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RESEARCH ARTICLE

Human appropriated net primary productivity as a metric for land use planning: a case study in the US Great Lakes region

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Abstract
Context Human appropriation of net primary productivity (HANPP) is employed as a measure of human pressures on biodiversity, though largely at global and national scales rather than landscape to regional scales where many conservation decisions take place. Though gaining in familiarity, HANPP is not widely utilized by conservation professionals.
Objectives This study, encompassing the US side of the Great Lakes basin, examines how regional distributions of HANPP relate to landscape-based biodiversity proxy metrics used by conservation professionals. Our objectives were (1) to quantify the HANPP of managed lands at the county scale; and (2) to assess spatial patterns of HANPP in comparison to landscape diversity and local habitat connectedness to determine if the metric can provide useful information to conservation professionals.
Methods We aggregated forest and cropland NPP data between 2005 and 2015 and coupled it with previously published potential vegetation maps to quantify the HANPP of each county in the study region. We mapped the outputs at 500 m resolution to analyze spatial relationships between HANPP and landscape metrics of biodiversity potential.
Results Area-weighted HANPP across our study region averaged 45% of NPP, down to 4.9% in forest-dominated counties. Greater HANPP correlated with reduced landscape diversity ($p < 0.001$, $r^2 = 0.28$) and reduced local habitat connectedness ($p < 0.001$, $r^2 = 0.36$).
Conclusion HANPP could be used as an additional tool for conservation professionals during regional-scale land use planning or conservation decision-making, particularly in mixed-use landscapes that both support important biodiversity and have high levels of primary production harvest.

Keywords Landscape · Land use/land cover · Cropland · Forest · HANPP · Human appropriated net primary productivity · Great lakes · Biodiversity

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Introduction

Humans have become the dominant influence on Earth's systems, modifying land cover and habitat, altering the global climate, and driving global biodiversity loss (Vitousek et al. 1997; Pimm and Raven 2000; DeFries et al. 2004). To accommodate the resource needs of the growing human population while also accommodating the resource needs of other species, conservation decision-makers need a deeper understanding of the effects of human activities on ecological conditions for other species. Many studies address the effects of land use on habitat quality, but fewer address the question of how human activities impact ecosystem energy dynamics.

Human appropriation of net primary productivity (HANPP) is a measure of human pressures on biodiversity (Haberl et al. 2004, 2009, 2012, 2014) because it represents the proportion of energy flow that was historically available to terrestrial food webs but has been appropriated for human use, primarily through the harvesting of primary production. As a global average, approximately 29% of aboveground potential natural NPP (NPP_0, defined below) was human appropriated in the year 2000 (Haberl et al. 2007). As human populations and needs continue to grow, there is considerable potential for human alteration of ecosystem energy dynamics to impact species. This is particularly true in cropland-dominated landscapes, which are responsible for ca. 50% of global HANPP and appropriate up to 85% of NPP_0 (Haberl et al. 2014). Calculating spatial patterns of HANPP across differing socioecological landscapes, such as those that support various cropping and forestry systems, could improve our understanding of interactions in human–environment systems at the landscape to regional scale.

In the present study, we strive to understand the relationship of HANPP to selected conservation metrics and land uses and to analyze patterns of HANPP across a region of conservation interest: a portion of the Great Lakes region of the Upper Midwest, USA (see below). Identifying "high conservation value regions" is of key interest to conservation professionals. Anderson et al. (2018) mapped climate resilient sites in the Great Lakes and Tallgrass Prairie regions at a 30 m resolution. The authors defined site resilience as "the capacity of a site to maintain biological diversity, productivity and ecological function as the climate changes" (Anderson et al. 2018). Sites that score higher on the site resilience index are more likely to retain biodiversity by providing more diverse and locally connected habitats. Site resilience is a relatively new and important parameter to consider in assessing conservation value. The site resilience index used by Anderson et al. (2018) integrated two variables—landscape diversity and local connectedness (each described below) —and used both as abiotic proxies for biodiversity. We obtained their spatial results and used these data in our analysis (hereafter we refer to these two proxies as "biodiversity metrics").

Ecosystem energy and HANPP in relation to biodiversity

NPP and HANPP are typically quantified in terms of biomass dry weight, but conceptually they represent flows of energy (Currie 2012; Haberl et al. 2014). The flow of energy in ecosystem food webs has been identified as a causal factor controlling species richness (the "species-energy hypothesis"; Wright 1983; Mittelbach et al. 2001; Hawkins et al. 2003). Previous studies have found an overall negative relationship between HANPP and biodiversity (Haberl et al. 2004, 2009, 2012; Vačkář et al. 2016). Our study is guided by the question of whether spatial variability in the amount of primary-producer energy that remains available to ecological food webs after human extraction of NPP may help to explain spatial patterns of biodiversity at landscape to regional scales.

Abiotic metrics as proxies for biodiversity

Ecosystem parameters for which data are widely available can be useful proxies for biodiversity because comprehensive spatial data on biodiversity and species richness are often unavailable at regional scales. Few studies have directly examined the relationship between HANPP and species richness for this reason (Haberl et al. 2014). Our study sought to develop and assess HANPP as an additional biodiversity metric for conservation professionals by comparing the spatial distributions of established biodiversity metrics and HANPP across our study region (see below).

Anderson and Ferree (2010) provided evidence that regional biodiversity correlates strongly with geophysical settings, including the number of geological classes, latitude, elevation range, dominant vegetation, and the amount of calcareous bedrock. Multiple studies have noted that different forest types and vegetation occur on different soil and topographic types (Host et al. 1987; Abrams 1992), and several case studies have used this "geodiversity" as a proxy for biodiversity (Anderson et al. 2015). Landscape diversity builds on the concept of geodiversity and was defined by Anderson et al. (2018) as an estimate of "the number of microclimates available within a given area. It is measured by counting the variety of landforms, and the density and connectivity of wetlands." Based on this definition, which envisions the variable as based on geophysical factors, we conceptualize landscape diversity as an independent spatial variable that may in part determine patterns of HANPP. Additionally, a number of studies have used landscape diversity or related measures as an indicator of regional capacity to support biodiversity (Lapin and Barnes 1995; Anderson and Ferree 2010; Stein et al. 2014; Lawler et al. 2015; Anderson et al. 2016, 2018).

Unlike landscape diversity, connectedness is a landscape variable driven by socioecological processes and human land-use (Lawler et al. 2015). The degree to which landscape features such as roads, deforestation, and urban and suburban build-up retard the movements and migrations of wildlife is captured in the concept of local connectedness, defined by Anderson et al. (2018) as "the number of barriers and the degree of fragmentation within the same area." It is assumed that pre-European settlement landscapes would have 100% local connectedness, as a lack of barriers and fragmentation would create the lowest value of resistance to species movement. As local connectedness may be affected by changes in land use and land cover (LU/LC) overtime, we conceptualized it as a dependent variable in relation to HANPP.

Study objectives

Here we examine the spatial relationship between established biodiversity metrics and the HANPP of the dominant terrestrial land uses over a range of intensities, i.e. forestlands and croplands, across our study region. Our purpose is to improve the understanding of these landscape to regional-scale metrics for use in decision-making for biodiversity conservation. Our first objective was to quantify spatial patterns of HANPP in forestland and cropland. Our second objective was to assess the spatial patterns of HANPP in comparison to spatial patterns of landscape diversity and local connectedness (as provided by Anderson et al. 2018) at the county scale across the region. Together, these two objectives both expand the body of research on distributions of HANPP to include a new region with interesting landscape patterns and begin to develop HANPP as a working metric for wildlife conservation.

Methods

Study Region—The U.S. Great Lakes Socioecological Gradient

Our study focuses on part of the Great Lakes region of the Upper Midwest, USA. The area that we consider (Fig. 1) includes most of the US side of the hydrologic basin of the Laurentian Great Lakes, including all of Michigan and portions of Wisconsin, Ohio, and Indiana. Two ecoregional provinces dominate this area: the Laurentian Mixed Forest (hereafter LMF) province in the north and the Eastern Broadleaf Forest (Continental) (hereafter EBFC) province in the south, with a few counties falling within the Prairie Parkland (Temperate) province and the Eastern Broadleaf Forest (Oceanic) province (Bailey 1994).

The extreme heterogeneity in land uses and landcover (LU/LC) make this location ideal for the study of socioecological system dynamics at landscape to regional scales. Crop production is one of the most important economic drivers in the region, bringing in more than $15 billion annually to the states of Michigan, Wisconsin, and Minnesota (Sousounis and Bisanz 2000). The southernmost portions of our study region comprise the northern edge of the US corn belt wherein field crops like corn and soybeans dominate, while in the mid-latitude and northern areas of our region, crops trend more toward vegetables, fruits, and hay (Sousounis and Bisanz 2000; Han et al. 2012). The northernmost areas of the study region are heavily forested with mixed coniferous and hardwood forests, shifting to boreal ecotones in Michigan's Upper Peninsula (Bogue 2000). In these areas there is farming, particularly hay (Han et al. 2012), but cropland is eclipsed by forestland. Across Michigan, the forest products industry is worth $20 billion, is

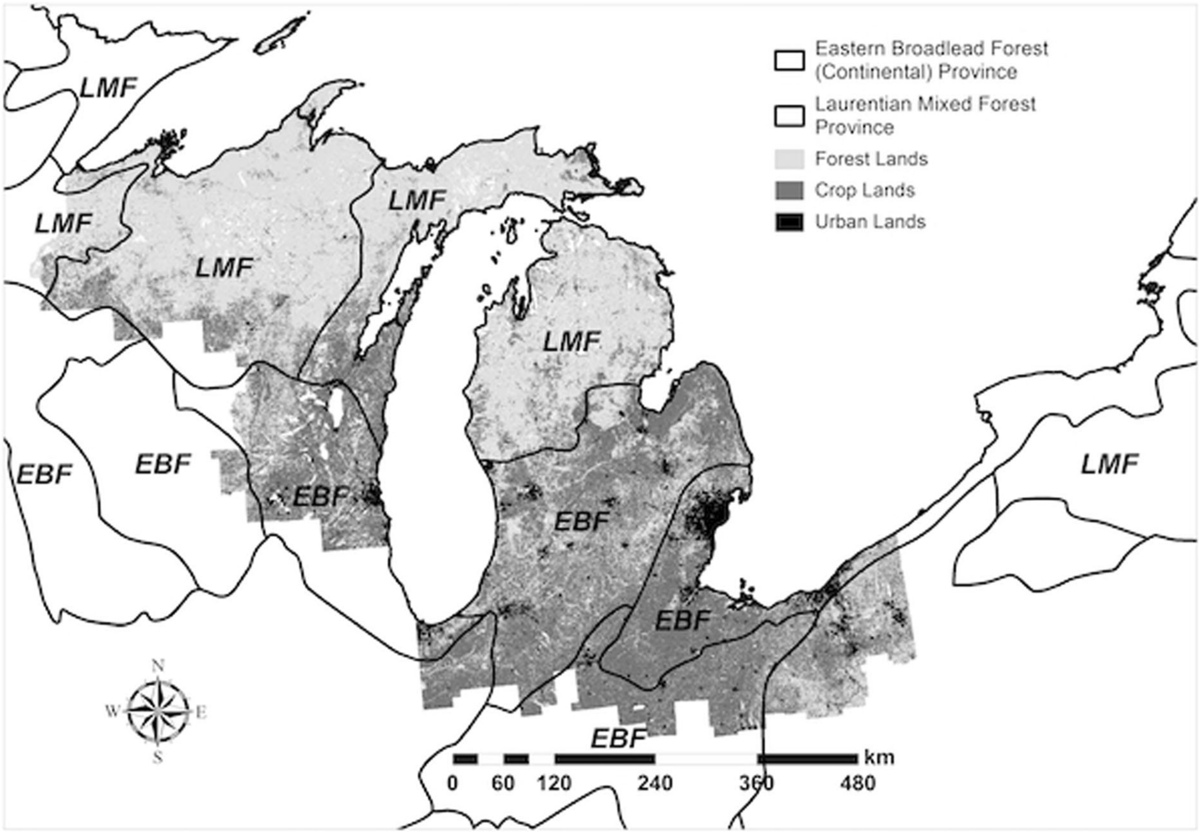

Fig. 1 Land cover map of the study region showing forest, crop, and urban lands, along with the region's dominant ecoregional provinces—the Eastern Broadleaf Forest (Continental; EBFC) and the Laurentian Mixed Forest (LMF). Approximately 38% of the study region is cropland and 46% is forestland (Homer et al. 2015; Bailey 1994)

responsible for 26,000 jobs, and removes approximately 20% of its raw materials from state forestlands (Michigan Department of Natural Resources 2018).

Regional demographic and economic change (Brown 2003; Theobald 2005; Robinson 2012) and growing interest in biofuels in the region may drive future land use decisions and increase land use intensity on both forestlands and croplands (Gustafson and Loehle 2008; Slater et al. 2010; Kells and Swinton 2014). Additionally, climate change could drive shifts in land use and forest composition (Breffle et al. 2013; Handler et al. 2014). Together these trends could impact how much biomass is extracted from the region and where that extraction takes place, i.e. regional patterns of land use and its intensity.

Changes in the nature and location of forest and croplands, and the intensity of biomass extraction on them, could affect the region's ability to provide supporting ecological services. The region has undergone a transition over the last 200 years from largely unmanaged forests and small amounts of cropland (i.e., during management by Native American tribal groups) to extremely high amounts of timber extraction in the north during the turn of the nineteenth century and growing domination of large-scale cropland in the south (Bogue 2000; Handler et al. 2014). The modern landscape comprises heterogeneous LU/LC types and varied ownership patterns—managed, fragmented forests with altered species compositions coupled with high amounts of cropland throughout much of the mid and southern regions of the Great Lakes (Whitney 1987; Handler et al. 2014). The choices inherent in this history, such as how much timber to harvest, where to plant crops, or what types of crops to plant, have shaped the present Great Lakes socioecological system (Steen-Adams et al. 2015). Creating future system trajectories that support biodiversity requires conservation professionals to balance human needs with the needs of other species; in this pursuit, multiple land use planning tools that complement each other and illuminate different aspects of human–environment interaction are a necessity.

Definition of HANPP

For this paper, we adopt a widely-used set of terms related to HANPP (Haberl 1997; Haberl et al. 2001, 2007; Haberl et al. 2014). HANPP is defined as "the combined effect of harvest and productivity changes induced by land use on the availability of NPP in ecosystems" (Haberl et al. 2007). In other words, this is a somewhat complicated metric to define operationally because it arises from two factors: changes in NPP from human land use compared to the potential natural vegetation ($HANPP_{luc}$), together with extraction of NPP by human harvest (NPP_h) (Eq. 1).

$$HANPP = HANPP_{luc} + NPP_h \tag{1}$$

$$HANPP = NPP_0 - (NPP_{act} - NPP_h) \tag{2}$$

$$HANPP_{luc} = NPP_0 - NPP_{act} \tag{3}$$

Combining Eqs. (1) and (2) shows that under this set of definitions, $HANPP_{luc}$ can be calculated from potential natural NPP (NPP_0) and actual NPP (NPP_{act}) for the unit of the landscape (Eq. 3). The definitions also address the fact that timber harvests do not remove the entirety of the forest with every harvest by calculating NPP_h of forestlands as a ratio of total forest inventory (Haberl et al. 2001, 2004). We consider both the above and below-ground compartments of NPP and focus on the percent of NPP_0 appropriated by human activities within a location (hereafter $\%HANPP_0$). We do not include removals of NPP (NPP_h) due to human-caused fires or livestock grazing (hay grown for pasture and feed is included as a crop, but we assume human harvest rather than harvest by livestock grazing).

Spatial unit of analysis

We rescaled all spatial data to a 500 m pixel resolution and reprojected the data into NAD83 Conus Albers. This projection minimizes spatial distortion within our study region (see Electronic Supplementary file 1, Section C, for more information on spatial data transformations). We use counties as our spatial unit of analysis (n = 188 counties) because forest and crop harvest data from the US Forest Service Forest Inventory and Analysis (FIA; Burrill 2018) and the US Department of Agriculture (USDA; "USDA/NASS QuickStats Ad-hoc Query Tool" 2007, 2012) are aggregated to the county scale. Attempting to use the data at a finer scale introduces high levels of uncertainty (S. Pugh, personal communication 2017). Additionally, using a scale based on counties as socio-political boundaries enables better policy-based planning and studies of demographic change. To compliment the county-scale analysis, we also stratified our data by ecoregions as defined by the US Forest Service (Bailey 1994). This allowed us to study counties varying in LU/LC within an ecoregion based in part on climate, growing season length, and soil type.

Data aggregation and synthesis

All spatial analyses were performed using ArcGIS version 10.5.1 (*ArcGIS* ArcMap 2017), and all data manipulations and statistical analyses were performed using R and Excel. In ArcGIS, the zonal statistics function was used to aggregate all values to a county level mean, at which point values were joined to county shapefiles (Fan 2018a, b, c, d).

For NPP_0 (Eq. 2), we used results from Haberl et al. (2007) which were calculated at 5 arc min resolution (about 10 km pixel resolution) and derived using the Lund-Potsdam-Jenna Dynamic Global Vegetation Model (LPJ DGVM; Sitch et al. 2003; Gerten et al. 2004). We reprojected and rescaled the data and used zonal statistics to calculate mean NPP_0 for each county.

Data for NPP_{act} (Eq. 2) was obtained from the MODIS Net Primary Productivity MOD17A3H V6 product (Running et al. 2015; see Electronic Supplementary file 1, section C, for more information) using Google Earth Engine. We averaged the MODIS data from 2005 to 2015 to help account for stochastic uncertainty among years.

We calculated NPP_h (Eq. 2) of croplands based on production and yield data primarily obtained from the USDA Agricultural Census ("USDA/NASS QuickStats Ad-hoc Query Tool" 2007, 2012). We used relationships from Hicke et al. (2004; Eqs. 4 and 5) to transform field crop production (Eq. 4) into field crop NPP values:

$$P = \sum_i \frac{PC_i \times MRY_i \times (1 - MC_i) \times C}{HI_i \times f_{AG,i}} \quad (4)$$

$$NPP = \frac{P}{\sum_i A_i}, \quad (5)$$

where i indicates different crop types, PC indicates the production of a crop in reported units (e.g. bushels), P is production in g C year^{-1}, and A is crop area. We obtained the other input values for the equation—harvest index (HI), fraction of above ground productivity (f_{AG}), moisture content (MC), and percent carbon (C) per unit dry mass—from data compiled by Lobell et al. (2002) and Prince et al. (2001; see Electronic Supplementary file 1, section A, Table A-1, for more detail). For fruit and vegetable crops, we used the equations and parameters presented in Monfreda et al. (2008; Eq. 6 and 7; see Electronic Supplementary file 1, section A, Table A-2, for more detail), where NPP_i represents the NPP of each crop i, EY represents estimated yield, DF is the dry fraction (1-moisture content), and RS is the root:shoot ratio.

$$NPP_i = \frac{EY_i \times DF_i \times C}{HI_i \times RS_i} \quad (6)$$

$$NPP = \sum_{i=1}^{n} \left(\frac{NPP_i}{fcrop_i}\right) \quad (7)$$

For the forest data, we downloaded data representing volume of live trees harvested from forestlands in ft^3 acre^{-1} from the FIA EVALIDator program for the years 2005–2015 (Burrill 2018; Electronic Supplementary file 1, section B). The use of ratio data accounted for the fact that not all forest is harvested every year. We transformed all NPP_h values for forests and crops into dry mass of carbon per unit area.

HANPP calculations

For forestland and cropland separately within each county, we calculated NPP_h at county-scale resolution across our study region (Eqs. 1–3). We calculated $\%HANPP_0$ for forests and croplands separately within each county as well as area-weighted $\%HANPP_0$ that combined forests and croplands within each county (Eq. 8, Table 1):

$$\%HANPP_0 = 100 \times \frac{(NPP_{hFor} \times Area_{For} + NPP_{hAg} \times Area_{Ag})}{NPP_0 * Area_{Total}} \quad (8)$$

NPP_{hFor} is the harvested NPP of forestlands per unit area, $Area_{For}$ is the area of forestlands, NPP_{hAg} is the harvested NPP of croplands per unit area, $Area_{Ag}$ is the area of croplands, and $Area_{Total}$ is the total area of managed forest plus crop lands in each county (see Electronic Supplementary file 2 for calculation output).

Data analysis

To analyze the relationships between $\%HANPP_0$ and landscape diversity or local connectedness, we used the spatial data produced by Anderson et al. (2018). We analyzed linear regressions between our HANPP results and the county mean values of the two biodiversity metrics, both across the entire study region and stratified by ecoregion. We identified four outlier counties in each relationship: Lake and Cuyahoga Counties in Ohio, Milwaukee County in Wisconsin, and Wayne County, Michigan. These counties contain major urban centers and thus exhibited outlier behavior in the relationships between HANPP and biodiversity metrics. Because our study focused on forest and croplands, we removed these four urban counties from our statistical analysis.

Additionally, we identified counties that combined high potential biodiversity—those with high levels of mean local connectedness or mean landscape diversity—with low intensity of human use-intensity as measured by $\%HANPP_0$. We did so by identifying the 25th, 50th, and 75th percentiles of both %HANPP0 and the two biodiversity metrics. We performed pairwise comparisons of different combinations of $\%HANPP_0$ and either connectedness or landscape diversity that were > 50th percentile or < 50th percentile using Wilcoxon rank sum test to examine the significance of the differences among groups (Table 2; Persha et al. 2011). Based on these statistics, we defined four groups of counties: those with high potential for effective biodiversity conservation were low-extraction, high-diversity (LEHD) counties and low-extraction, high-connectedness (LEHC) counties; and high-extraction, high-connectedness or high-diversity (HEHC or HEHD) counties where there is a

Table 1 Summary statistics of area-weighted $\%HANPP_0$ and $\%HANPP_0$ separated into forest and croplands

	Range	Mean	Median	Mode	SD
$\%HANPP_0$	3.2–150	47	48	76	32
$\%HANPP_0$ of forestlands	0.049–17	4.7	4.2	12	3.0
$\%HANPP_0$ of croplands	21–200	80	76	80	23

Table 2 Results of the pairwise comparisons using Wilcoxon rank sum test examining the differences among groups of different combinations of $\%HANPP_0$ and either connectedness or landscape diversity

County group	$\%HANPP_0$ percentile	Indicator	Indicator percentile	Mean 2010 population estimate of county group	Mean road density estimate (m ha^{-1})	Mean %forest cover
LEHC	< 50th	Connectedness	≥ 50th	$41{,}400^{a}$	17.6^{a}	67.6^{a}
HEHC	> 50th	Connectedness	≥ 50th	$57{,}300^{b}$	21.6^{b}	25.1^{b}
LELC	< 50th	Connectedness	≤ 50th	$253{,}000^{c}$	29.1^{c}	40.5^{c}
HELC	> 50th	Connectedness	≤ 50th	$97{,}600^{bc}$	26.2^{bc}	14.2^{d}
LEHD	< 50th	Landscape diversity	≥ 50th	$41{,}300^{a}$	17.0^{a}	67.8^{a}
HEHD	> 50th	Landscape diversity	≥ 50th	$54{,}100^{b}$	21.6^{a}	23.5^{b}
LELD	< 50th	Landscape diversity	≤ 50th	$213{,}000^{b}$	28.3^{b}	45.3^{c}
HELD	> 50th	Landscape diversity	≤ 50th	$102{,}000^{b}$	26.5^{b}	13.9^{d}

Each group is a combination of two variables either above or below the 50th percentile. Low-extraction, high-diversity (LEHD) and low-extraction, high-connectedness (LEHC) counties have high potential for effective biodiversity conservation. High-extraction, high-connectedness/diversity (HEHC and HEHD) counties have high biodiversity potential due to scores on the indices above the 50th percentile, but also has high $\%HANPP_0$ values

potential for biodiversity-supporting habitat but that also activities that extract large proportions of ecosystem NPP. The remaining counties did not have potential for biodiversity conservation.

Results

Spatial distribution of $\%HANPP_0$

Within the study region, forestlands accounted for an average of 4.7% of appropriated NPP_0, while croplands accounted for an average of 80% of appropriated NPP_0; the overall mean area-weighted $\%HANPP_0$ was 45%. Counties with the highest $\%HANPP_0$ values were in Ohio—the north end of the U.S. corn belt—the fertile regions of southeastern Wisconsin, and areas near Saginaw Bay in Michigan (Fig. 2). These counties all have extensive and highly productive croplands. Areas with lower $\%HANPP_0$ include an east–west corridor in southern Michigan, the northern portion of Michigan's Lower Peninsula, and the entirety of Michigan's Upper Peninsula (Fig. 2) The east–west corridor in southern Michigan corresponds to a band of urban areas and their associated exurban fringes, while the northern areas of low $\%HANPP_0$ corresponded to regions of dense forest cover (Fig. 1). The lowest $\%HANPP_0$ occurred in counties with $<$ 50% cropland and positive mean connectedness (Fig. 3).

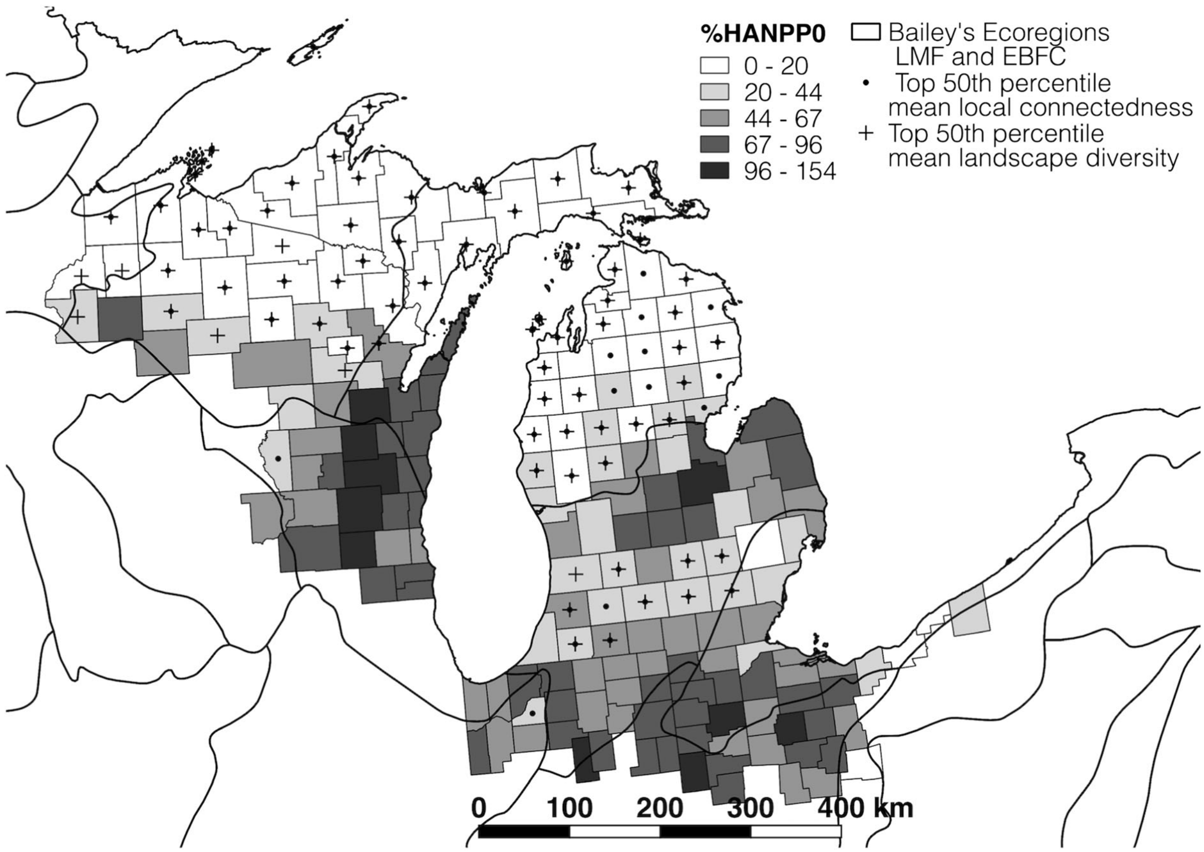

Fig. 2 Map showing the spatial distribution of $\%HANPP_0$ in relation to counties with low-extraction, high-connectedness and low-extraction, high diversity (LEHC and LEHD). The two dominant ecoregional provinces are shown, with the LMF province covering the northern portions of Michigan and Wisconsin and the EBFC covering the southern portions of these states and northern Ohio and Indiana. Most of the LEHC or LEHD counties are in the LMF province and coincide with area-weighted $\%HANPP_0$ between 3.2 and 44%. The exception is a band in southern Michigan, which coincides with a band of mixed LU/LC, including multiple cities (Detroit, Ann Arbor, Lansing, Grand Rapids, Kalamazoo, Flint, and Jackson, MI; and Ekhart, OH) and their associated suburban and exurban fringes (Fig. 1). These counties have an area-weighted $\%HANPP_0 \leq 44\%$ but are in the EBFC province

Relationship between $\%HANPP_0$ and biodiversity metrics

A strong overall pattern in our results was that both landscape diversity and local connectedness exhibited lower values in counties that are experiencing high NPP extraction as measured by $\%HANPP_0$ (Fig. 2; Table 3). This pattern is stronger between local connectedness and $\%HANPP_0$ ($r^2 = 0.36$, $p < 0.001$), than between landscape diversity and $\%HANPP_0$, particularly in the LMF ecoregional province where 51% of the spatial variation in mean local connectedness is explained by spatial variation in $\%HANPP_0$ ($r^2 = 0.51$; Table 3; Figs. 3 and 4). Forestland is more abundant than cropland in the LMF counties, and lower road densities and population (see Electronic Supplementary file 1, section D, for more detail) present fewer opportunities for both forest fragmentation and large-scale resource extraction.

The relationship between $\%HANPP_0$ and landscape diversity is weak ($r^2 = 0.28$) but highly significant ($p < 0.001$). Stratifying by ecoregion, this relationship was stronger in the LMF ecoregional province than in the EBFC ecoregional province (Table 3).

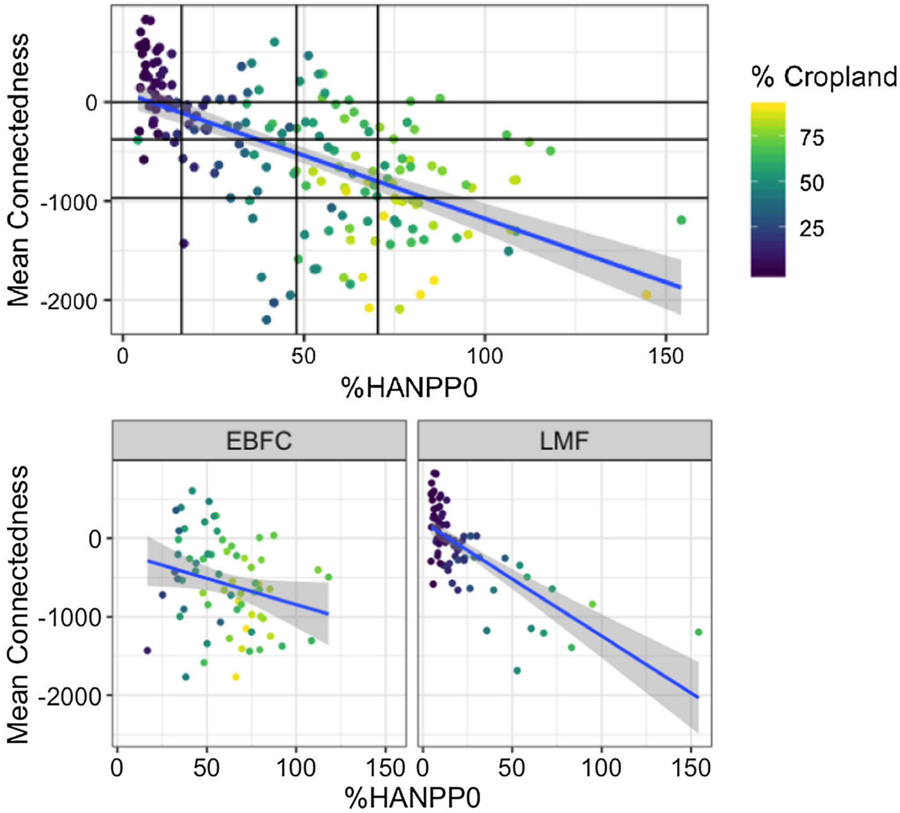

Fig. 3 The relationship between mean local connectedness and weighted %HANPP0, with 25th, 50th, and 75th percentile lines shown on the top graph for the whole study region and the counties stratified by ecoregion in the bottom two graphs. Each point represents a single county in our study region and the grey area around the line of best fit it the 95% confidence interval in the slope of the line. Negative values represent below average connectedness, and positive values are above average. We found that for the whole study region, the relationship between mean connectedness and %HANPP$_0$ is moderate ($r^2 = 0.36$) and significant ($p < 0.001$). The relationship is much stronger in the LMF province, with 51% of the variation in mean connectedness explained by %HANPP$_0$. In contrast, r^2 is only 0.06 in the EBFC province. Counties within the bottom 50th percentile of %HANPP$_0$ and in the top 50th percentiles of connectedness are low-extraction, high-connectedness (LEHC) counties. These counties are largely forested ($\geq$ 50%) and in the LMF province

Table 3 Ordinary least squares regression results examining the relationship between %HANPP$_0$ and the biodiversity metrics

Regression	*p* value	r	r^2
%HANPP$_0$ ~ mean local connectedness	< 0.001	− 0.61	0.36
LMF	*< 0.001*	*− 0.72*	*0.51*
EBFC	*0.0077*	*− 0.26*	*0.060*
Mean landscape diversity ~ %HANPP$_0$	< 0.001	− 0.53	0.28
LMF	*< 0.001*	*− 0.52*	*0.26*
EBFC	*< 0.001*	*− 0.18*	*0.02*

Regressions were done for the whole study region and for the two main ecoregions, Laurentian Mixed Forest (LMF) and Eastern Broadleaf Forest (Continental) (EBFC)—these subregional regressions are shown in italics. All relationships were stronger in the LMF province than in the EBFC province

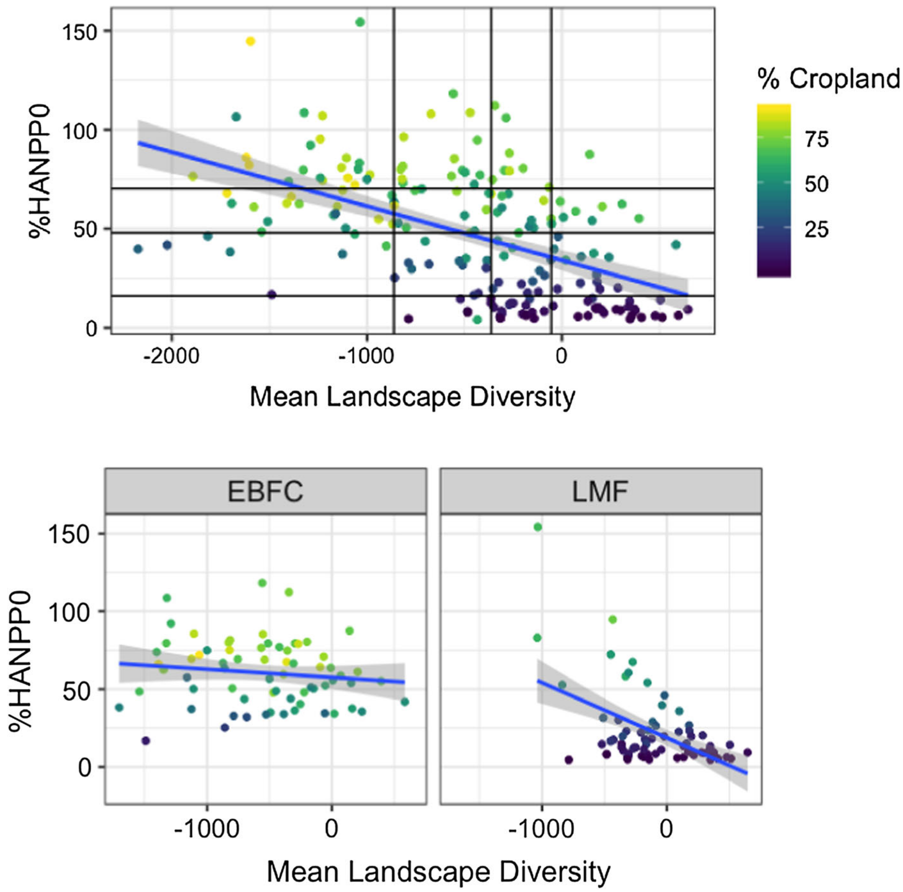

Fig. 4 The relationship between mean landscape diversity and %HANPP$_0$, with the 25th, 50th, and 75th percentiles shown for the whole study region in the top graph and the counties stratified by ecoregion in the bottom two graphs. Each point represents a single county in our study region and the grey border around the line of best fit represents the 95% confidence interval in the slope of the line. Negative values represent below average landscape diversity, and positive values are above average. For the whole region (top graph), the relationship between %HANPP$_0$ and landscape diversity is weak ($r^2 = 0.28$) but significant ($p < 0.001$). R^2 is not improved by stratification by ecoregion (bottom graphs), but the LMF province shows a higher r^2 than the EBFC province. Counties within the bottom 50th percentile of %HANPP$_0$ and in the top 50th percentiles of connectedness/diversity are low-extraction, high-diversity (LEHD) counties. These counties are largely forested (> 50%) and in the LMF province

Identifying counties with greatest potential for biodiversity conservation

We identified counties that fell within the bottom 50th percentile of %HANPP$_0$ (LEHD) and in the top 50th percentiles of landscape diversity or connectedness (LEHC; Table 2, Figs. 3 and 4). These counties have below average NPP extraction as a stressor and exhibit above-average proxies for biodiversity conservation. For efforts to preserve existing biodiversity, these counties may have the greatest likelihood for success. While we stratify them into two groups, these groups are not independent, and some counties overlap. For both LEHD and LEHC stratifications, most counties are in the northern portion of Michigan's Lower Peninsula, Michigan's Upper Peninsula, and northern Wisconsin. They have > 50% forested landcover and ≤ 10% crop landcover (see Electronic Supplementary file 1, section D, Tables D-1 and D-2, for more detail). Among crops, hay for forage or pasture is the most widely planted in these counties. Socioeconomic data indicate that counties in these categories have human population densities well below the regional average of 107,500 persons per county and had the lowest road densities of all categories (Table 2). These socioeconomic data provide further evidence of lower human-use intensity in these groups of counties.

Those counties falling in the opposite arrangement—high-extraction, low-connectedness (HELC) and high-extraction, low-diversity (HELD)—we categorized as high risk and likely high cost for biodiversity conservation due to the combined lack of biodiversity-supporting habitat and high intensity of resource extraction. Socioeconomic data indicated that these categories of counties had intermediate human population densities and road densities. These characteristics are consistent with these groups of counties containing large amounts of rural agricultural land, evidenced by the lowest values of forest cover (ca. 14% on average; Table 2).

Counties falling in the top 50th percentile of $\%HANPP_0$ and in the top 50th percentile of mean local connectedness or mean landscape diversity (HEHC and HEHD respectively) we classified as high risk and high priority for biodiversity conservation. These counties have high potential to support biodiversity but are also being intensely used in terms of the human harvest of primary production. Conservation might be costly in these areas, but valuable, depending on the cause of the high $\%HANPP_0$ values and the socioeconomic drivers impacting landowner decision-making in the region. These counties had above-average human population densities, near-average road densities, and below-average forest cover (Table 2). Interestingly, this category of counties shows that above-average landscape diversity and connectedness can be maintained in the presence of above-average $\%HANPP_0$, even where human populations are above average, as long as the land conversion to cropland is limited (25% forest cover is preserved).

Discussion

Quantification of HANPP on managed lands in the US Great Lakes region

Most HANPP studies have been performed at a global or national scale (Haberl et al. 2007, 2014, 2009, 2004; Krausmann et al. 2013; Plutzar et al. 2016), with fewer examining the regional or local scales (O'Neill et al. 2007; Andersen et al. 2015; Marull et al. 2016), yet the landscape and regional scales are important in much conservation decision-making. Our analysis quantified HANPP in a region where it has not previously been examined at this resolution and specificity, adding a new dataset to the body of regional and local HANPP research.

We found that $\%HANPP_0$ distribution across our study region aligned well with the global means of $\%HANPP_0$ in forest and crop systems, which are approximately 7% and up to 85%, respectively (Haberl et al. 2014). In our region, the mean $\%HANPP_0$ of cropland was about 80% and the mean $\%HANPP_0$ of forest lands was about 5%. The mean $\%HANPP_0$ of forestlands in the Great Lakes region is similar to the global average, but it differs from that of other regions. In Austria (Haberl et al. 2001) and Nova Scotia (O'Neill et al. 2007)—two case studies in similarly temperate climates—aboveground $\%HANPP_0$ on forestland was found to be about 25%, which is five times higher than the average in our study region. This difference could be due to decreased activity in the forest products industry in our region over the last several decades (Shivan and Potter-Witter 2011; Janowiak et al. 2014). For cropland, our analysis resulted in mean $\%HANPP_0$ across the region on par with global means, however our county-level results showed a pattern of extreme spatial variation, ranging from 3.2 to 154% (Table 1). This large range of use-intensity indicates that not all crop-dominated landscapes are subject to high amounts of extraction of ecosystem energy. For instance, hay grown for pasture or feed dominated (in terms of area covered) in counties with $\%HANPP_0 \leq 30\%$, indicating that land can be used for agriculture without removing high amounts of trophic energy. As the data are county-scale, however, interpretation of results must take into account that there are unknown interactions among socioecological variables (such as interactions between different crop systems, choices to use fertilizer or irrigation, methods of harvesting) at the sub-county scale that could be affecting how much or how little NPP is removed from a system.

Increasing the percentage of forestland in the landscape matrix is a possible strategy for increasing landscape-scale ecosystem energy retention. We found consistently low $\%HANPP_0$ on forestlands ($\leq 17\%$), and in counties with $\geq 30\%$ forestland the area-weighted $\%HANPP_0$ was uniformly low ($< 45\%$). This included counties outside of the forestland-dominated LMF province, most notably the east–west band of counties with mixed LU/LC, some of which are LEHC or LEHD counties and others that include urban areas such as Detroit, Flint, Ann Arbor, Lansing, Kalamazoo, and Grand Rapids. Previous research has shown a correlation between exurban expansion and an increase in tree cover and gross primary productivity; exurban landscapes also display carbon storage levels higher than those in croplands (Brown et al. 2008; An et al. 2011; Currie et al. 2016). Together with our findings this research suggests retention of forestland or afforestation can increase the potential for a mixed LU/LC landscape to support biodiversity at a county scale, even in counties where human population densities are above average.

Despite the notable amount of NPP left unharvested in managed forestlands, the regional mean $\%HANPP_0$ was strongly influenced by the $\%HANPP_0$ values in counties dominated by cropland. Thus, areas of forestland within a mixed LU/LC matrix may still occur in an area of regionally high average $\%HANPP_0$, although areas of forest may increase landscape patterns that benefit biodiversity. If a conservation goal were to decrease regional average $\%HANPP_0$, this may not be achievable without large-scale conversion of cropland to forest, residential land, or other land cover. Smaller reductions in $\%HANPP_0$ might be achievable using crop types or planting and harvesting practices that are purposefully chosen to increase the amount of NPP left in the ecosystem. In mixed LU/LC areas of biodiversity concern, intensive row crops (e.g. corn, soybeans, sorghum) could be replaced or intermixed with lower-intensity perennial crops, such as hay and alfalfa systems with lower harvest rates (Asbjornsen et al. 2014). In addition to leaving more biomass to benefit wildlife foodwebs, replacement of annual row crops with perennial crops could provide increased wildlife habitat, as found by Graham et al. (2017) for the case of pollinator habitat in an agricultural landscape in Illinois.

Relationship between HANPP and biodiversity metrics

Percent $HANPP_0$ exhibited relationships with both landscape diversity and habitat connectedness. However, there was a stronger relationship with connectedness than with landscape diversity. Our study indicates that differing geophysical conditions do not affect biomass removal rates as much as biomass removal rates affect the spatial patterns of habitat connectivity and fragmentation (and thus the permeability of the landscape for wildlife movement). This may be due to the relatively low degree of diversity of geophysical conditions in our study region (e.g., as compared to mountainous landscapes). The relatively low landscape diversity in our region limits the extent to which spatial variability in land cover diversity acts as a signal that we can compare against patterns of NPP extraction. The relationship between $\%HANPP_0$ and landscape diversity was much stronger in the Laurentian Mixed Forest (LMF) ecoregional province ($r^2 = 0.26$, Table 2), a region that is heavily forested and has greater elevational change, more remaining wetlands, and more diverse geology than the Eastern Broadleaf Forest (Continental; EBFC) ecoregional province. The difference between ecoregional provinces suggests that the diversity of geophysical settings could potentially act as a driver of $\%HANPP_0$ patterns in regions with greater variation in landscape diversity. This idea is supported by previous research in which topographical elements such as slope, altitude, and roughness (the topological variability of a landscape) were predictive of spatial patterns of $\%HANPP_0$ (Wrbka et al. 2004). The relatively weak relationship overall between landscape diversity and $\%HANPP_0$ also suggests these variables contain different types of information about human impacts on landscapes. Although the relationship between $\%HANPP_0$ and mean local connectedness was stronger, only 36% of the variance in mean local connectedness among all counties could be explained by $\%HANPP_0$. Again, the relationship was stronger in the LMF province ($r^2 = 0.51$) than in the EBFC province ($r^2 = 0.06$).

Wrbka et al. (2004) similarly found that landform patterns—aspect, roughness, and elevation, variables related to topography—have a moderate to weak relationship with spatial patterns of HANPP, and that the relationship varies notably among geo-ecological units. The research group hypothesized the weak relationship was because their study area consisted of "cultural landscapes," in which the disturbance regime and major energy and material fluxes are controlled by humans. How this control plays out, e.g. what management strategies are used on the land, is constrained not just by the geophysical makeup of the landscape but by interacting social and economic forces. These may be more or less important than ecological constraints in determining management practices at different times and in different spaces.

Our analysis consistently showed a much stronger relationship between %$HANPP_0$ and the biodiversity metrics in the LMF ecoregional province than in the EBFC, which contained more counties dominated by cropland and urban/exurban land, the most intensively used LU/LC types worldwide (Haberl et al. 2014). The LMF province, on the other hand, contains counties with high percent forest cover that is managed more irregularly (i.e., forest harvests occur only once every few decades or longer, large tracts of forest have protected status that limits resource extraction, and many private forest landowners choose not to harvest their forests at all; Janowiak et al. 2014; Shivan and Potter-Witter 2011). One explanation is that the socioeconomic forces Wrbka et al. (2004) predicted as a third explanatory variable may be more relevant in regions dominated by more intensive extraction of NPP, in which socioeconomic profits and losses are higher and with more immediate effects.

HANPP as a tool for conservation decision-making

Conservation professionals have a wealth of tools and variables at their disposal to aid them in evaluating where to focus conservation efforts. To date, HANPP has largely been studied as an academic metric with few examples of application to conservation planning. Our analysis indicates that there is significant variability in the spatial distribution of %$HANPP_0$ that is not fully explained by the distribution of mean landscape diversity and that there is a similar (although lesser) variability in mean local connectedness that is not explained by %$HANPP_0$. This supports the idea that %$HANPP_0$ may contain additional information about landscape-scale socioecological interactions for conservation professionals when used in conjunction with other metrics of human impacts on biodiversity.

One way %$HANPP_0$ operates as a biodiversity metric is as an ecosystem stress indicator. Extensive research has been done in the Great Lakes region on developing ecosystem stress indicators, and percent crop LU/LC has been identified as a major terrestrial stressor on aquatic ecosystems (Johnson et al. 2015). Given that high values of crop LU/LC result in high %$HANPP_0$ and evidence that tree biomass removal (e.g. clear cut harvesting) is related to degraded downstream water quality (Ensign and Mallin 2001; Wang et al. 2006), significant biomass removal from terrestrial landscapes may be an indicator of stress on downstream aquatic ecosystems. In terrestrial ecosystems, one question for conservation professionals is how much energy extraction can occur on a landscape before it crosses a threshold of rapidly declining ecosystem services. Haberl et al. (2004) found declines in species richness when %$HANPP_0$ rose above 50%, which in turn impacts biodiversity conservation. We have found that the mean area-weighted %$HANPP_0$ across forest and croplands in our study region was about 46%, suggesting the region may be close to a threshold of energy extraction past which species richness could decline.

HEHC or HEHD counties are potentially at-risk—they have a high potential for supporting present biodiversity due to their landscape patterns, but are also being heavily used for resource extraction. These are counties where conservation might be costly, but valuable, depending on the cause of the high %$HANPP_0$ values and the socioeconomic drivers impacting landowner decision-making in these counties. Both these counties and HELC or HELD counties are those that may need ecological restoration either to improve local biodiversity support or create corridors connecting habitats of higher conservation value (Jones et al. 2015).

Habitats of higher conservation value are more likely to be found in the counties in our study region that have an average %$HANPP_0$ below the 50% threshold. These LEHC/D counties are largely focused in the northern, heavily forested counties (Figs.1 and 2) and may be less costly to conserve as they already have landscapes that can support biodiversity and are not the site of intense resource extraction. In addition to having the highest mean percent forest cover, this county group has significantly lower mean road density and mean population (Table 2; see Electronic Supplementary file 1, Section D, Tables D-1 and D-2, for more detail) than the other county groups. In a conservation triage situation (Gerber 2016) where limited aid must be allocated to regions where the aid will do the most good, the habitats in these counties are ones conservation professionals may want to focus on to protect and connect.

The difference between regional mean %$HANPP_0$ values and county-level mean %$HANPP_0$ values invites the question of how landscape-scale extraction patterns translate into local biodiversity impacts. There is evidence that different species may be differentially impacted by land sparing conservation strategies—conserving large tracts of unused land and allowing for smaller areas of more intense extractive management—or land sharing conservation strategies—ensuring human-dominated lands are managed for extraction in an ecologically-friendly way (Gonthier et al. 2014; Kremen 2015). Because of different responses to land management from different species, both strategies can prove useful in different contexts and complimentary in landscape-level conservation planning (Kremen 2015). What configuration of crop and forest matrices and what threshold extraction level are best for meeting biodiversity objectives may thus depend on the species and ecosystem services of greatest conservation concern.

Conclusion

As a snapshot of the mean LU/LC and the accompanying landscape patterns of the US Great Lakes basin in the first 15 years of the twenty-first century, this analysis provides an initial quantification of the spatial patterns of HANPP in our study region and shows how HANPP can complement established biodiversity metrics. We observed a moderate, negative relationship between $\%HANPP_0$ and mean landscape diversity and local connectedness and a strong pattern of high $\%HANPP_0$ in cropland-dominated counties and low $\%HANPP_0$ in forestland-dominated counties. These relationships support previous research suggesting that HANPP is negatively correlated with landscape characteristics that likely control species richness and support previous research putting forth HANPP as a metric of human impact on biodiversity (). Our findings suggest HANPP has the potential to be useful to conservation professionals during regional-scale land use planning or conservation decision-making, particularly in landscapes with a combination of high site potential for biodiversity and high resource extraction activity. Further developing HANPP as a metric may illuminate which LU/LC development should be advocated for or against in the pursuit of biodiversity conservation in managed, mixed use landscapes.

Future research could continue to improve HANPP as a metric for understanding how resource extraction impacts conservation goals. To maintain current levels of site resiliency, further understanding is needed of socioecological processes and landowner decision-making, and how they interact with ecosystems to create specific matrices of LU/LC and use-intensity. Additionally, the forests of the Great Lakes region are managed by a combination of private and public interests; taking a closer look at how different crop and forest management styles impact biomass extraction levels at local scales is an important next step in regional HANPP analysis to support biodiversity conservation.

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