	12.86	907
135	Pomo (Eastern)*	39.00	−123.00	Foraging	1171	21	8	14.19	847
136	Yokuts (Lake)*	35.00	−119.50	Foraging	231	26	8	14.92	452
137	Paiute (North)	43.50	−119.00	Foraging	366	21	−4	12.67	226
138	Klamath	42.63	−121.67	Foraging	1072	15	−2	11.60	449
139	Kutenai	49.00	−116.67	Foraging	722	19	−4	12.32	333
140	Gros Ventre	48.00	−108.00	Pastoralism	340	18	−10	11.78	285
141	Hidatsa	47.00	−101.00	Intensive agriculture	391	22	−9	12.46	300
142	Pawnee	42.00	−100.00	Horticulture	468	22	−5	12.74	332
143	Omaha*	41.43	−96.50	Horticulture	704	24	−4	13.11	388
144	Huron	44.50	−79.00	Horticulture	782	21	−4	12.67	301
145	Creek*	32.93	−86.00	Horticulture	1269	26	7	14.74	503
146	Natchez*	31.50	−91.42	Horticulture	1417	28	11	15.76	577
147	Comanche*	34.00	−101.50	Pastoralism	622	26	7	14.74	320
148	Chiricahua*	32.00	−109.50	Pastoralism	382	25	8	14.80	280
149	Zuni*	35.67	−108.75	Intensive agriculture	234	23	0	13.35	200
150	Havasupai	35.83	−112.17	Intensive agriculture	556	19	0	12.67	195
151	Papago*	32.00	−112.00	Intensive agriculture	364	30	11	15.93	146
152	Huichol*	22.00	−105.00	Horticulture	365	16	9	13.20	696
153	Aztec*	19.00	−99.17	Intensive agriculture	868	21	16	16.77	1193
154	Popoluca*	18.25	−94.83	Horticulture	3085	28	23	21.08	724
155	Quiche*	15.00	−91.00	Horticulture	765	25	20	19.23	1299
156	Miskito*	15.00	−83.00	Horticulture	3293	27	25	23.60	1217
157	Bribri*	9.00	−83.25	Horticulture	3047	24	22	21.20	847
158	Cuna (Tule)*	9.25	−78.50	Horticulture	3305	28	27	26.00	713
159	Goajiro*	11.92	−71.75	Pastoralism	456	30	28	26.00	542
160	Haitians*	18.83	−72.17	Intensive agriculture	1242	29	25	22.67	812
161	Callinago*	15.50	−60.50	Intensive agriculture	1678	27	24	22.36	1821
162	Warrau*	9.08	−62.00	Foraging	2441	16	14	14.80	908
163	Yanomamo*	2.42	−65.00	Horticulture	3148	25	26	27.14	1118
164	Carib (Barama)*	7.42	−60.17	Horticulture	1486	29	27	25.20	966
165	Saramacca*	3.50	−55.75	Horticulture	2180	29	27	25.20	1032
166	Mundurucu*	−6.50	−56.50	Horticulture	2770	26	24	22.80	1231
167	Cubeo (Tucano)*	1.25	−70.50	Horticulture	3148	25	26	27.14	1055
168	Cayapa*	1.00	−79.00	Horticulture	3148	25	26	27.14	1049
169	Jivaro*	−3.00	−78.00	Horticulture	2623	27	24	22.36	1541
170	Amahuaca*	−10.33	−72.25	Horticulture	1880	25	22	20.91	959
171	Inca	−13.50	−72.00	Intensive agriculture	804	12	9	11.45	485
172	Aymara	−16.00	−65.75	Horticulture	963	10	5	10.00	1131
173	Siriono*	−14.50	−63.50	Foraging	1141	24	20	19.33	459
174	Nambicuara*	−13.00	−58.75	Horticulture	1388	28	23	21.08	821
175	Trumai*	−11.83	−53.67	Horticulture	1411	27	23	21.33	584
176	Timbira*	−6.50	−46.00	Horticulture	940	27	24	22.36	498
177	Tupinamba*	−22.79	−44.50	Horticulture	1653	28	26	24.40	942
178	Botocudo*	−19.00	−42.50	Foraging	1291	22	18	18.00	790
179	Shavante*	−13.50	−51.50	Foraging	1411	27	23	21.33	340
180	Aweikoma*	−28.00	−50.00	Foraging	1806	20	10	14.44	1060
181	Cayua*	−23.50	−55.00	Horticulture	1325	25	18	18.00	611
182	Lengua*	−23.00	−58.50	Horticulture	1205	29	20	18.94	579
183	Abipon*	−28.00	−59.50	Pastoralism	1175	26	14	16.40	715
184	Mapuche*	−38.50	−72.58	Intensive agriculture	162	23	5	14.00	765
185	Tehuelche*	−40.50	−68.00	Pastoralism	135	27	4	14.39	287
186	Yahgan	−55.50	−69.50	Foraging	622	9	2	9.47	178

Asterisk indicates warm-climate subsample.

Table 2
Descriptive statistics for all subsistence categories and subcategories using both the entire SCCS sample and the warm-climate subsample

Category	Subcategory	Mean NPP	Median NPP	*N*	SD	Min	Max
Entire SCCS sample							
Forager		600	466	36	431	85	1727
All Agriculture		737	700	150	455	0	1821
	Pastoralism	341	209	23	344	0	1150
	Horticulture	990	1035	72	371	295	1685
	Intensive agriculture	573	484	55	404	27	1821
Total		711	652	186	453	0	1921
Warm-climate subsample							
Forager		879	790	17	456	189	1730
All Agriculture		793	812	129	455	0	1821
	Pastoralism	388	283	16	379	0	1150
	Horticulture	1008	1039	69	360	295	1685
	Intensive agriculture	606	525	44	454	27	1821
Total		804	801	146	454	0	1821

All results are in units of g/m^2 per year.

of foragers who live far north of the equator in quite cold habitats where agriculture is not feasible, especially in North America. When we limit our analysis to the warm-climate subsample, foragers have a slightly higher habitat quality than agriculturalists, but there is again no significant difference. Our warm-climate subsample includes not only the tropics but also temperate climates at latitudes up to about 40–45°. This encompasses the areas that have been occupied by human ancestors throughout hominin evolution, while the areas to the north and south of our warm-climate subsample have only been occupied mostly in the past 5–20,000 years, though some archaic sapiens and even perhaps some *Homo erectus* populations occupied habitats that were quite cold and even further north than 45° [30].

The same logic that suggests foragers should occupy more marginal habitats than agriculturalists also suggests horticulturalists and pastoralists should occupy more marginal habitats than intensive agriculturalists. It is intensive agriculturalists who have the largest populations and became the most politically dominant once state-level organization was achieved. As our results show, however, horticulturalists occupy more productive habitats, and pastoralists occupy less productive habitats than intensive agriculturalists. Different sorts of subsistence occur in different types of habitats. Intensive agriculture often occurs where irrigation is necessary. Horticulture does not, since by definition, horticulture precludes irrigation. Pastoralists can do well in habitats with low NPP because large ungulates do well in grasslands. We cannot automatically assume that habitats that are good for one type of subsistence are good for all types. Foragers do well in habitats that are poor for plant cultivation since they may eat underground tubers and game animals that do well in such habitats. Because foragers may get much of their food from the ocean or rivers or by hunting large game in cold climates, or small game in deserts, they occupy a very wide range of habitats, which produces a wide range of technology, behavior, and social organization [21].

NPP is a crude estimate of actual human food abundance. A better measure would include secondary (animal) biomass as well. Most animals consumed by humans, however, subsist

Table 3
Results of independent samples *t*-tests on each pair of forager and agriculturalist subcategories

		Foraging		Pastoralism		Horticulture	
		All	Warm	All	Warm	All	Warm
All agriculture	*t*	1.64	−0.73				
	df	184	144				
	p	0.102	0.468				
Pastoralism	*t*	2.43*	3.35**				
	df	57	31				
	p	0.018	0.002				
Horticulture	*t*	−4.88***	−1.25	−7.44***	−6.14***		
	df	106	84	93	83		
	p	<0.0005	0.215	<0.0005	<0.0005		
Intensive agriculture	*t*	0.60	2.17*	−2.41*	−1.77	6.04***	5.32***
	df	89	59	76	58	125	111
	p	0.761	0.034	0.18	0.083	<0.0005	<0.0005

'All' refers to the entire SCCS sample and 'Warm' to the warm-climate subsample. All tests assume equal variance. Asterisks denote significance levels.

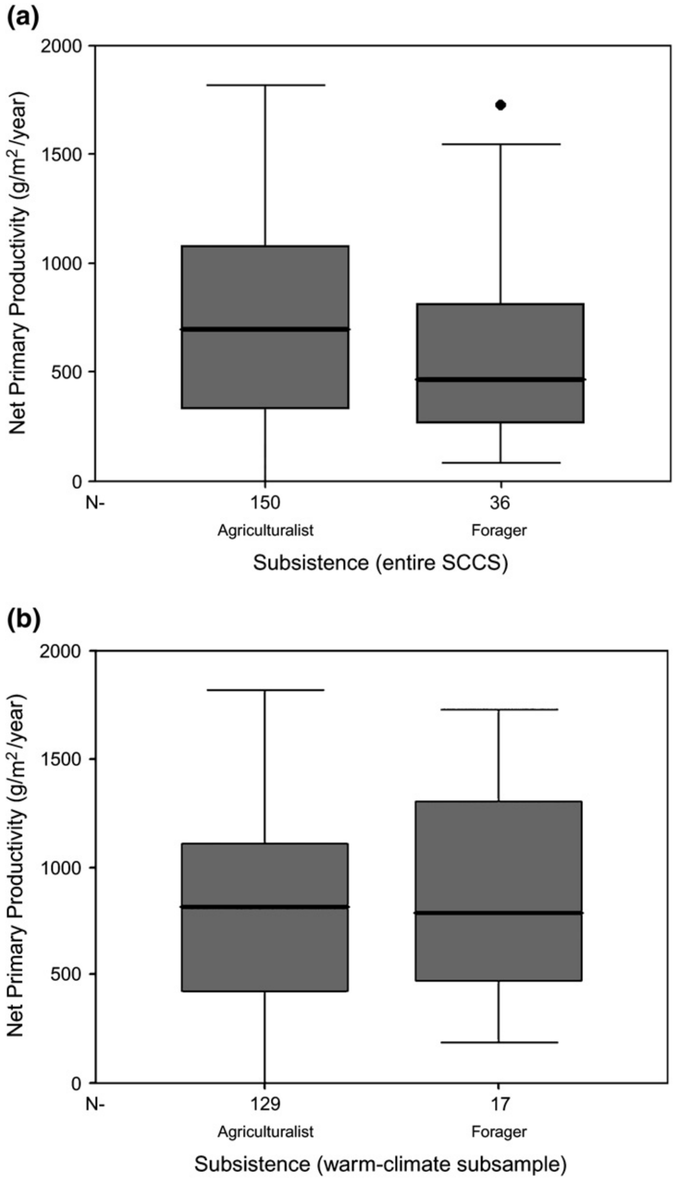

Fig. 2. (a) Net primary production (NPP) of habitats for foragers and agriculturalists using the entire SCCS sample. Box boundaries show quartiles, bold lines within indicate median, and whiskers indicate range excluding outliers. (b) Net primary production (NPP) of habitats for foragers and agriculturalists using the warm-climate subsample. Box boundaries show quartiles, bold lines within indicate median, and whiskers indicate range excluding outliers.

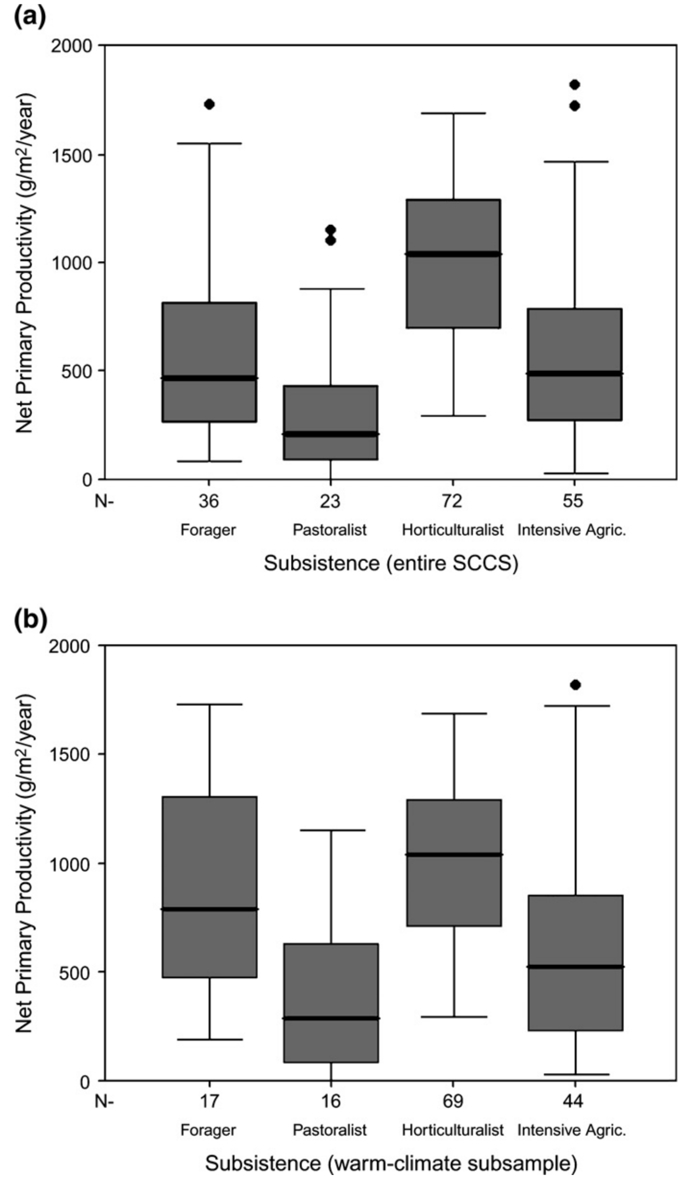

Fig. 3. (a) Net primary production (NPP) of habitats for all subsistence strategies using the entire SCCS sample: foragers and the subcategories of agriculturalists. Box boundaries show quartiles, bold lines within indicate median, and whiskers indicate range excluding outliers. (b) Net primary production (NPP) of habitats for all subsistence strategies using the warm-climate subsample: foragers and the subcategories of agriculturalists. Box boundaries show quartiles, bold lines within indicate median, and whiskers indicate range excluding outliers.

on plants, thus secondary biomass should be related to primary production, and indeed, Binford [9] found a strong correlation between them. It is not clear whether secondary biomass should vary with respect to agricultural versus forager habitats but omitting animal biomass only results in an underestimate of forager habitat productivity. The habitats of arctic terrestrial and marine mammal hunters have little to no plant biomass, so including secondary biomass would increase our measure of their habitat quality. Semi-arid grasslands are also known for their abundant large game (e.g., Serengeti plains), so some areas of low plant production can support high animal biomass. This probably means we have underestimated the mean habitat quality for foragers, and pastoralists as well. In sum, it seems that more refined measures of habitat quality would likely increase estimates of the habitat quality of foragers.

There are a few other limitations to our analyses. First, the MODIS data are from 2000–2004 and not from the time period during which the ethnographic data were collected. Primary production is partially calculated using estimates of leaf area in present day vegetation, and the land use practices in the region may have changed dramatically from when the ethnographies were conducted. It does not seem this would introduce any systematic bias since land use changes could effect both foragers and agriculturalists; some forager habitats may have been cleared of forest, some agricultural habitats may have been paved, and both may have experienced increases in the amount of cultivation. Second, we used the precise latitude and longitude given in the SCCS at the center of each society's area (except for those few found to be in error). A better method would be to use the average NPP of the whole area occupied by each ethno-linguistic group. That method would require more precise data on the locations and size of area occupied by each society than is given. Third, the SCCS sample is small. Future analyses should calculate NPP for all the societies in the Ethnographic Atlas and then control for phylogeny using a language tree. The larger sample could provide a more nuanced analysis of habitat differences across subsistence types and within the forager category.

Our results do not imply that ethnographic foragers are unproblematic analogs of earlier foragers. There are several reasons why they may be a skewed sample from which to draw inferences about the means and ranges of certain trait values during earlier times. These include the climate and faunal changes that occurred at the beginning of the Holocene. Foley [12] has proposed that these changes created two new niches that had not existed before, one niche being agriculture, and the other being the ethnographic foragers. Contact with agriculturalists could have altered ethnographic foragers in important ways. For example, foragers may have been pacified by their more powerful neighbors or simply acculturated via trading relations [6,19,38]. Some researchers contend that certain contemporary foragers exist, not in spite of, but because of their contacts with, and trading dependence on, agriculturalist neighbors [5,13]. However, since some foragers have been in contact with agricultural populations for thousands of years; others less than 100 years, the influence of contact is highly variable. Despite the importance of dramatic climate change that occurred at the Pleistocene-Holocene boundary, the most important difference between ethnographic foragers and the ancestral population that lived in Africa around 200,000 years ago, must surely be the more complex technology of ethnographic foragers. For example, societies like the Northwest Coast anadromous fishers built weirs across rivers and smoke houses to store salmon just within the past 5000 years [2,34]. The bow, which is so widespread among ethnographic foragers, was only adopted very recently by many foragers, and even among those who have used it the longest it may not be of great antiquity, but nonetheless could have had revolutionary significance [18,21,29].

There are many reasons why ethnographic foragers may be of limited use in understanding Pleistocene foragers, but our results suggest that living in more marginal habitats is not a reason that need concern us, at least not to the extent often assumed and not when we focus on warmer climates. Considering that modern humans, and many earlier hominin species, appear to have evolved in Eastern Africa, somewhere between Egypt and South Africa, where the mean NPP across all societies (foragers and agriculturalists) that occupy this area in the SCCS is 775 g/m^2 per year, it is likely that most of our ancestors have evolved in an environment characterized by primary production levels close to those that characterize foraging societies in the warm-climate subsample (877 g/m^2 per year). The warm-climate foragers in the ethnographic record appear to be a better sample for drawing socio-ecological inferences about earlier foragers than many skeptics have assumed.

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A. Appendix A

A.1. Warm climate subsample

Effective temperature (ET) $= (18 \times W - 10 \times C)/(W - C + 8)$ where W is the mean temperature (°C) of the warmest month, and C is the mean temperature (°C) of the coldest month. Societies with an ET > 13 were included in the subsample. If no temperature data were recorded for a society, we used approximate temperatures from weather stations near the coordinates to determine whether or not to include the society in the subsample. Two societies could not be definitively classified (the Chinese and the Abkhaz) and were by default left out of the warm-climate subsample.

A.2. Subsistence classification

Foragers were classified as societies where contribution to local food supply is characterized by $<$10% agriculture (v3 $<$ 4), $<$10% animal husbandry (v5 $<$ 4), trade accounting for $<$50% and no more than any single local source (v1 $<$ 6) We also excluded the equestrian hunters (v858 $\neq$ 5 [Mounted Hunting]). All other societies were considered to use some form of domestication, and classified as agriculturalists. The category of agriculturalists was further divided into three subcategories: those using pastoralism and mounted hunting (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 those foragers that rely on trade for $>$50% of their subsistence [v1 $\geq$ 4]), and intensive agriculture (v858 = 11 [Intensive Agriculture with no plow] or 12 [Intensive Agriculture with plow]).

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