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Supporting Online Material

www.sciencemag.org/cgi/content/full/316/5833/1862/DC1 Materials and Methods SOM Text Tables S1 and S2 References

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Domesticated Nature: Shaping Landscapes and Ecosystems for Human Welfare

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Like all species, humans have exercised their impulse to perpetuate and propagate themselves. In doing so, we have domesticated landscapes and ecosystems in ways that enhance our food supplies, reduce exposure to predators and natural dangers, and promote commerce. On average, the net benefits to humankind of domesticated nature have been positive. We have, of course, made mistakes, causing unforeseen changes in ecosystem attributes, while leaving few, if any, truly wild places on Earth. Going into the future, scientists can help humanity to domesticate nature more wisely by quantifying the tradeoffs among ecosystem services, such as how increasing the provision of one service may decrease ecosystem resilience and the provision of other services.

omestication of plants and animals may be the single most important feature of the human domination of our planet. Domestication involves the selection of traits that fundamentally alter wild species to become more useful to us. For example, wheat has been selected for larger and more seeds per plant, hatchery-raised trout are selected for rapid growth, and dogs have been selected for an ability to live and even communicate with humans (1).

Humans did not, however, stop with simply domesticating a few chosen species; we have domesticated vast landscapes and entire ecosystems. Moreover, just as domesticated plants and animals have predictable and repeatable traits among different species, domesticated ecosystems also reveal common traits. In particular, when humans tame nature they seek enhanced productivity, convenient commerce, and protection from predators and storms. However, along with domestication, there is often concurrent and inadvertent selection for maladaptive features in either species or ecosystems. For example, selecting for rapid growth in crop plants may result in plants with reduced investment in structural and chemical defenses (2). Similarly, hatchery trout that are selected for rapid growth often have smaller brains (3). Whereas plant and animal breeders are well aware that domestication involves tradeoffs in vigor, the notion of tradeoffs resulting from the domestication of entire landscapes has only recently received serious scientific attention.

Conservation has often been framed as the science aimed at protecting nature, and especially protecting nature from people. We restate here what others have already emphasized: There really is no such thing as nature untainted by people (4). Instead, ours is a world of nature domesticated, albeit to varying degrees, from national parks to high-rise megalopolises. Facing this reality should change the scientific focus of environmental science. Instead of recounting doom-and-gloom statistics, it would be more fruitful to consider the domestication of nature as the selection of certain desirable ecosystem attributes, such as increased food production, with consequent alteration to other ecosystem attributes that may not be desirable. Under this paradigm, our challenge is to understand and thoughtfully manage the tradeoffs among ecosystem services that result from the inescapable domestication of nature.

The Global Footprint of Humans

Domesticated nature in its simplest form means nature exploited and controlled. To that end, roughly 50% of the world's surface area has been converted to grazed land or cultivated crops (5). More than half of the world's forests have been lost in that land conversion (5). The whole notion of a "virgin rainforest" may be erroneous, with extensive prehistoric human activity evident in what were once thought to be untouched forests in the Amazon and Congo (6). In addition to clearing

land for agriculture, humans target wild species for harvest or elimination. On every continent, humans have eliminated the largest mammals, leaving behind a fauna of smaller species (7).

Nature can be dangerous. To protect themselves and their domesticated animals, humans have been especially quick to kill predators, driving almost every large terrestrial carnivore in the world to near extinction (8). To protect property and lives, humans suppress wildfires (9). To reduce storm surges, humans fortify marine shorelines with jetties and sea walls. In Europe alone, 22,000 km² of the coastline are artificially covered with concrete or asphalt, and where the coasts are severely retreating or eroding, over half are artificially stabilized by jetties or other structures (10). To control rivers for irrigation, hydropower, and flood mitigation, humans have built so many dams that nearly six times as much water is held in storage as occurs in free-flowing rivers (5).

Humans have so tamed nature that few locations in the world remain without human influence. Global maps of human impact indicate that, as of 1995, only 17% of the world's land area had escaped direct influence by humans (4), as indicated by one of the following: human population density greater than one person/km²; agricultural land use; towns or cities; access within 15 km of a road, river, or coastline; or nighttime light detectable by satellite (Fig. 1). The huge magnitude of human impacts is recent, but the presence of impacts such as purposeful wildfires goes back thousands of years (9). The reality of the human footprint renders discussions about what areas of the world to set aside as wild and protected areas as somewhat irrelevant; more germane is a discussion of what tradeoffs we are willing to accept as a result of the domestication of nature.

The Tradeoffs of Domestication

There is no question that humans have been successful in their efforts to avoid predators, produce food, and create trade, thereby enhancing their well-being. Contrary to Malthus's predictions, food production has kept up with, and even outpaced, human population growth (11). In South America, rangelands maintain 10 times as much herbivore biomass as natural ecosystems (12). This massive increase in food supply has been achieved by focusing efforts on planting and consuming a small variety of plants. As of 1999, barley, maize, rice, and wheat occupied almost 40% of global cropland (13). With these agricultural advances, the hand-tomouth lifestyle of preagricultural humans has been

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Fig. 1. The human footprint on Earth. Human impact is expressed as the percentage of human influence relative to the maximum influence recorded for each biome. Data include human population density, land transformation (including global landcover, roads, and cities), electrical power infrastructure (NOAA night-lights data), and access (via roads,

navigable rivers, and coastline) to the land. Map created from data downloaded at www.ciesin.columbia.edu/wild_areas from the Human Footprint dataset generated by the Center for International Earth Science Information Network (CIESIN) at Columbia University and The Wildlife Conservation Society.



Shipping Lanes

Fig. 2. Earth's shipping lanes and network of roads. Each shipping lane data point represents the location where an expendable probe was dropped for sampling of ocean temperature from 14 October 2004 to 15 October 2005. Shipping lanes map created from data downloaded at www.aoml.noaa.gov/phod/trinanes/BBXX from the SEAS BBXX database of the Global Ocean

Road Networks

Observing System Center from the Atlantic Oceanographic and Meteorological Laboratory of the National Oceanic and Atmospheric Administration. The road network is a 1:1 million scale representation of the paved and unpaved roads of the world. Map created from Environmental Systems Research Institute's (ESRI) Digital Chart of the World (DCW) global vectors, created in 1992.

exchanged for access to energy-rich, easily stored grains and the ability to harvest meat and dairy products from livestock at will.

The gains associated with domestication of crops and grazing animals have been counterbalanced by tradeoffs. The maximization of food production in croplands and grazing lands is commonly achieved by altering ecological processes in ways that severely impair natural services distant from the agricultural land itself. Modern agroecosystems require the input of fertilizers that ultimately find their way into watersheds and river basins, leading to blighted coastal zones and deadly algal blooms (14). Modern agroecosystems are also depleted in biodiversity and habitat heterogeneity, often with a reduction in resilience as a result of their biological monotony. For example, when converting diverse natural forests to monoculture plantation forests, we maximize production of wood fiber, with the unintended consequence of increased pest and pathogen outbreaks (15). In addition, although levees and channelization reduce "natural floods" and protect farmlands in fertile flood plains, these attempts to control and contain natural hydrological disturbances lead to the loss of wetlands where rivers meet the ocean, with the result that extreme weather causes greater damage than would otherwise be the case if wetlands were present to mitigate storm surges (16).

The industrialization of fisheries during the 20th century has also required fundamental tradeoffs. For example, for decades the fishing industry has culled the historically large stocks of fish in the Benguela ecosystem off the northern coast of Namibia. Removing these fish has resulted in blooms of undesirable large jellyfish. Before the 1970s, large jellyfish were relatively uncommon in fishing nets. Now, the tonnage of jellyfish caught outweighs that of commercial fish landings by a factor of three (17). The long-term overharvesting of the Benguela ecosystem has converted a naturally diverse and productive system into one that produces mainly jellyfish. More generally, the simplification and alteration of marine ecosystems by human use repeatedly reduces the stability of food production and the resilience of these ecosystems to disturbances (18).

Production also creates surplus, which is traded and becomes the basis for commerce. To facilitate commerce, humans built ports along the world's major coasts and covered vast amounts of land with roads (Fig. 2). Unfortunately, through the conversion of oceans and land into shipping routes and highways, we have created paths for the movement of invasive species, with economic costs amounting to at least \$100 billion per year in the United States alone (19). Commerce is also altering global disease transmission. Disease has always been a part of nature, but the advent of rapid trade and travel means that diseases such as severe acute respiratory syndrome can appear in China and within months spread to 26 countries on five continents (20). Humans now inadvertently transport a wide variety of unwanted organisms,

ranging from invasive plants to pathogens to zebra mussels that clog power intake pipes (21).

Reducing direct risks to humans would, at first glance, seem always to represent a net gain. However, evidence is accruing that human attempts to manage natural disasters and risk can backfire. For example, as a result of fire suppression, fires are less frequent, but they are also more severe and destructive than wildfires that occur at a more natural frequency (9). In coastal systems at risk of storm damage, fortified seawalls can protect against a large wave, but hardened coastlines interfere with the ability of marshes and wetlands to simply retreat inland in the face of current sea level rise (10). Hikers and ranchers are at less risk from predators if mountain lions and grizzly bears are absent, but ecosystems without top carnivores experience dramatic eruptions of herbivore populations that create ecological havoc. For example, regions of Zion National Park in Utah lacking cougars are overgrazed by mule deer populations that in turn exacerbate streambank erosion, resulting in sedimentation of streams that

urban regions are a relatively small percent of Earth's total land, they are rapidly increasing in extent: By 2030, there will be 1.75 billion more urban residents (22), resulting in new urban land cover representing a total area the size of California (23). Urban regions reflect the endpoint of landscape domestication, showing trends that may soon appear in other areas. Urban conditions systematically select for a flora and fauna that are often quite different from those in rural settings (24). Cities harbor species that humans introduce for their functionality or aesthetic appeal, such as lawn grasses and ornamental flowering plants. Urban species come from a subset of families that humans find useful, and the varieties introduced often have been artificially selected to have specialized traits, including stress tolerance and showy flower displays (25, 26). Cities also are havens for species that tend to follow humans without our intentional aid, such as rats, dandelions, and starlings. These species are often "weedy" generalists, tolerant of a wide range of environmental conditions, able to live in marginal

Maximized Productivity		Impacts & Tradeoffs	
Increased Food Production:		Disturbed nitrogen cycle, Marine dead zones	
Increased Animal Production:		Riparian zones damaged; Overuse of antibiotics	
Increased Fisheries Yield:		Ecosystems simplified; Increase in undesirable species	
Reduced risk		Impacts & Tradeoffs	
Fire Suppression:		Larger, more intense fires	
Flood Control:		Wetlands shrink downstream, fish habitat lost	
Predator Removal:		Herbivore populations increase and damage systems	
Coastal Engineering:		Constrained natural adaptation to rising sea level	
Promote Commerce		Impacts & Tradeoffs	
Enhanced Trade:		Spread of disease & invasive species	
		Habitats fragmented, anima	Il dispersal hindered
		Productivity	Impacts and Tradeoffs
		ncrease in Cropland (1700 – 1990)	14% global loss of Forest/Woodland (1700 – 1990)
		ncrease in Pasture (1700 - 1990)	30% global loss of Savanna/grassland (1700 - 1990)
	4-fold increas (US; 1950s –	e in irrigation and water withdrawal 1980)	40 cm/yr average decline in water table of the 451,000 km² Ogallala Aquifer (US; 1993 – 2003)
	123MT fish harvested globally (in 1997)		27MT of this directly discarded as by-catch (in 1997)
	3-fold increas	e in farmed fish (1990 – 1997)	It takes >5kg of wild fish to produce 1kg farmed finfish (1997

Fig. 3. The tradeoffs associated with major dimensions of nature domestication. The benefits of domestication under the three major human modifications of ecosystems are presented alongside concomitant negative impacts or tradeoffs (upper left). For the goal of maximizing productivity, more specific examples of tradeoffs are detailed with quantitative information (lower right). References: land use change (41), water extraction (42), Ogallala (43), fisheries (44).

is harmful to fish (21). Safety from the dangers of nature is often achieved at considerable cost to other ecosystem functions.

Landscape Domestication: From Cities to Wilderness

Cities represent the most domesticated landscapes on the planet, in which every element of the environment has been consciously or unconsciously selected to accord with human desires. Although

habitat, and with a high reproductive rate (27, 28). Urban growth favors these two types of species, at the expense of relatively rare and sensitive species, resulting in regional biotic homogenization (29).

At the other end of the domestication continuum from cities are national parks, nature reserves, and wilderness areas. As of 2006, over 14% of Earth's land area has been designated as a natural protected area, but most of this landscape is under human influence and use (30). Indeed, land set aside as wilderness areas represents only 1% of Earth's land surface (30). The most common form of nature preservation is the creation of nature parks or national parks, which although designated as protected often serve large populations of human visitors (31, 32). Among the world's most visited parks, the Fuji-Hakone-Izu Park in Japan (more than 100 million visitors annually) is 122,690 km² in area and includes spas, hotels, golf courses, and trams (31, 33). The Great Smoky National Park, another frequented park, is suffering from invasive species and erosion problems due to heavy human traffic. Like most nature reserves, Great Smoky National Park requires constant human attention and management to maintain its forests. For instance, to combat a non-native woolly adelgid that is attacking and killing the park's hemlock, park managers have imported predatory beetles from Japan (34). This ironic situation of preserving natural ecosystems by importing non-native species to control undesirable species has been repeated hundreds of times around the world. Even the world's so-called wilderness areas have been tamed by humans. For instance, the high-altitude Uintas wilderness area in Utah is naturally fishless but has been stocked with rainbow and eastern brook trout, resulting in a supposedly "improved wilderness" (35). In the modern world, wilderness is more commonly a management and regulatory designation than truly a system without a human imprint.

Shaping the Path of Domestication

If nature is viewed as a bundle of ecosystem services, then domesticated landscapes represent the promotion of certain ecosystem services over others to provide for lower risk, greater productivity, and convenient commerce. The Millennium Ecosystem Assessment summarized the global trends for 16 ecosystem services and reported that two-thirds of those services are currently declining (5). These declines in ecosystem services are an outcome of selecting and taming nature in a way that leads to increases in food and timber production. To a conservationist interested mainly in biodiversity, we have degraded nature, but to an agronomist, we have altered wild land to make it better serve humans. If one accepts that virtually all of nature is now domesticated, the key scientific and social questions concern future options for the type of domesticated nature humans impose upon the world.

Cities are a good place to start when considering broader implications of domesticated ecosystems. The cumulative resource demands of cities are often expressed as the total land area required to supply those resources, called the "ecological footprint" (36). Every city imports resources and exports waste into a region that is spatially much larger than the city's area. However, there is substantial variation in per capita ecological footprints between rich and poor regions, with the average resident of the United States using six times the area of the average sub-Saharan African (37). Differences in urban form also affect per

capita resource use rates, in which lower-density cities in the United States have 2.4 times the car use as higher-density cities in Europe (38). Most notably, as incomes and consumption have increased, there has been an increase in the per capita ecological footprints in most middle- to high-income cities. It is clear that cities are the main consumers of most ecosystem services. This is important because the desire and value for these services determines the traits that humans select for preservation or elimination. For example, if humans want to maximize food production, landscapes will be domesticated to accommodate a few highproductivity species, plus the human-associated species able to survive in these modified landscapes. If people want more wildlife for recreational hunting, populations of predators of game species will be reduced, and the edge habitat that a few game species prefer will be increased. The choices and actions of urban dwellers influence nature far removed from cities, yet urban dwellers are increasingly unaware of these impacts.

More than 25 years ago, when discussing different views of forestry management and land use, Raup cautioned against the romantic glorification of "wilder is better" (39). Indeed, apart from reproduction, the most natural of all human activities may be the domestication of nature. Some paths of domestication will result in improved ecosystems both for people and for other species; other paths of domestication will result in ecosystems that are clearly better for humans but not for other species; and some paths of domestication will result in ecosystems that are too degraded to benefit people or other species. The key scientific goals for the study of domesticated nature are to understand what tradeoffs exist between the promotion or selection of different ecosystem services and to determine to what extent we can change a negative tradeoff to a positive one by altering the details of our domestication process (Fig. 3). With this understanding will come a science of nature domestication that might guide human activities to minimize the negative aspects and accentuate the human benefits.

When it comes to domesticated species, the theory of quantitative genetics provides a framework for managing tradeoffs among traits in a way that minimizes unfit varieties or breeds. Unfortunately, there is no parallel theory for domesticated ecosystems. One possibility might be the application of resilience theory, which suggests a link between simplified ecosystems and a loss of resilience (40). A second possibility would entail an examination of tradeoffs, perhaps even switches to alternative ecosystem states after some threshold is crossed. Tradeoffs are most likely to create problems when they occur as an abrupt change, with little warning. Because managers and researchers have tended to focus on impacts rather than tradeoffs, there has been no systematic examination of tradeoffs in a way that leads to a useful theory. Without a solid understanding of tradeoffs among ecosystem services, we can expect conservationists to rely on protecting nature from people as the primary form of stewardship. Unfortunately, stewardship based on keeping people out of nature is likely to be unstable with population expansion. A more durable stewardship would manage tradeoffs among ecosystem services so that nature and people simultaneously thrive.

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