

Ecological Applications, 15(6), 2005, pp. 1864–1878
© 2005 by the Ecological Society of America

THE THREE PHASES OF LAND-USE CHANGE: IMPLICATIONS FOR BIODIVERSITY

MICHAEL A. HUSTON¹

Department of Biology, Texas State University, San Marcos, Texas 78666 USA

Abstract. Traditional economic models of land-use change have focused on factors such as distance to population centers, available labor supply, population density, and patterns of existing infrastructure, such as roads. While such models can reproduce urban sprawl, they do not address such fundamental issues as the causes of initial human settlement locations, variation in the growth rates of different urban centers, and the ecological consequences of different economic drivers. A complementary approach, based on properties of the environment related to net primary productivity, predicts the temporal and spatial patterns of development and land-use change associated with three distinct phases of economic development: agricultural, industrial, and information/communication. Initial land-use patterns, established in response to environmental constraints on agriculture, are selectively amplified based on the subsequent requirements for industrialization. These environmental constraints are later relaxed during the information/communication phase of development, which affects portions of the landscape that were little affected by the first two phases. This sequence of events produces a predictable change in the distribution of human population density and land-use intensity that impacts different components of biodiversity over time. The agricultural phase tends to eliminate those components of biodiversity that depend on high-productivity environments, while preserving those components that can survive on marginal lands. However, the transition from an industrial to an information-driven economy breaks the linkage between productivity and land-use intensity, and allows intensification of human impacts in areas that had been protected by the constraints imposed by agricultural and industrial economies. As a consequence, the remaining reservoirs of biodiversity on marginal lands are now being threatened as formerly remote rural areas are being developed for recreational and residential use, particularly in the western United States.

Key words: *biodiversity; industrial economy; information-driven economy; land-use pattern; land-use change; primary productivity.*

INTRODUCTION

Accelerating human alteration of landscapes around the world has led to increasing concern about the ecological consequences of land-use change (Goudie 1981, Turner et al. 1990, Vitousek et al. 1997). Traditional economic models of land-use change have focused on factors such as distance to population centers, available labor supply, population density, and patterns of existing infrastructure, such as roads (e.g., Christaller 1933, 1972, Lösch 1938, Stutz and de Sousa 1998). A complementary approach, based on soil properties and other environmental conditions that influence the abundance and diversity of plants and animals, can be used to predict the temporal and spatial patterns of human

development and land-use change, as well as their potential impact on different components of biodiversity.

While human populations are ultimately subject to the same constraints as other animal species, the development and application of technology has led to increasing relaxation of these constraints at the local (but not global) level, with profound implications for the impacts of humans on the environment. The history of human civilization and environmental impacts is the history of this relaxation of local environmental constraints, and can be divided into three main phases.

The first phase, driven by primary productivity, is the agrarian stage that has occupied most of human history. This stage includes the hunter-gatherer culture, in which primary and secondary production both contribute to population growth, and the subsequent agricultural culture, in which primary productivity is the main driver.

The second phase marks the beginning of independence from the local environmental constraints on primary productivity. The development of efficient trans-

Manuscript received 10 September 2003; revised 1 September 2004; accepted 8 November 2004. Corresponding Editor: M. G. Turner. For reprints of this Invited Feature, see footnote 1, p. 1849.

¹ E-mail: houstonma@txstate.edu

portation initiates the transition from the agrarian to the industrial phase, in which the transport of both foods and raw materials allows human population centers to be located away from the centers of agricultural production. This phase occurred in the developed countries during the 19th century and the first three-fourths of the 20th century, and is still occurring in the less developed countries.

The third phase is characterized by a further increase in independence from the centers of agricultural and industrial production as a result of electronic communication and increased transportation efficiency. This information stage allows the new types of production, of information and services, to be totally removed from the centers of agricultural production and traditional transportation corridors, thus freeing the human population to occupy any portion of the landscape, regardless of its primary or secondary productivity. This phase began in the later decades of the twentieth century, and is occurring primarily in the most developed countries or wherever there is sufficient accumulation of wealth to allow establishment of the information infrastructure.

These three phases produce very different patterns of human population distribution and thus very different patterns of land use and impacts on the environment and biodiversity. These patterns depend on the availability and distribution of the resources necessary for human population growth.

PARALLELS BETWEEN ANIMAL ECOLOGY AND HUMAN ECOLOGY

The distribution of organisms over the Earth's terrestrial surface is highly predictable in relation to environmental conditions. At very large spatial scales, most terrestrial organisms are found within a limited range of temperature and precipitation conditions, typically classified into biomes or life zones in response to differences in temperature and precipitation, ranging from deserts to rainforests (e.g., Holdridge 1947). Most aquatic organisms are found within a narrow range of temperature and other physical and chemical properties of water bodies. At regional scales, groups of organisms can be classified as being typical of particular ecoregions or other biogeographical subdivisions, classified on the basis of distinct combinations of climate, soils, and topography (e.g., Omernik 1987, 1995, Bailey 1989, 1995, Omernik and Bailey 1997). At still smaller scales, plants and animals are arrayed in zones or patches along mountain slopes and hillsides, based on elevation, soils, landforms, slope, and aspect (Whittaker 1956, 1960, Kessell 1979). At each of these scales, the most conspicuous organisms are the plants, which generally give their names to the patterns. Nonetheless, most animal species are closely associated with plant communities or specific types of landscapes, leading to high predictability in the distribution of most

species of both plants and animals (Scott et al. 2002, Kalkhan and Stohlgren 2000, Bashkin et al. 2003).

Beyond their effect on the probable presence or absence of a specific type of organism, environmental conditions related to primary and secondary productivity are often associated with variation in the size, health, and fecundity of individuals, as well as the population density and range size of any particular species (e.g., Gaston and Blackburn 1996, Jetz and Rahbek 2002). The single species of genus *Homo* on the planet is widely distributed, but quite predictable in terms of the environmental conditions where population densities are highest.

Like other animals, humans require sufficient energy (food intake) to maintain individual metabolism and to reproduce successfully. As omnivores, humans have the advantage of being able to consume both plants (primary producers) and animals (secondary producers). In addition to food, humans and most other terrestrial animals require the constant availability of fresh water, as well as temperature conditions suitable for normal metabolic activity.

To a greater extent than any other species, humans are able to modify their environment by creating shelter that protects them from unfavorable conditions and increases their potential for survival and population growth. While the local availability of energy and other resources can impose limits on the ability of technology to moderate the physical environment, the capability of humans to create shelter makes them relatively independent of physical environmental conditions. As long as adequate food, water, and oxygen are available, humans are capable of surviving in virtually any environment.

Despite our unique capabilities, we are nonetheless subject to the same basic limitations as other animals, and the same fundamental laws of population dynamics apply to us as well as to other species. Both population growth rates and maximum population size (carrying capacity) depend upon resource availability. Human populations grow rapidly and reach high densities where food availability is high and other conditions are favorable (Hyams 1952), but are constrained to low growth rates and low densities where primary and secondary productivity are low or other conditions are unfavorable (e.g., Meggers 1971).

In humans, as in grizzly bears, a much larger area is needed to provide food for an individual or a population under unproductive conditions than under productive conditions (Schwartz et al. 2003). Primary and secondary production during periods with suitable temperatures for growth are typically limited by the availability of water and nutrients. Because these resources are often correlated across landscapes, favorable conditions for the population growth of humans and other animals are often found in the same portions of the landscape.

NPP-DRIVEN (AGRARIAN) DYNAMICS
OF LAND-USE CHANGE

In the agrarian stage, the patterns of anthropogenic land-use change are regulated by the same constraints that affect the population growth of most organisms. The fundamental constraint is net primary production (NPP), the rate of production of plant mass that supports virtually all animal life. Both the rate of production and the predictability of that production are critical for determining the densities of animals (including humans) that can be supported in any particular area. High plant productivity can support high animal biomass while low productivity only supports low biomass. However, if the high productivity is not stable over time, both within years and between years, populations must have mechanisms to avoid the starvation and increased mortality that would cause population declines during unfavorable conditions. Such mechanisms include hibernation, migration, and storage of food energy as living body mass or dried, canned, or frozen dead plant and animal tissue.

Plant productivity varies in response to the interaction of nutrient availability, water availability, temperature, light, and carbon dioxide (e.g., Larcher 1980). At large spatial scales, such as biomes, most of the variation in plant productivity is in response to climatic factors such as length of growing season, temperatures during the growing season, and the amount and seasonality of precipitation (Walter 1979). At smaller scales from local to regional (e.g., ecoregions) topography and geology have a more important effect on spatial variability, along with the effects of climate and microclimate. Across this range of scales, these well-known growth factors produce a highly predictable pattern of net primary productivity that shapes the distribution of biodiversity, agricultural production and human health, and economic activity (e.g., Huston 1993, 1994).

Soils with high mineral nutrient availability are generally found where rates of geological activity are high, such as areas of volcanic activity, uplift of mineral-rich igneous rocks, or glaciation that exposes and pulverizes nutrient-rich bedrock. Topographically constrained patterns of erosion and deposition produce highly predictable distributions of rich and poor soils, with poorer soils characteristic of erosional areas such as ridges and hillslopes, and richer soils in valley bottoms and alluvial floodplains. These processes create the spatial patterns of net primary productivity that influence the abundance and diversity of all plants and animals, as well as human agricultural activity over a broad range of spatial scales.

The key feature of the agrarian stage of land use is that human population growth rates and population densities are regulated by local environmental constraints, which produces a strong correlation between environmental conditions and human population den-

sities and environmental impacts. Humans, and other large mammals, preferentially use those portions of the landscape that have high net primary productivity (NPP). This preferential use occurs across all spatial scales. At the fine scale of selection of which areas to cultivate, subsistence farmers use cues such as plant sizes and species to identify the most productive soils, which are often the alluvial soils that are typically, but not always, found in valleys. On Walker Branch Watershed near Oak Ridge, Tennessee, now a forest research site, cultivated fields and pastures were preferentially located on ridgetop positions (Fig. 1B, red and pink areas). The counterintuitive ridgetop location of these fields was highly correlated with the presence of an ancient alluvial soil (and associated ancient colluvium) that persisted as an inverted landform in a few locations (Fig. 1C, aqua and dark gray areas) on the landscape, remnants of stream valleys that drained the ancestral Smoky (Unaka) Mountains 40 miles (24.8 km) to the south (Lietzke 1994). These unusual soils occupy only 11% of the total watershed area. Cultivated fields were preferentially located on this ancient alluvium and associated colluvium on ridgetops (2.5× random expectation) and also on recent alluvium in the valley bottoms (1.5×) (Fig. 1A). Subsistence farmers preferentially used this unusual, relatively fertile, ancient soil that scientists only recognized as distinct from the younger residual soils after near three decades of research.

At regional scales, where environmental patterns often appear as vegetation zones or ecoregions (determined by elevation, climate, and soils), the most productive zones generally have the highest human population densities during the agricultural phase. In five Central American countries, population densities were highest in the dry forest and moist forest life zones (Fig. 2), which typically have higher soil fertility than the wet and rain forest life zones. Because of more rapid weathering and leaching in high rainfall areas, rainfall and soil nutrient available are inversely correlated in many tropical regions (Craig and Halais 1934, Hall and Swaine 1976, Huston 1980).

Preferential use of high-NPP areas results in higher rates of food or energy acquisition, and higher total food and energy uptake. The individual and population level consequences of higher energy intake include improved health, longevity, and reproductive rates for all animals, including humans, plus the benefits of agriculture-based trade, such as more material goods, better education, better health care, etc.

High population growth rates of herbivores, carnivores, and omnivores, including humans, lead to locally high population densities and pressure for dispersal or migration. The total population that can be supported in any area is obviously a function of the total size of the area, and the mean population density that can be supported per unit area. Large areas of

fertile soil with high NPP can support large populations. Small areas of good soil surrounded by infertile soils will support only small populations, but may continuously produce excess individuals which disperse, as described by the “source–sink hypothesis” (Pulliam 1988).

The land-use impacts of a population are a function of the density of the population in relation to resource availability (carrying capacity), so that a population with a high relative density that extends over a large area can potentially have a strong impact over a large area. Animal populations that reach high densities can cause severe impacts as a result of overharvesting their food base, potentially leading to secondary impacts such as soil degradation or erosion. Examples include the degradation of arctic marshes by high densities of snow geese on their historical nesting grounds (Kerbes et al. 1990, Iacobelli and Jeffries 1991), as well as high levels of deer herbivory in the eastern United States (McShea et al. 1997, Russell et al. 2001). Humans can have a similar impact through destructive agricultural practices. However, human land-use practices are generally designed to increase the usable NPP of the landscape, typically by shifting the vegetation to smaller plants or earlier successional stages, which have a higher ratio of production to respiration, and often higher nitrogen concentrations. This is accomplished by conversion of forests to grasslands, use of annual crops rather than native perennials, or shortening the rotation length of forest harvests. Natural analogs of this type of human manipulation of NPP include certain native grazers, such as prairie dogs, which maintain younger vegetation by continual cropping, leading to improved forage quality and potentially higher local NPP (Detling 1998, Fahnestock and Detling 1999, Green and Detling 2000).

Even at the global scale, the pattern of human-caused land disturbance is closely related to soil properties that influence NPP (Fig. 3). Human land disturbance, by deforestation and cultivation, is greatest in regions with fertile soils, where human populations can achieve high densities and high population growth rates that allow dispersal and occupation of all usable portions of the landscape. High proportions of land cultivation are found in eastern North America, eastern Europe, India, and China, (Fig. 3A, dark red and black colors indicate highest percentage of cultivation) where soils are fertile (Fig. 3B, dark green indicates highest fertility as measured by total exchangeable bases) and human population densities are high. In contrast, the major areas of tropical rain forest, which have nutrient-poor soils (Fig. 3B, dark orange colors indicated lowest fertility) and low human population densities (Meggers 1971), until recently have had relatively low levels of human disturbance (Ramankutty and Foley 1999) (Fig. 3A). At the global scale, the proportion of the land

surface that is cultivated is highly correlated with soil fertility, one measure of which is illustrated in Fig. 3D.

NPP-DRIVEN IMPACTS ON BIODIVERSITY

A fundamental fact of the distribution of biodiversity on earth is that plant diversity and animal diversity reach their maximum levels under different conditions (Fig. 4). It is now recognized that highest plant diversity occurs under relatively unproductive conditions, where net primary productivity is relatively low as a result of low availability of nutrients, light, and/or water (Fig. 4B, cf. Grime 1973*a, b*, 1979, 2001, Huston 1979, 1980, 1985, 1994). This somewhat surprising reduction of plant diversity under highly productive conditions is the result of competitive exclusion, in which rapidly growing species overgrow and eliminate individuals of smaller, slower-growing species (Berdse 1994, Mahdi et al. 1989). The diversity of animals, particularly of large herbivores and carnivores, depends on species being able to maintain population sizes sufficiently large to survive natural disturbances and climatic fluctuations. Because of the loss of energy with each trophic transfer, animals at higher trophic levels have much less available energy than do organisms at lower trophic levels, and consequently, the total biomass of animals that can be supported is much less than that of the plants. This energetic limitation on population size and survival means that the largest populations of animals, and potentially, the largest number of species, will occur at the highest levels of net primary productivity (Fig. 4F, e.g., Owen 1988, Dodson et al. 2000). These populations are highly susceptible to mortality-causing disturbances, particularly under unproductive conditions (Fig. 4E). Thus, plant diversity is generally highest under relatively unproductive conditions (Fig. 4B), while the diversity of large vertebrates and carnivores reaches its maximum under the most productive conditions (Fig. 4F), where human populations also reach their highest density.

The inevitable correlation between NPP and human population density during the agrarian phase of development restricts the major environmental impacts to those portions of the landscape with high NPP. These include riparian and alluvial areas, productive grassland (prairies, veld, and steppe), and productive forests on fertile soils, such as the forests of the Great Lake States and glaciated portions of North America (e.g., Cronon 1983, Whitney 1994). In these regions, the major impacts have been on the organisms most dependent on high NPP, which are primarily large vertebrates, particularly at higher trophic levels. The large native herbivores, elk and bison, have been totally eliminated from the areas where they once occurred in great abundance, primarily because the native vegetation has been converted to annual crops, and domesticated herbivores substituted for native ones (e.g., Licht 1997). In addition, the large carnivores that once preyed on these

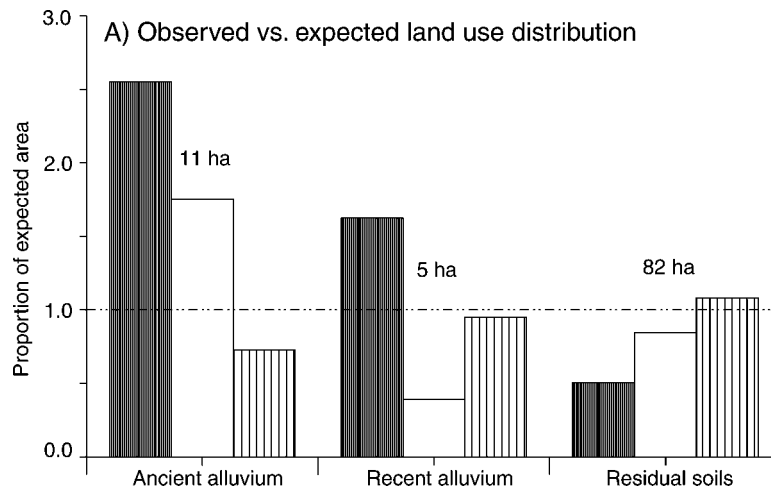


FIG. 1. Small-scale (local) distribution of agricultural land uses in relation to soil properties on Walker Branch Watershed near Oak Ridge, Tennessee, USA. Natural vegetation was oak–hickory–chestnut deciduous forest with subsistence agricultural activities of cultivated corn, beans, tobacco, and flowers; cleared pastures; woodland pastures; and woodlots. (A) Proportional distribution of cultivated fields (black bars), pastures (open bars), and forest (hatched bars) in relation to three major soil types. The expected proportion with no preference is 1.0. The total area of each soil type is indicated above the bars. (B) Circa 1935 distribution of forest, pastures, and cultivated fields (pinks and red) across the 100-ha watershed. (C) Distribution of soil types. Residual soils (pastel colors) were formed in situ from dolomitic bedrock, and are now low-pH, nutrient-poor, red-clay ultisols (Lietzke 1994), as is the recent colluvium (light gray) formed by downslope movement of these soils. Ancient alluvial soils (blue-greens) and their colluvium (dark gray) represent an inverted landform, now restricted to ridgetops.

native herbivores have been eliminated by a combination of hunting and elimination of their prey base (Rogers and Caro 1998, Woodroffe and Ginsberg 1998, Woodroffe 2000).

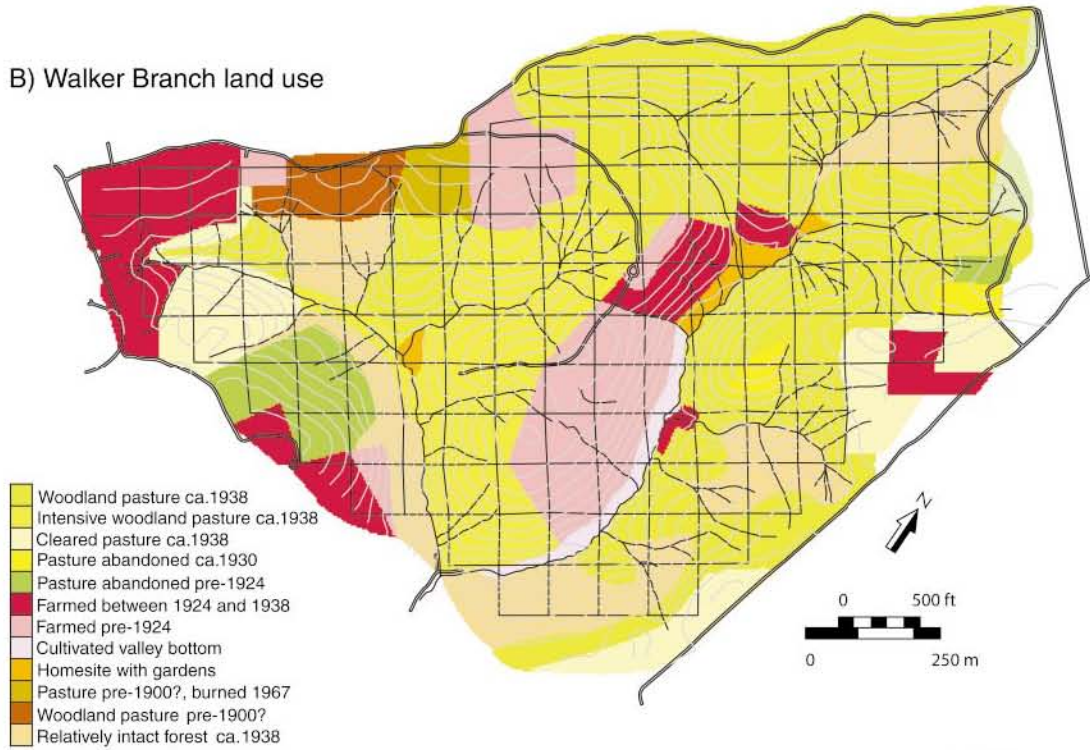
In spite of the extensive replacement of native vegetation and elimination of the large mammal fauna, there have been very few global extinctions, of either plants or animals (both terrestrial and aquatic) that had their highest abundances in the most productive areas of North America (Flather et al. 1994). Most plant species of the high-NPP regions were widely distributed, and now survive in the peripheral areas of their original range, and in the less productive, marginal areas that serve as refuges within their core areas (Huston 1994). Similarly, large vertebrates such as elk, bison, and black bear survive in the much less productive western portions of their original range, where population densities are lower, but still sufficient for survival (Flather and Hoekstra 1989, Vaughan and Pelton 1995). The most notable extinctions were of two bird species that once occurred in extremely high numbers, the passenger pigeon, and to a lesser degree, the Carolina parakeet. The passenger pigeon was almost certainly the most abundant bird species on earth, nesting and feeding in the productive eastern deciduous forests of the Great Lake states (Schorger 1955, Ehrlich et al. 1992). Extensive clearing of the forests, along with market hunting of the passenger pigeon, drove both of these species to extinction in a remarkably short period of time (Whitney 1994, Russell 1997). These two dramatic and tragic extinctions were of gregarious, no-

madic species that were highly adapted to the productive forests of eastern North America (Blockstein and Tordoff 1985). Conversion of the most productive forests to cultivated fields and pastures made their survival impossible.

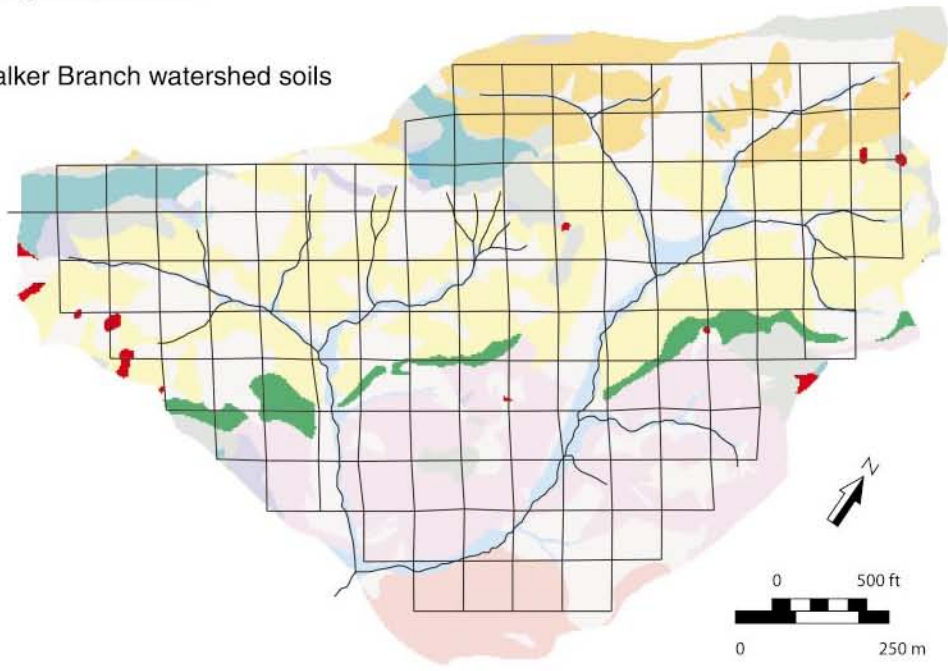
In striking contrast to the productive midwestern regions, the lower NPP regions of the western grasslands and mountains were relatively little impacted during the agrarian phase (Fig. 3A). The large areas of infertile, dry, and/or cold soils supported very low human population densities and consequently low total populations over large regions. While there were some impacts of grazing, logging, and mining, the overall impact was relatively small, and these western regions remain as our primary remnants of natural landscapes, and our primary refuges for plant and animal biodiversity, preserved in our national parks, forests, and grasslands (Huston 1993, Scott et al. 2001). Large mammal densities were never as high as in the more productive grasslands, savannahs, and forests of the central (midwestern) region, and plant species richness at large scales is augmented by a much higher density of narrowly distributed (endemic) plants and small animals than in the more productive parts of the country (Flather et al. 1994, Huston 1994).

Within these large, unproductive regions, the small proportion of the landscape that is highly productive is extremely important to regional biodiversity. These productive areas, such as isolated springs, wet meadows, marshes, and riparian zones along streams and rivers, are critical for the survival of both local endemic

B) Walker Branch land use



C) Walker Branch watershed soils



-----RESIDUUM-----			ALLUVIUM		
Copper Ridge	Chepultepec	Longview	Kingsport	Mascot	RECENT
Decatur	Typic Paleudults	Waynesboro	ANCIENT	RECENT	ANCIENT
-----ANCIENT ALLUVIUM-----			-----COLLUVIUM-----		SEDIMENTS

FIG. 1 Continued.

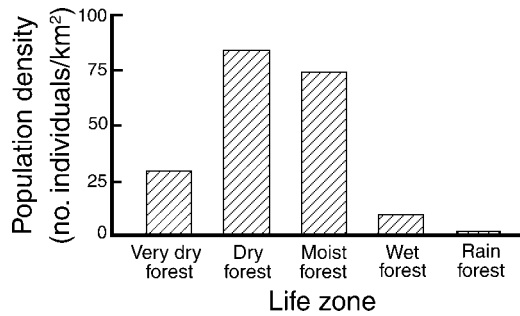


FIG. 2. Regional pattern of human population distribution among major vegetation life zones (sensu Holdridge 1947) in Central America (based on Tosi and Voertman 1964).

species and widespread species that depend on these refuges during critical times of the year. Unfortunately, these productive, well-watered areas are the preferred location for human settlements and agricultural activities (Hansen et al. 2002, 2005), and consequently have been severely impacted throughout most of the west. These areas are extremely important as travel corridors and productive zones for feeding and reproduction (Hansen et al. 2000, Hansen and Rotella 2002a), yet they are rarely included in the publicly owned lands (Scott et al. 2001), and tend to be increasingly utilized for a wide range of human activities (Hansen and Rotella 2002a, b, Hansen et al. 2002).

In spite of massive disturbances over large areas of productive soils, and intensive disturbances of restricted productive areas in regions with low average productivity, the impacts of human activities during the agrarian phase are restricted to specific portions of the landscape and are less severe than might be expected. Even on the less productive portions of the landscape abandoned after the agrarian phase, most of the “legacy effects” of past agriculture (e.g., Foster et al. 2003) are relatively short-term changes in vegetation that will be erased over time by plant succession and soil development. Nonetheless, there have been large areas impacted by agricultural soil erosion (e.g., Trimble 1974), and even small-scale agricultural activities can affect the rate of forest succession and patterns of tree diversity for decades or centuries (Lafon et al. 2000). Fortunately, avoidance of the unproductive portions of the landscape leaves refuges that allow the continued survival of most of the plant and animal species that originally occupied North America. Unfortunately, aquatic species have been much more severely impacted than terrestrial species (LaRoe et al. 1995, Flather and Hoekstra 1989), primarily because many aquatic species have very limited ranges.

TRANSPORTATION-DRIVEN (INDUSTRIAL) DYNAMICS OF LAND-USE CHANGE

The transportation-driven phase of economic development and population growth occurs as population

densities increase, trade develops, and industrial activity begins to complement agriculture as a source of wealth. With the expansion of transportation networks that can move food, human populations are no longer tied as closely to local sources of agricultural production, and thus the connection of population to local NPP begins to weaken.

Human population distribution is freed from dependence on local food production and begins to shift toward locations where transportation concentrates food and other resources. Excess population from high-NPP areas begins to disperse to nodes in the transportation network, which quickly develop into urban/industrial centers. Population densities in the high-NPP agricultural areas often decrease as transportation, technology, and resource inputs increase the efficiency of agricultural production, as illustrated by the decline of family farms as they are consolidated into much larger industrial farms in the midwestern U.S. (Lobao and Meyer 2001).

This pattern of human population and land-use intensity is illustrated by historical census data from the 99 counties in the state of Iowa. (Fig. 5). Earliest settlement spread from the Mississippi River, with the highest population densities in the extreme southeast, where the town of Keokuk is located at the confluence of the Des Moines River with the Mississippi River (Fig. 5A). As shown at 40-yr intervals (Fig. 5B, C, D), population increased most rapidly around Des Moines, located in the center of the state at the confluence of the Raccoon and Des Moines rivers and the southernmost extent of the Wisconsin glaciation (thumb-shaped outline in Fig. 5). All of the counties that developed high populations (Fig. 5D) have major cities located on rivers, at confluences, rapids, or mouths, illustrating the important role of transportation centers for concentrating resources and populations. Associated with the concentration of population in transportation/industrial centers was a decline in population in rural areas. As of 1970, more than half of the counties in the state had been experiencing population decline since 1900 or earlier (Fig. 5E). Similar rural population declines are occurring throughout the midwest and east of the United States (Brown et al. 2005).

This pattern of population change is closely related to soil properties associated with the major landforms of the state (Prior 1991). Des Moines is located at the southern terminus of the Wisconsin glacial advance (10 500 to 30 000 yr BP), which covered the north-central portion of the state, and also affected the areas east and west of the main glacial lobe as a result of glacial drift. These areas, comprising approximately the northern half of the state, have much younger and more fertile soils than the southern half of the state, which was most recently glaciated 130 000 to 300 000 years ago (Illinoian Glaciation). Counties on the relatively poor soils in the southern part of the state suf-

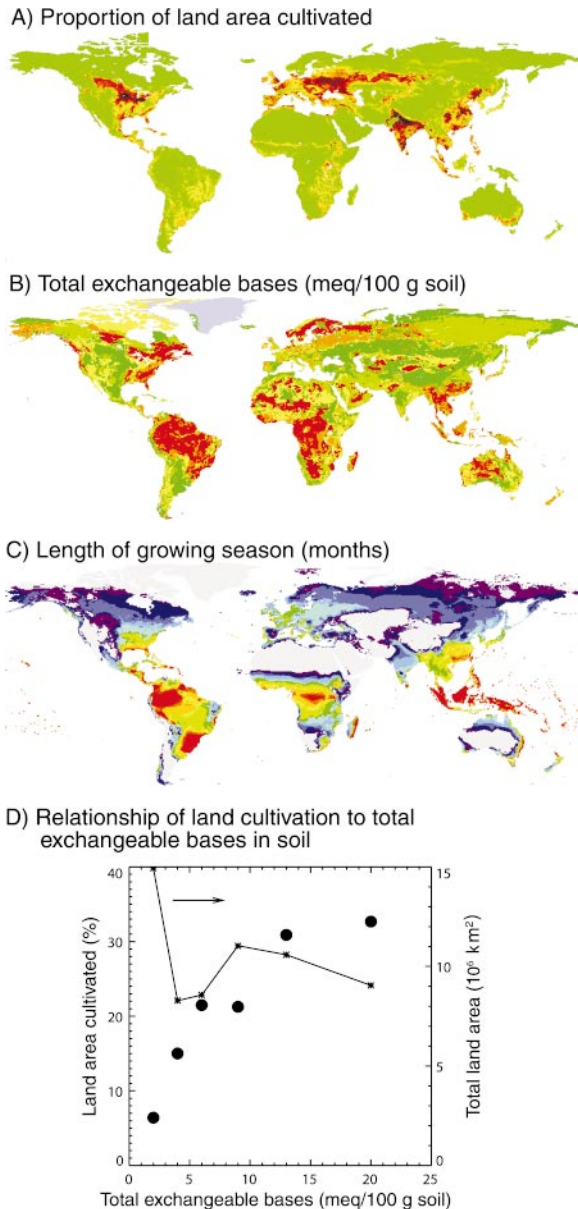


FIG. 3. Global distribution of land cultivation in relation to soil fertility at 0.5° (latitude–longitude) resolution. (A) Global pattern of the percentage of land surface in crops (based on Ramankutty and Foley 1997). Green indicates little or no cultivation, increasing through yellow to red to black at highest levels approaching 100% of land area within a $0.5^\circ \times 0.5^\circ$ cell. (B) Global distribution of one measure of soil fertility (TEB, total exchangeable bases: K, Ca, Mg), approximated for the upper 1 m of soils (based on data from Batjes 1997, 2002). Red indicates TEB of 1–3 meq/100 g soil, increasing through orange and yellow to dark green, indicating TEB of ≥ 16 meq/100 g soil. (C) Global distribution of estimated average growing season length (based on temperature and precipitation data from New et al. [2000]). Red indicates an 11- or 12-month growing season decreasing through yellow, green, and blue to less than one month in gray areas. (D) Scatterplot of land cultivation (percentage of total area in crops) in relation to total exchangeable bases for land areas with estimated growing season of three months

fered the greatest population decline (Fig. 5F), having reached their highest population densities in 1900 or earlier (Fig. 5E). The declining counties in the north-eastern corner of the state occur on a landscape last glaciated over 500 000 years ago, with the oldest soils in the state and a hilly landscape with deep valleys considered by many to be the most scenic area of the state. The shift from rural areas with poor soils to urban areas would be even more dramatic were it not for the mitigating effects of government subsidies (i.e., dollars) flowing from the urban and fertile areas to the less fertile rural areas (e.g., Licht 1997).

As technology improves, the rate and efficiency of transportation increases, and increased wealth improves access to the best technologies. For most of the history of human civilization, water was by far the most efficient means of transportation, and most of the world's great cities are located at the nodes of water transportation systems, particularly harbors and the mouths or confluences of major rivers. The first major relaxation of the waterway constraint was the development of the railway system, followed shortly by the development of the internal combustion engine and highways (Stutz and de Sousa 1998). These new modes of transportation often reinforced the historical centers that had already developed near favorable water transport.

As transportation rates and efficiency increase, the limitations of distance decrease and urban/industrial areas can be located farther from the sources of food production. This further reduces the constraint of local NPP on population size and increases the importance of regional NPP, with the size of the region being determined by the efficiency (and thus the cost) of transportation. Local variation in NPP becomes relatively unimportant, but total regional NPP, constrained by soils, temperature, and water, still limits the size of the human population at the regional scale. With increasing wealth and a global transportation system, local human population size can be independent of even regional NPP, as in the oil-rich, but arid, Arabian peninsula.

Environmental properties still influence the size and spatial distribution of human populations, but the constraints on local population are now the availability of transportation pathways, both the natural pathways provided by oceans, lakes, and rivers, and the man-made pathways of railways and roads (Russell 1997). Natural barriers such as mountain ranges may still isolate some areas from effective transportation, as can arid con-

←

or longer. Dots indicate the average percentage of cropland in soils within a specific range of values of TEB (e.g., 1–3 meq/100 g, 3–6 meq/100 g). Total land area in each class of TEB (with growing season ≥ 3 mo) is indicated by the asterisks (right y-axis).

FIG. 4. General patterns of species diversity at three trophic levels in relation to potential net primary productivity (which is determined by the interaction of soil properties with climate) and in relation to mortality caused by natural and anthropogenic processes. The upper graph illustrates maximum predicted diversity as indicated by the dark diagonal area, with diversity decreasing to either side, according to the dynamic equilibrium model of species diversity (Huston 1979, 1994). These predictions have been confirmed by two recent reviews of the effect of grazing mortality on plant diversity (Proulx and Mazumder 1998, Worm et al. 2002). Energy losses resulting from trophic transfer are indicated by the positions of each trophic level along the x-axis (productivity) in the lower graphs, left-hand panels (A, C, E) illustrate the effect of a disturbance gradient on trophic classes of organisms with differing population growth rates (plants highest, carnivores lowest). Right-hand panels (B, D, F) illustrate the effect of a productivity gradient on the three trophic levels when experiencing approximately the same disturbance regime. Note that patterns caused by these processes are expected to disappear as the sample area becomes very large (see Huston 1999).

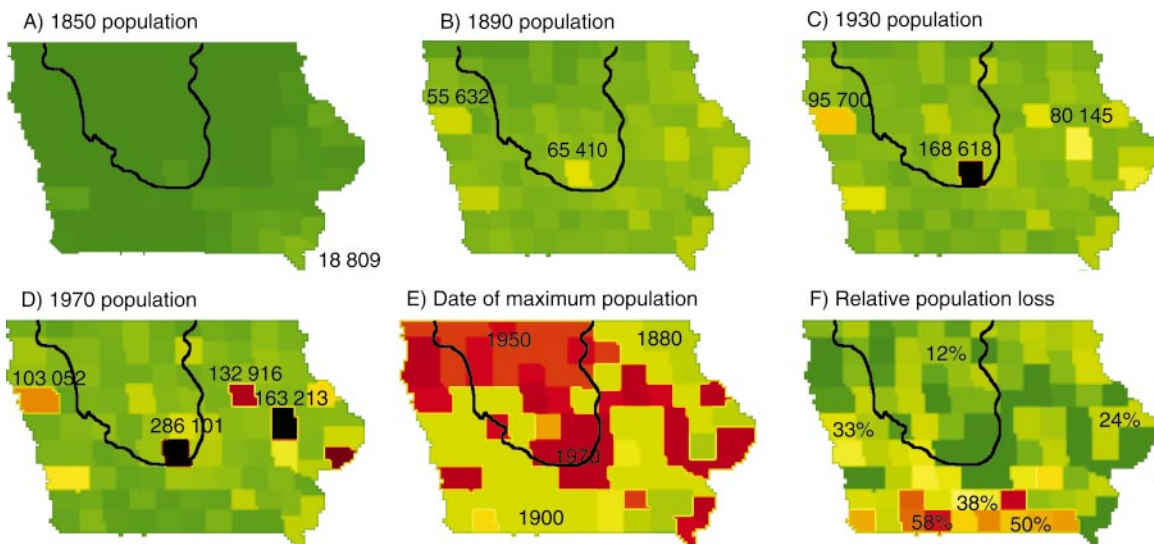
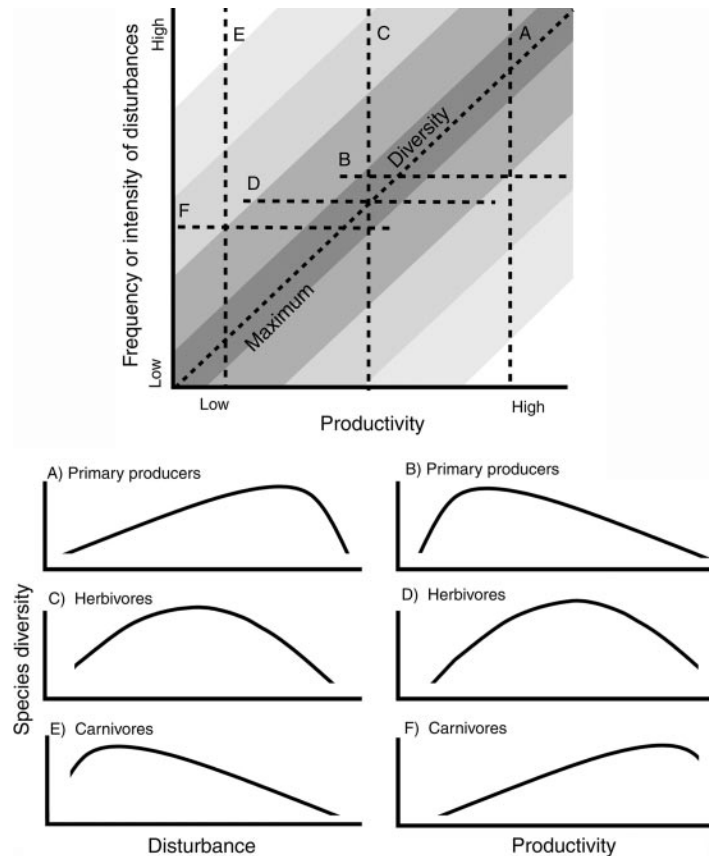


FIG. 5. Shifts of human population from rural areas with poor soils toward urban areas and regions of higher soil fertility in Iowa, based on 1850–1970 county-level U.S. census data (Inter-university Consortium for Political and Social Research 2001). (A–D) Spatial distribution of total population (not including native Americans) by county at 40-yr intervals. Dark green indicates lowest densities, increasing through pale green, yellow, and red to highest levels in black. (E) Census date at which each county reached its maximum population up to 1970. Earliest dates are indicated by pale green, later dates by red and dark red. (F) Relative population loss between maximum population and population in 1970. Greatest loss is indicated by darker reds, decreasing through orange, yellow, and pale green to dark green, indicating no loss.

ditions, which reduce the density of navigable waterways.

Infrastructure developed during one phase of development can create a legacy that influences rates and patterns of development in subsequent phases. However, the influence of infrastructure can be quite ephemeral unless a site has some permanent advantage, such as favorable water transportation or geographical constraints that force land transportation through a specific location. North America, and the rest of the world, is dotted with towns that flourished until the river channel shifted, the cattle drives stopped, the rail line was abandoned, or the local highway was replaced by an interstate highway built nearby (e.g., Burns 1982).

In the industrial stage, human population densities are highest at the transportation nodes where food and raw materials are concentrated, particularly where multiple types of transportation converge, conforming to traditional place-centered economic models. This transportation-driven resource concentration allows much higher local population densities than were possible in the agrarian phase, and consequently, local environmental impacts can be much more severe. Population distributions and impacts are still based on preferential land use, and are thus nonrandom and highly predictable.

In many cases, the land areas selected because of transportation-related properties are also high-NPP lands that were originally selected for food production. Examples are the productive alluvial lands along rivers, including the deltas where rivers flow into lakes or oceans. In addition to the location of population centers, rail corridors and roadways often follow the naturally created low gradients along streams and rivers, reducing the suitability of these areas for biodiversity as well as for agriculture. Urban/industrial development can even displace agriculture from high-NPP lands, not because of the NPP, but because of the proximity to transportation and industry. This is occurring on the fertile soils around Des Moines, Iowa (Fig. 5D), as well as in many other cities throughout the country (Brown et al. 2005).

Environmental impacts during the industrial stage are less strongly related to local NPP than during the agrarian stage, although some high-NPP areas can be heavily impacted, as discussed above. The new features of industrial stage environmental impacts are (1) increasing impact on terrestrial areas with low NPP and (2) increasing impacts on aquatic resources and water quality caused by concentrated human populations (Wang et al. 2001, Stepenuck et al. 2002, Hansen et al. 2005). Natural resource extraction, particularly of the energy resources that drive the transportation and industrial economies, can have a major negative impact on local environmental conditions, particularly in unproductive areas where vegetation growth and recovery are slow. Consequently, low NPP areas that escaped

impact during the agrarian stage can be heavily affected by resource extraction and urban/industrial growth.

Improved transportation and industrial technologies allow major changes in agriculture that increase its impact in both highly productive areas already in agricultural land uses, and in less productive areas that escaped impact during the agrarian phase. Industrial production of nitrogen fertilizers, irrigation technologies, and drainage of wet areas (ditching and tiling) allow increased productivity and often increased negative environmental impacts on both terrestrial and aquatic systems, in productive areas. More significant in terms of biodiversity impacts is the extension of agriculture to previously unimpacted lands that were unsuitable for agriculture because of aridity (e.g., the Texas Panhandle or Central Valley of California), or excessive wetness (e.g., the Florida Everglades). These agricultural subsidies generally produce only short-term economic benefits, and production generally decreases over time as a result of factors such as erosion, declining water tables, salinization, micronutrient depletion, or soil subsidence. Even on the short term, these subsidies are effective primarily in areas that already have all the required plant resources except for one that can be added at relatively low cost, such as irrigation in an area with high levels of required soil nutrients.

An indirect environmental benefit of the industrial stage is reduction of the human population density in agricultural regions (Lobao and Meyer 2001). This occurs both because of the increased efficiency of agricultural production made possible by transportation and new technologies (Weiss 1993, also, hybrid seeds and the "green revolution"), and by the economic activity and jobs in the urban/industrial centers. This depopulation results in the abandonment of marginal agricultural lands (e.g., Fig. 5F, southern and northeastern Iowa), which has led to substantial forest regeneration in the northeastern U.S. (Hall et al. 2002, Foster et al. 2003, Brown et al. 2005), as well as reduced grazing impacts and grassland re-establishment in the western grasslands (Licht 1997). The local recovery of many native animal species is associated with re-establishment of native vegetation (Askins 1993, 2000). An additional consequence of these population shifts and land-use transitions is an increasing concentration of agricultural production on the most suitable, high-NPP lands. This intensive, and potentially sustainable, concentration of agricultural production reduces the "environmental footprint" of food production, and allows the preservation of less productive lands that can support substantial biodiversity. If food production were less efficient, or if human populations continue to grow, these marginal lands would be brought into production, with negative consequences for biodiversity (Avery 1995, Huston 1995, Waggoner and Ausubel 2001).

COMMUNICATION-DRIVEN DYNAMICS
OF LAND-USE CHANGE

The communication-driven (information) stage of economic development removes most of the remaining locational constraints on the generation and use of wealth (Levitt 2002). During both the agrarian and industrial stages wealth generation, and consequently human population density, was restricted to specific locations. The initial restriction to productive lands was later expanded to include the urban/industrial centers at transportation nodes. Over the last few decades of the 20th century, developed countries have seen the creation of an information infrastructure that allows the transmission of vast amounts of information without any direct physical connection between source and recipient. Processing and exchange of this information has created a new means for generating wealth that allows human populations to be redistributed even more independently of environmental constraints.

Nonetheless, some constraints do remain. Humans still require food and water, which must be available from local sources or through transportation from distant sources. In addition, material for construction of shelter and other necessities must be available. Consequently, populations become independent of either local production of food and other resources, or effective transportation systems, but not both. This shift is facilitated by continuously improving transportation, which allows rapid long-distance transport of not only food and natural resources, but luxury products as well. Local generation of wealth, by information processing or other means, is not even a necessity, since wealth generated in urban/industrial centers can be easily transferred electronically for use in areas far from traditional sources of wealth (e.g., Jacobs 1984).

Redistribution of human population in the communication-driven stage is almost completely independent of local and even regional net primary productivity. Preferential use of the landscape is driven by aesthetic concerns, such as views of natural scenery and the beauty of local features such as vegetation, rocks, and streams (Hansen et al. 2005). People can now build homes on hillsides and ridgetops, which often have low productivity but high biodiversity value, without any concern for being able to obtain food, wealth, or even water from the local environment. High productivity areas, such as stream valleys and lakeshore, may also have desirable aesthetic properties that make them more valuable as home sites than for agricultural production. Rural growth has become almost totally independent of soil properties and NPP.

The greatest impact of this change has been in regions with low NPP, such as the western mountains, deserts, and shrublands (see Brown et al. 2005: Fig. 1, Hansen et al. 2005). These areas tend to have much higher densities of naturally rare "endemic" species of plants and animals than more productive areas of

the country. Because of rapid urban and rural growth these western endemics now comprise a large proportion of the species listed as threatened and endangered (Flather et al. 1994). These unproductive areas were largely ignored during the agrarian and transportation stages, but have now become increasingly popular "amenity destinations" for human populations that are heavily dependent on resources brought in from outside the region (Rasker and Hansen 2000).

The low productivity of these environments makes them particularly sensitive to disturbances caused by human activities. Populations of plants and animals tend to be smaller, and to recover more slowly than in more productive areas, making them more susceptible to mortality caused by land clearing, road development, and other activities. These plant communities tend to be easily invaded by exotic species (Huston 1994, 2004), and the introduction of exotic predator species such as dogs, cats, and foxes can have a devastating effect on native vertebrates (Abbott 2001, Hansen et al. 2005). Even at low average density, humans can have severe impacts in these less productive regions because human land use is concentrated in the small percentage of the landscape that is critical for ecosystem function and biodiversity because of its water availability and higher productivity (Hansen et al. 2005), and also because high interannual variability of productivity contributes to overgrazing (Freudenberger and Noble 1997).

Changes in natural disturbance regimes, such as increases or decreases in fire frequencies, or flood control, can also have major impacts (Huston 2003, Hansen et al. 2005). The small proportion of the landscape that has high NPP, primarily riparian corridors, springs, and marshes, is particularly susceptible to impacts such as fragmentation, blockage of riparian dispersal corridors, and conversion to other uses. A decrease in the disturbance regime on any but the least productive portions of the landscape is likely to result in an accumulation of biomass, including fuel for fires, and a reduction of plant diversity due to competition during succession. The combination of "forest fringe" development with fire suppression has contributed to the increased costs of western forest fires in terms of economic losses and loss of human life. Many of these problems are concentrated in the ponderosa pine zone, which, in the absence of fire suppression has a relatively high frequency of low severity fires (Agee 1993), but quickly produces a sufficient fuel load to support high severity crown fires (Moore et al. 2004).

Most of the public lands in the United States occur in these agriculturally marginal, low-productivity landscapes (Huston 1993, Scott et al. 2001), which are the primary reservoir for much of our biodiversity, especially large vertebrates and predators. Many species that survive in these environments depend on rare, high productivity riparian and wetland areas for feeding and

reproduction (Hansen and Rotella 2002a). Unfortunately, these productive areas tend to be privately owned and not included in the publicly-owned national parks and forests. Disturbance and development of these productive environments have potential negative effects on biodiversity that far exceed their proportional representation on low-productivity landscapes.

CONCLUSION AND IMPLICATIONS

The three stages of technological development, human population dynamics, and land-use change described in this paper form a well-known historical sequence that has already occurred in the developed countries of the world. All countries in the world have experienced the agrarian phase, but in some countries this phase still dominates economic activity and land use (Huston 1993). In the less-developed countries, all three stages may exist simultaneously and the industrial phase may be shortened or skipped completely in some areas.

These three phases produce very different patterns of human population distribution and thus very different patterns of land use and impacts on the environment and biodiversity. Each phase has predictable patterns, with impacts that range from local to global, depending on the availability and distribution of the resources necessary for human population growth.

The impact of the agrarian phase is strongly constrained by local conditions, to the extent that areas with low primary productivity are little impacted by human land use. Agrarian land-use transformations affect primarily common species in productive areas, and have their greatest negative effects on the population sizes of large vertebrates.

The transportation/industrial phase is less dependent on net primary productivity than the agrarian phase, and begins to extend the environmental impacts of human land use to the lower productivity areas that were avoided during the agrarian phase. One side-effect of this stage is a reduction of rural population densities, and subsequent recovery of natural vegetation and some wildlife species, that often occurs as economic activity and jobs shift to the urban/industrial centers.

The human population distribution during the communication phase is independent of local primary production, but is nonetheless constrained by regional or national levels of productivity that determine the total human population, as well as influence the financial resources available for transportation and communication infrastructure. One consequence of this phase is an increase in rural population densities, particularly in low-productivity, high "amenity value" areas, which attract people with sources of wealth that are independent of local environmental conditions. The increase of human population and disturbance on low-productivity areas can have a severe impact on the rare and/or endemic species that occur predominantly in

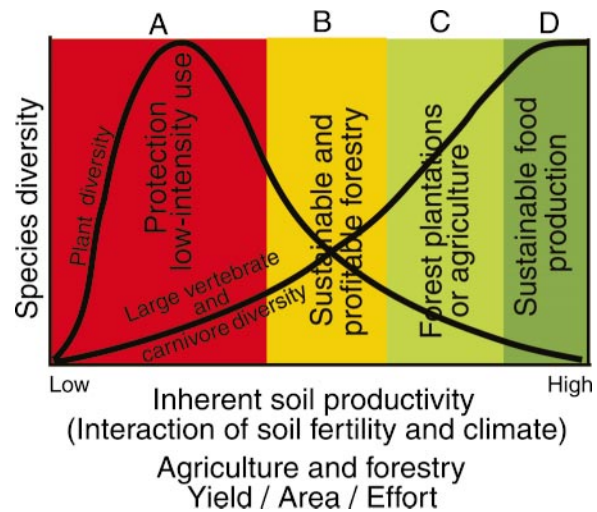


FIG. 6. Sustainable distribution of land uses in relation to natural variation in primary productivity (determined by interaction of soil properties and climate) and the general patterns of plant and large animal diversity. (A) Areas with low primary productivity tend to have low abundance and diversity of carnivores and large vertebrates, and a wide range of plant diversity, ranging from very low to the highest levels found anywhere. Low productivity limits sustainable land uses to protection, with substantial benefits in terms of hydrologic function, conservation, and carbon sequestration. (B) Moderate productivity allows higher abundance and diversity of large vertebrates, and potentially sustainable forestry. (C) High productivity allows potentially sustainable agriculture and plantation forestry on lands that, in the absence of human disturbance, could support a high abundance and diversity of large vertebrates, but relatively low plant diversity. (D) The highest levels of productivity support the highest abundance and diversity of carnivores and large vertebrates, but most of these lands are now used for intensive agriculture. High-productivity sustainable agriculture in these areas requires the least land area per unit of food production, and potentially reduces pressure to cultivate less productive lands that may have higher plant diversity. While the loss of plant diversity through cultivation of high-productivity lands is relatively low, the loss of carnivore and large vertebrate diversity is extremely high (based on Huston 1994, 1995).

these environments. Until recently, these low-productivity areas have been the primary refuges for the biodiversity that escaped the impacts of the agrarian stage.

This productivity-based approach to understanding human population dynamics and land-use dynamics helps explain the current distribution of land use in relation to patterns of biodiversity. In addition, it helps clarify which components of biodiversity are most likely to be impacted during different stages of technological and economic development, and by different types of land uses. These principles suggest a preferred distribution of land uses in relation to productivity (Fig. 6) that tends to minimize negative impacts on the diversity of plants and small animals, but inevitably has strong negative effects on the large vertebrates that compete most directly with human land uses. Because the agricultural value of land tends to reflect the po-

tential primary productivity of the land, it is not surprising that the most cost-effective solutions for conservation of threatened and endangered species tend to select large expanses of unproductive, low value lands in the semiarid west and southwest (Ando et al. 1998). Understanding the inevitable tradeoffs that are made between human land use and biodiversity conservation is essential for conservation planning and sustainable land management.

ACKNOWLEDGMENTS

This manuscript was improved by comments from Bill Schramm, Andy Hansen, and two anonymous reviewers. I especially thank Navin Ramankutty for providing his global map of crop area and the Inter-university Consortium for Political and Social Research for access to their summary of U.S. census data. Sidey Timmins and Tris West provided help with GIS programming. M. Huston was partially supported by the EPA Science to Achieve Results (STAR) Program Grant R-82889701-0, by a grant from the National Council for Science for Sustainable Forestry (NCSSF) to Interdisciplinary Solutions for Environmental Sustainability, Inc. (ISESI), Oak Ridge, Tennessee, and by the U.S. Department of Energy Office of Biological and Environmental Research. Although the research described in the article has been funded in part by the U.S. Environmental Protection Agency's STAR Program, it has not been subjected to any EPA review and therefore does not necessarily reflect the views of the Agency, and no official endorsement should be inferred.

LITERATURE CITED

- Abbott, I. 2001. The Bilby *Macrotis lagotis* (Marsupialia: Peramelidae) in south-western Australia: original range limits, subsequent decline, and presumed regional extinction. *Records of the Western Australian Museum* **20**:271–305.
- Agee, J. K. 1993. *Fire ecology of Pacific Northwest forests*. Island Press, Washington, D.C., USA.
- Ando, A., J. Camm, S. Polasky, and A. Solow. 1998. Species distributions, land values, and efficient conservation. *Science* **279**:2126–2128.
- Askins, R. A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. *Current Ornithology* **11**:1–34.
- Askins, R. A. 2000. *Restoring North America's Birds: lessons from landscape ecology*. Yale University Press, New Haven, Connecticut, USA.
- Avery, D. T. 1995. *Saving the world with pesticides and plastic: the environmental triumph of high-yield farming*. Hudson Institute, Indianapolis, Indiana, USA.
- Bailey, R. G. 1989. *Ecoregions of the continents*. USDA Forest Service, Washington, D.C., USA.
- Bailey, R. G. 1995. *Description of the ecoregions of the United States*. Miscellaneous Publication 1391. USDA Forest Service, Washington, D.C., USA.
- Bashkin, M., T. J. Stohlgren, Y. Otsuki, M. Lee, P. Evangelista, and J. Belnap. 2003. Soil characteristics and plant exotic species invasions in the Grand Staircase—Escalante National Monument, Utah, USA. *Applied Soil Ecology* **22**:67–77.
- Batjes, N. H. 1997. A world data set of derived soil properties by FAO-UNESCO soil unit for global modeling. *Soil Use and Management* **13**:9–16.
- Batjes, N. H. 2002. *ISRIC-WISE global data set of derived soil properties on a 0.5 by 0.5 degree grid. (Version 2. 0)*. ISRIC Report 2002/03. International Soil Reference and Information Centre, Wageningen, The Netherlands.
- Berendse, F. 1994. Competition between plant populations at low and high nutrient supplies. *Oikos* **71**:253–260.
- Blockstein, D. E., and H. B. Tordoff. 1985. Gone forever—a contemporary look at the extinction of the Passenger Pigeon. *American Birds* **39**:845–851.
- Brown, D. G., K. M. Johnson, T. R. Loveland, and D. M. Theobald. 2005. Rural land-use trends in the conterminous United States, 1950–2000. *Ecological Applications* **15**:1851–1863.
- Burns, N. 1982. *The collapse of small towns on the Great Plains; a bibliography*. Emporia State Research Studies, Emporia, Kansas, USA.
- Christaller, W. 1933. *Die zentralen Orte in Süddeutschland*. Gustav Fischer, Jena, Germany. [Translated, in part, by Charlisle W. Baskin, 1966. *Central places in southern Germany*. Prentice Hall, Englewood Cliffs, New Jersey, USA.]
- Christaller, W. 1972. How I discovered the theory of central places: a report about the origin of central places. Pages 601–610 in P. W. English and R. C. Mayfield, editors. *Man, space and environment*. Oxford University Press, Oxford, UK.
- Craig, N., and P. Halais. 1934. The influence of maturity and rainfall on the properties of lateritic soils in Mauritius. *Empire Journal of Experimental Agriculture* **2**:349–358.
- Cronon, W. 1983. *Changes in the land: Indians, colonists, and the ecology of New England*. Hill and Wang, New York, New York, USA.
- Detling, J. 1998. Mammalian herbivores: ecosystem-level effects in two grassland national parks. *Wildlife Society Bulletin* **26**:438–448.
- Dodson, S. I., S. E. Arnott, and K. L. Cottingham. 2000. The relationship in lake communities between primary production and species richness. *Ecology* **81**:2662–2679.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1992. *Birds in Jeopardy: the imperiled and extinct birds of the United States and Canada*. Stanford University Press, Stanford, California, USA.
- Fahnestock, J. T., and J. K. Detling. 1999. Plant responses to defoliation and resource supplementation in the Pryor Mountains. *Journal of Range Management* **52**:263–270.
- Flather, C. H., and T. W. Hoekstra. 1989. *An analysis of the wildlife and fish situation in the United States, 1989–2040*. USDA Forest Service, General Technical Report RM-178.
- Flather, C. H., L. A. Joyce, and C. A. Bloomgarden. 1994. *Species endangerment patterns in the United States*. USDA-FS General Technical Memo RM-241. Fort Collins, Colorado, USA.
- Foster, D. R., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. 2003. The importance of land-use and its legacies to ecology and environmental management. *BioScience* **53**:77–88.
- Freudenberger, D., and J. Noble. 1997. Consumption, regulation, and off-take: a landscape perspective on pastoralism. Pages 35–48 in J. Ludwig, D. Tongway, D. Freudenberger, J. Noble, and K. Hodgkinson, editors. *Landscape ecology, function, and management: principles from Australia's rangelands*. CSIRO Publishing, Melbourne, Australia.
- Gaston, K. J., and T. M. Blackburn. 1996. Global scale macroecology: interactions between population size, geographic range size and body size in Anseriformes. *Journal of Animal Ecology* **65**:701–714.
- Goudie, A. 1981. *The human impact on the natural environment*. MIT Press, Cambridge, Massachusetts, USA.
- Green, R. A., and J. K. Detling. 2000. Defoliation-induced enhancement of total aboveground nitrogen yield of grasses. *Oikos* **91**:280–284.
- Grime, J. P. 1973a. Competitive exclusion in herbaceous vegetation. *Nature* **242**:344–347.

- Grime, J. P. 1973*b*. Control of species density in herbaceous vegetation. *Journal of Environmental Management* **1**:151–167.
- Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley, New York, New York, USA.
- Grime, J. P. 2001. Plant strategies, vegetation processes, and ecosystem processes. Second edition. Wiley, New York, New York, USA.
- Hall, J. B., and M. D. Swaine. 1976. Classification and ecology of closed-canopy forest in Zghana. *Journal of Ecology* **64**:913–951.
- Hall, B., G. Motzkin, D. R. Foster, M. Syfert, and J. Burk. 2002. Three hundred years of forest and land-use change in Massachusetts, USA. *Journal of Biogeography* **29**:1319–1335.
- Hansen, A. J., R. L. Knight, J. Marzluff, S. Powell, K. Brown, P. H. Gude, and K. Jones. 2005. Effect of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecological Applications* **15**:1893–1905.
- Hansen, A. J., R. Rasker, B. Maxwell, J. J. Rotella, A. Wright, U. Langner, W. Cohen, R. Lawrence, and J. Johnson. 2002. Ecology and socioeconomics in the New West: a case study from Greater Yellowstone. *BioScience* **52**:151–168.
- Hansen, A. J., and J. J. Rotella. 2002*a*. Biophysical factors, land use, and species viability in and around nature reserves. *Conservation Biology* **16**:1–12.
- Hansen, A. J., and J. J. Rotella. 2002*b*. Rural development and biodiversity: a case study from Greater Yellowstone. Pages 123–140 in J. Levitt, editor. *Conservation in the Internet age*. Island Press, New York, New York, USA.
- Hansen, A. J., J. J. Rotella, M. L. Kraska, and D. Brown. 2000. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. *Landscape Ecology* **15**:505–522.
- Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. *Science* **105**:367–368.
- Huston, M. A. 1979. A general hypothesis of species diversity. *American Naturalist* **113**:81–101.
- Huston, M. A. 1980. Soil nutrients and tree species richness in Costa Rican forests. *Journal of Biogeography* **7**:147–157.
- Huston, M. A. 1985. Patterns of species diversity on coral reefs. *Annual Review of Ecology and Systematics* **16**:149–177.
- Huston, M. A. 1993. Biological diversity, soils, and economics. *Science* **262**:1676–1680.
- Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, UK.
- Huston, M. A. 1995. Saving the planet: report on a farm policy conference. *Bulletin of the Ecological Society of America* **76**:97–99.
- Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* **86**:393–401.
- Huston, M. A. 2003. Understanding the effects of fire and other mortality-causing disturbances on species diversity. Pages 51–84 in N. C. Burrows and I. Abbott, editors. *Fire in south-western Australian forests: impacts and management*. Backhuys Publishers, Leiden, The Netherlands.
- Huston, M. A. 2004. Management strategies for plant invasions: manipulating productivity, disturbance, and competition. *Diversity and Distributions* **10**:167–178.
- Hyams, E. 1952. *Soil and civilization*. Thames and Hudson, London, UK.
- Iacobelli, A., and R. J. Jefferies. 1991. Inverse salinity gradients in coastal marshes and the death of stands of *Salix*—the effect of grubbing by geese. *Journal of Ecology* **79**:61–73.
- Inter-university Consortium for Political and Social Research. 2001. Historical, demographic, economic and social data: the United States 1790–1970. ICPSR 0003, 0007, 0008, 0009, 0014, 0017. Inter-university Consortium for Political and Social Research, Ann Arbor, Michigan, USA.
- Jacobs, J. 1984. *Cities and the wealth of nations*. Random House, New York, New York, USA.
- Jetz, W., and C. Rahbek. 2002. Geographic range size and determinants of avian species richness. *Science* **297**:1548–1551.
- Kalkhan, M. A., and T. J. Stohlgren. 2000. Using multi-scale sampling and spatial cross-correlation to investigate patterns of plant species richness. *Environmental Monitoring and Assessment* **64**:591–605.
- Kerbes, R. H., P. M. Kotanen, and R. L. Jefferies. 1990. Destruction of wetland habitats by lesser Snow Geese—a keystone species. *Journal of Applied Ecology* **27**:242–258.
- Kessell, S. R. 1979. *Gradient modeling: resource and fire management*. Springer-Verlag, New York, New York, USA.
- LaFon, C. W., M. A. Huston, and S. P. Horn. 2000. Effects of agricultural soil loss on forest succession rates and tree diversity in East Tennessee. *Oikos* **90**:431–441.
- Larcher, W. 1980. *Physiological plant ecology*. Springer-Verlag, Berlin, Germany.
- LaRoe, E. T., G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. 1995. *Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems*. U.S. Department of the Interior, National Biological Service, Washington, D.C., USA.
- Levitt, J., editor. 2002. *Conservation in the Internet age*. Island Press, New York, New York, USA.
- Licht, D. S. 1997. *Ecology and economics of the Great Plains*. University of Nebraska Press, Lincoln, Nebraska, USA.
- Lietzke, D. A. 1994. *Soils of Walker Branch watershed*. ORNL/TM-11606. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Lobao, L., and K. Meyer. 2001. The great agricultural transition: crisis, change, and social consequences of twentieth century US farming. *Annual Review of Sociology* **27**:103–124.
- Lösch, A. 1938. The nature of economic regions. *Southern Economic Journal* **5**:71–78.
- Mahdi, A., R. Law, and A. J. Willis. 1989. Large niche overlaps among coexisting plant species in a limestone grassland community. *Journal of Ecology* **77**:386–400.
- McShea, W., H. B. Underwood, and J. H. Rappole. 1997. *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C., USA.
- Meggers, B. J. 1971. *Amazonia: man and culture in a counterfeit paradise*. Smithsonian Institution Press, Washington, D.C., USA.
- Moore, M. M., D. W. Huffman, P. Z. Fule, and W. W. Covington. 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. *Forest Science* **50**:162–176.
- New, M., M. Hulme, and P. D. Jones. 2000. Representing twentieth century space–time climate variability. Part II. Development of a 1961–1990 mean monthly terrestrial climate fields. *Journal of Climate* **13**:2217–2238.
- Omernik, J. M. 1987. Ecoregions of the coterminous United States. *Annals of the American Association of Geographers* **77**:118–125.
- Omernik, J. M. 1995. Level III ecoregions of the continent. U.S. EPA National Health and Environmental Effects Research Laboratory, Washington, D.C., USA.

- Omernik, J. M., and R. G. Bailey. 1997. Distinguishing between watersheds and ecoregions. *Journal of the American Water Resources Association* **33**:935–949.
- Owen, J. G. 1988. On productivity as a predictor of rodent and carnivore diversity. *Ecology* **69**:1161–1165.
- Prior, J. C. 1991. *Landforms of Iowa*. University of Iowa Press, Iowa City, Iowa, USA.
- Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient poor versus nutrient rich ecosystems. *Ecology* **79**:2581–2592.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**:652–661.
- Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochemistry* **13**:997–1027.
- Rasker, R., and A. J. Hansen. 2000. Natural amenities and population growth in the Greater Yellowstone region. *Human Ecology Review* **7**:30–40.
- Rogers, C. M., and M. J. Caro. 1998. Song sparrows, top carnivores and nest predation: a test of the mesopredator release hypothesis. *Oecologia* **116**:227–233.
- Russell, E. W. B. 1997. *People and the land through time: linking ecology and history*. Yale University Press, New Haven, Connecticut, USA.
- Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plant, plant populations, and communities: a review. *American Midland Naturalist* **146**:1–26.
- Schorger, A. W. 1955. *The Passenger Pigeon: its natural history and extinction*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Schwartz, C. C., S. D. Miller, and M. A. Haroldson. 2003. Grizzly bear. Pages 556–586 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. *Wild mammals of North America*. John Hopkins University Press, Baltimore, Maryland, USA.
- Scott, J. M., F. W. Davis, R. G. McGuire, R. G. Wright, C. Groves, and J. Estes. 2001. Nature reserves: do they capture the full range of America's biological diversity? *Ecological Applications* **11**:999–1007.
- Scott, J. M., P. J. Heglund, M. Morrison, M. Raphael, J. Hauffer, and B. Wall, editors. 2002. *Predicting species occurrences: issues of scale and accuracy*. Island Press, Washington, D.C., USA.
- Stepenuck, K. F., R. L. Crunkilton, and L. Z. Wang. 2002. Impacts of urban landuse on macroinvertebrate communities in southeastern Wisconsin streams. *Journal of the American Water Resources Association* **38**:1041–1051.
- Stutz, F. P., and A. R. de Souza. 1998. *The world economy: resources, location, trade, and development*. Third edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- Tosi, J., and R. F. Voertman. 1964. Some environmental factors in the economic development of the tropics. *Economic Geography* **40**:189–205.
- Trimble, S. W. 1974. *Man-induced soil erosion on the Southern Piedmont 1700–1970*. Soil Conservation Society of America, Madison, Wisconsin, USA.
- Turner, B. L., II, W. C. Clark, R. W. Kates, R. F. Richards, J. T. Matthews, and W. B. Meyer, editors. 1990. *The Earth as transformed by human action: global and regional changes in the biosphere over the past 300 years*. Cambridge University Press, Cambridge, UK.
- Vaughan, M. R., and M. R. Pelton. 1995. Black bears in North America. Pages 100–103 in E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. *Our living resources: a report to the nation on the distribution, abundance, and health of U. S. plants, animals, and ecosystems*. U.S. Department of Interior, National Biological Service, Washington, D.C., USA.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**:494–499.
- Waggoner, P. E., and J. H. Ausubel. 2001. How much will feeding more and wealthier people encroach on forests? *Population and Development Review* **27**:239–257.
- Walter, H. 1979. *Vegetation of the Earth and ecological systems of the geo-biosphere*. Springer-Verlag, New York, New York, USA.
- Wang, L. Z., J. Lyons, and P. Kanehl. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. *Environmental Management* **28**:255–266.
- Weiss, T. 1993. Long-term changes in United States agricultural output per worker, 1800–1900. *Economic History Review* **46**:423–441.
- Whitney, G. G. 1994. *From coastal wilderness to fruited plain: a history of environmental change in temperate North America from 1500 to the present*. Cambridge University Press, Cambridge, UK.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* **26**:1–80.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou, Oregon and California. *Ecological Monographs* **30**:279–338.
- Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* **3**:165–173.
- Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* **280**:2126–2128.
- Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem functioning. *Nature* **417**:848–851.