URBANIZATION AS A THREAT TO BIODIVERSITY: TROPHIC THEORY, ECONOMIC GEOGRAPHY, AND IMPLICATIONS FOR CONSERVATION LAND ACQUISITION

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ABSTRACT—Habitat loss is often cited as the primary cause of species endangerment in the United States, followed by invasive species, pollution, and direct take. Urbanization, one type of habitat loss, is the leading cause of species endangerment in the contiguous United States and entails a relatively thorough transformation from the "economy of nature" to the human economy. Principles of economic geography indicate that urbanization will continue as a function of economic growth, while principles of conservation biology indicate that the most thorough competitive exclusion occurs in urban areas. These findings suggest the need for an *ecologically* macroeconomic approach to conservation land acquisition strategies.

"Habitat loss" is often cited as the primary cause of species endangerment in the United States, followed by invasive species, pollution, disease, and direct take. However, various types of habitat loss are readily identified, such as logging, mining, agriculture, and urbanization (table 1). When these types of habitat loss are considered separate causes of species endangerment, invasive species are identified as the leading cause of species endangerment in the United States, including Hawaii and Puerto Rico (Czech *et al.* 2000). On the mainland United States, however, urbanization is the

Table 1.— Causes of endangerment for the first 877 (of the current 1,262) species in the United States and Puerto Rico classified as threatened or endangered by the United States Fish and Wildlife Service (from Czech et al. 2000).

Cause	Number of species endangered by cause
Interactions with nonnative species	305
Urbanization	275
Agriculture	224
Outdoor recreation and tourism development	186
Domestic livestock and ranching activities	182
Reservoirs and other running water diversions	161
Modified fire regimes and silviculture	144
Pollution of water, air, or soil	144
Mineral, gas, oil, and geothermal extraction or exploration	140
Industrial, institutional, and military activities	131
Harvest, intentional and incidental	120
Logging	109
Road presence, construction, and maintenance	94
Loss of genetic variability, inbreeding depression, or hybridization	92
Aquifer depletion, wetland draining or filling	77
Native species interactions, plant succession	77
Disease	19
Vandalism (destruction without harvest)	12

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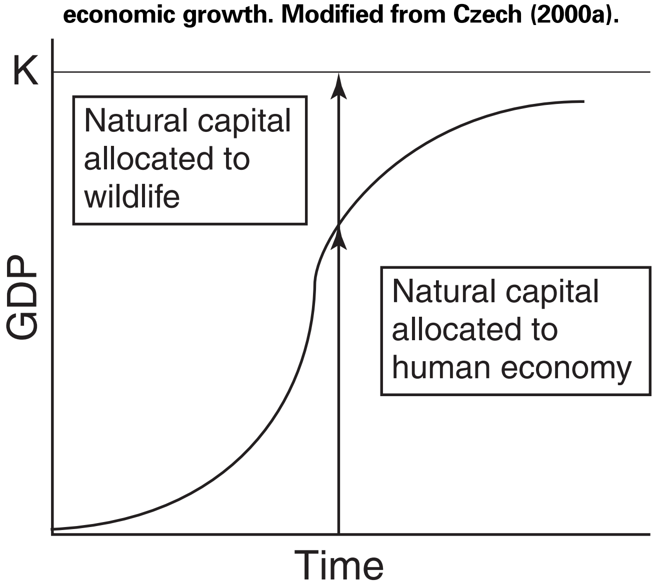
leading cause of endangerment, although it may be overtaken by invasive species in the coming decades. Urbanization and nonnative species invasions are often related, because urbanization disturbs habitats, opens niches to invasive species, and leads to introduction (sometimes intentional) of invasive species.

In most cases of habitat loss, natural capital such as soil, water, timber, grass, or minerals is extracted and reallocated from the "economy of nature" (comprised of nonhuman species) to the human economy (fig 1). In the economy of nature, such natural capital had been used for producing nonhuman individuals and species (Czech 2000a). After its reallocation to the human economy, natural capital is used for producing human goods and services.

In some cases of habitat loss, natural capital is simply cleared away to make room for human economic infrastructure, enterprises, and residences, although some of the natural capital may be salvaged and used, on or offsite, in various economic sectors. This "liquidation" of natural capital is analogous to the tearing down of a warehouse and the disposal of its contents; some is used but much is simply destroyed and replaced (Daly 1996). Natural capital liquidation is often associated with reservoirs and water developments, road construction, and urbanization.

Urbanization is a common type of habitat loss that entails a relatively thorough transformation from the economy of nature to the human economy. The purpose of this paper is to summarize the impact of urbanization on species conservation in the United States and to analyze the impact of urbanization in the context of ecological trophic theory and basic principles of economic geography. A discussion of trophic theory and economic geography principles may help to shed light on management and policy implications for species conservation.

Figure 1.—Reallocation of natural capital from economy of nature to human economy in the process of economic growth. Modified from Czech (2000a).



ECONOMIC TROPHIC LEVELS

In the economy of nature, most species exist within distinct trophic levels, or positions within a food chain. The producer trophic level consists of plants, which produce food and fiber via the process of photosynthesis for their own survival and reproduction (Begon *et al.* 1996). Primary consumers consume producers, secondary consumers consume primary consumers, tertiary consumers consume secondary consumers, and so on. In general, animals consume organisms residing in one or more lower trophic levels. Few species eat purely animal flesh, but animals that consume substantial quantities of plants in addition to other animals are called omnivores.

Some species such as scavengers, decomposers, and parasites do not readily fit into particular trophic levels. They may be designated as "service providers" in the economy of nature (Daily 1997).

In ecological economics, human economies are seen to follow the same basic rules as the ones governing the economy of nature. Therefore, the human economy also has a trophic structure (Czech 2000b). The "producers" in the human economy are the agricultural and extractive sectors. The "primary consumers" are the heaviest manufacturing sectors such as mineral ore refining. Ever-lighter manufacturing sectors, all the way up to industries such as computer-chip manufacturing, constitute higher level consumers.

As in the economy of nature, various economic actors participate up and down the trophic levels. These "service providers" in the human economy include bankers, janitors, insurance providers, health care providers, waiters, and others.

The most habitat-transforming or habitat-liquidating economic sectors constitute the trophic levels in the human economy while the service sectors are directly analogous to the service providers in the economy of nature.

A rule of thumb in ecology states that the biomass making up a trophic level is approximately 10 percent of the biomass making up the next-lower trophic level (Begon *et al.* 1996). Therefore, plants dominate the economy of nature in terms of biomass, while the "super-carnivores" are relatively rare and have the lowest biomass.

The human economy follows similar rules. Although farming is no longer a dominant occupation, agricultural land (much of which is now corporately owned) still dominates the landscape. Forests and rangelands, where logging and cattle ranching are the most common economic activities, also are prominent features of the landscape. In other words, larger areas are required for the operation of the lower trophic levels in the human economy, as in the economy of nature. The manufacturing and service sectors of the human economy tend to be located in the most economically efficient areas, i.e., in or near urban centers (Hanink 1997).

Urbanization involves the proliferation of light-to-medium manufacturing sectors and service sectors, all supported by the agricultural and extractive sectors operating in rural areas. Largely for the sake of economic efficiency, urban areas also tend to comprise residential areas for the labor force.

NICHE BREADTH, CARRYING CAPACITY, AND COMPETITIVE EXCLUSION

Beginning with the assumption that the human economy is a subset of the ecosystem, the principles most relevant to conservation land acquisition that merge conservation biology with ecological economics are niche breadth, carrying capacity, and competitive exclusion. The principle of competitive exclusion is that no species succeeds except at the expense of other species (Pianka 1974). The underlying assumption is that each species has a carrying capacity, and therefore, the collective set of species has an aggregate carrying capacity. No species can claim a larger share of aggregate carrying capacity without infringing upon the niches and therefore carrying capacities of other species.

In the neoclassical economic growth model, carrying capacity for the human economy is not required (Jones 1998) nor is there an requirement for aggregate carrying capacity. The resulting policy implications are perhaps the most alarming aspect of neoclassical economic growth theory and hint at the ecological shortcomings of neoclassical economics (Hall *et al.* 2000). The neoclassical growth theory of unlimited potential is mathematically equivalent to the belief that a limited, stationary scale of human economy could be compacted into a perpetually smaller land mass. Neoclassical growth theory violates well-established principles of conservation biology, thus the need for an *ecologically* macroeconomic approach to conservation land acquisition (Czech 2002).

None of this implies that aggregate carrying capacity is static. Aggregate carrying capacity varies with astrophysical, geological, and evolutionary processes (Fortey 1998). For example, aggregate carrying capacity (for life as we know it) on a hypothetical planet with a temperature of absolute zero will increase as temperatures warm due to astrogeological events, but it will decrease beyond a certain temperature and disappear at a prohibitively hot temperature. Meanwhile, species evolve niches that help to alleviate competitive pressures (Begon *et al.* 1996), thereby increasing aggregate carrying capacity. Even then, an ultimate or final aggregate carrying capacity is entailed by the first and second laws of thermodynamics (Georgescu-Roegen 1971). What is immediately relevant to conservation land acquisition, however, is that when a species succeeds in an unprecedented manner, at a much faster rate than can be explained by astrophysical, geological, and evolutionary processes, the principle of competitive exclusion is fully engaged. The implication is that, due to the tremendous breadth of the human niche and the technologically boosted rate of its expansion, the scale of the human economy increases at the competitive exclusion of wildlife in the aggregate (Czech *et al.* 2000). Evidence for this relationship is both theoretical and empirical (Trauger *et al.* 2003). This relationship is, in fact, the reason why conservation lands have become necessary. As with most conservation tools, and by the definition of conservation, a system of conservation lands ultimately amounts to a brake on economic growth.

ASSOCIATION OF URBANIZATION WITH OTHER CAUSES OF SPECIES ENDANGERMENT

Urbanization has led to the imperilment of at least 275 threatened and endangered species in the United States and Puerto Rico (Czech *et al.* 2000). Urbanization is strongly associated with other prominent causes of endangerment such as roads and industrial development (Czech *et al.* 2000). This association helps to identify urbanization as both a proximate cause of species endangerment and a co-symptom of the ultimate cause, i.e., economic growth, which results in a higher extent and intensity of urbanization in addition to the various other habitat-transforming economic sectors more common to exurban areas.

ECONOMIC GEOGRAPHY AND LAND PRICES

With economic growth as a national goal and facilitated by a capitalist democracy in which the majority are fully supportive, the scale of the American economy is expanding and will continue to do so for the foreseeable future. This economic expansion has quantitative and qualitative effects on land use. One of the quantitative effects is rising land prices. This rise occurs because all economic sectors rely to some extent directly on a land base from which to conduct activities; farms, factories, and Internet work stations all use space. The productive or agro-extractive trophic level is most land-intensive in terms of acreage required per monetary unit of transaction (Cramer and Jensen 1994). Land prices rise as the scale of the economy expands because (1) the Earth provides a finite land base and therefore land scarcity increases as more land is claimed for economic production; (2) demand for land increases with economic growth due to the trophic structure of human economy, and; (3) prices rise with scarcity and demand (Dobson *et al.* 1995).

Land prices do not rise uniformly nationwide, however. They rise fastest in areas where the combination of scarcity and demand rises fastest. Land scarcity is a function of economic activity and is most pronounced where lands are already fully employed for economic activity, but in some cases land scarcity results from ecological processes (e.g., desertification). Demand for land may be for production or consumption.

A growing economy, especially a relatively self-sufficient economy such as that of the United States, represents an integrated expansion of its trophic structure (Boulding 1993). It must first have an adequate productive level: farming, mining, logging, ranching, and fishing. The surplus arising from this productive or agro-extractive level enables the division of labor and resulting manufacturing sectors such as those that produce farm implements and extractive equipment. Next, transportation, financial, and information services proliferate. Value is added to products along each step of the way. For example, the value of a unit of iron increases when manufactured into an implement and increases further still when displayed by a retailer at the appropriate marketplace.

The addition of value associated with the trophic structure of the human economy corresponds with a per acre intensification of economic activity. It may take an acre to produce the iron, a quarter of an acre to convert the iron into an implement, and a hundredth of an acre to display it in the marketplace. Because of the simultaneous value-adding and spatial compaction of economic activity, price per acre rises through the trophic levels of the human economy. This helps explain why land prices increase from agro-extractive to manufacturing to servicing properties. It also helps to explain why the destruction of wildlife habitats tends to become more complete proceeding from farm fields to metropolitan centers. As the intensity of economic activity increases, so does competitive exclusion (Czech *et al.* 2000).

Meanwhile, the higher trophic levels tend to conglomerate and eventually make up urban areas due to the efficiencies offered by urbanization. Indeed, this is the economic explanation for urbanization (Monkkonen 1988). When agro-extractive surplus (and therefore relative non-scarcity of agro-extractive land) exists, as it has throughout all major periods of American history, hands are freed for the division of labor, demand for urban properties is highest, and urban land prices are highest. Simultaneously, because of the intensified competitive exclusion occurring in urban areas, urban areas tend to support the least biodiversity.

IMPLICATIONS FOR BIODIVERSITY CONSERVATION VIA LAND ACQUISITION AND PROTECTION

The immediate implications of urbanization and relative land prices to a conservation land acquisition strategy are straightforward: conservation lands are generally most expensive in urban areas, least expensive in rural areas, and intermediate at the interface where manufacturing tends to dominate. Exceptions tend to be associated with consumption-based demand. For example, during periods of economic expansion supporting many wealthy individuals, demand for rural properties with outstanding aesthetic characteristics increases. Prices for these "amenity" properties increase accordingly. Nonetheless, while land prices in these areas may be higher than those of nearby agro-extractive lands, they are seldom as high as commercial urban land prices.

Some of the highest land prices are in areas where production and consumption are both intense, whether urban or rural. For example, downtown casinos and beachfront resorts are extremely valuable properties, especially during economic booms when demand for luxury services remains high (Frank 1999).

In general, however, the positive relationship of economic activity and land prices means that, with a limited acquisition budget, more land may be acquired by focusing on rural areas. This is not the same as saying that the conservation value of rural acquisitions is higher than the conservation value of urban acquisitions, but it is one piece of a puzzle pointing in that direction.

The *long-term* implications of urbanization and relative land prices are not so simple and must take into account the political economy of the United States and economic globalization. In a society with a national goal of economic growth and the proven means (including relative self-sufficiency and international trade advantages) to pursue that goal, one of the implications is that more land will go into economic production. History also has shown that the ratio of rural to urban land will continue to decline as agriculture becomes more efficient (Cramer and Jensen 1994). This history may ultimately be threatened by declining agricultural productivity due to erosion and other factors, but to the extent that it continues, an increasing proportion of land will be urban (Czech and Krausman 2001). Furthermore, as the United States depends increasingly on raw materials from other nations, as with timber and several mineral resources, much of the national economy and landscape could become dominated by manufacturing and services in urban areas. Areas of the world where this process is further along include Japan and Hong Kong. The relationship between urbanization and species endangerment indicates that, as urban areas proliferate, so will species endangerment. The proliferation of species endangerment will be exacerbated by the increasing fragmentation of habitats by the urban areas themselves and by loss of the connecting infrastructure (Noss and Csuti 1994).

Any potential land acquisition may be considered to fall on a spectrum of economic structure from totally undeveloped (e.g., pristine wilderness) to totally developed (e.g., urban core). At this stage of the nation's development, neither extreme is likely to be considered for conservation acquisition, because wilderness tends to already be protected and urban cores tend not to have the ecological integrity sought after for the sake of biodiversity conservation. Nevertheless, a long portion of the spectrum is relevant. For example, one may compare the acquisition of a ranch in northern-central Montana (relatively wild) with the acquisition of a beachfront property in southeast Florida (relatively urbanized).

When considering the level of economic activity in developing a conservation land acquisition strategy, it is logical that one end of the development spectrum, or perhaps an area somewhere along the spectrum, may be identified that maximizes the conservation value of acquisitions. Selecting lands along the entire spectrum would be nonstrategic unless there was no known or detectable relationship between stage of development and conservation value. The logical starting point, therefore, is to consider each end of the spectrum in terms of relative conservation value.

A conservation land acquisition strategy that prioritizes-intentionally or unintentionally-lands in heavily developed, urbanized areas will result in the acquisition of high-priced lands where species are becoming endangered. This could be a prudent strategy in the context of a *stable* economy. While costs would be high, so would benefits; viz., conservation of endangered species. Indeed, the high conservation value of the parcels in question is why many conservation land acquisitions in recent years have been made in and near urban areas such as Austin (Texas), San Diego (California), and Key West (Florida). However, there is no indication that the implications of a *growing* economy have been considered. Based on the preceding discussion of conservation biology, ecological economics, and economic geography, in a growing economy: (1) the land area harboring endangered species will increase at an increasing rate as fragmentation, human disturbance, pollution, and other threats associated with urbanization proliferate; (2) land prices will increase most rapidly precisely where species become endangered most rapidly; (3) the areas where the highest prices are paid will be the same areas where species survival is least likely, and (4) higher operating costs associated with intensive user demands, law enforcement, and boundary maintenance in urban areas will reduce the long-term conservation value of urban acquisitions.

In the context of economic growth, the prudence of a strategy that prioritizes lands in relatively undeveloped, rural areas is indicated by the following characteristics: (1) while fragmentation, human disturbance, pollution, and other threats proliferate, rural areas will generally be affected last and least; (2) land prices will increase least rapidly where species become endangered least rapidly; (3) the areas where the lowest prices will be paid will be the same areas where species survival is most likely; and (4) lower operating costs in rural areas will tend to increase the long-term conservation value of rural acquisitions.

Even in a stable economy, an argument could be made for the prudence of prioritizing rural lands. While benefits related to biodiversity conservation might be lower per unit area, so would costs, resulting in a larger addition of conservation lands per funding cycle and, perhaps, greater overall biodiversity conservation. Theoretically, however, these conservation lands would not be required in a stable economy because a stable economy would not require an expanding land base for economic production and consumption. In other words, the rural lands would not be subject to a higher level of competitive exclusion than that already operating. Acquisition of high-priced lands instead would have the simple effect of re-situating economic activities away from urban areas, but only to the extent required by the scale of the stable economy. Perhaps the strongest case that could be made for prioritizing rural lands in the context of a stable economy would be as an "insurance policy" for a potential shift in national policy or performance from economic stability to economic growth.

The prudence of prioritizing rural lands for acquisition in a stable economy is like theoretical icing on an empirical cake, however, because the United States is not poised for economic stabilization. While today's economy consists of some rapidly developing areas where species endangerment is rampant, in a growing economy all areas not set aside for conservation will eventually be developed and the list of endangered or otherwise imperiled species will grow. The implication is that the acquisition of as much area as possible, as soon as possible, will minimize species endangerment in the long run.

Based on the comparison thus far, and in the context of economic growth, the more appropriate conservation land acquisition strategy would prioritize lands in undeveloped, rural areas. What has not been considered, however, is the relationship of biodiversity to land prices. Some of the most expensive areas, such as estuarine shorelines along the Gulf of Mexico, are "biodiversity hotspots" (Dobson *et al.* 1997). Meanwhile, less expensive areas, such as lodgepole pine forests in the northern Rockies, often support relatively little biodiversity. Unfortunately, the relationship of biodiversity to land prices is far from straightforward, as the history of wetlands development exemplifies. Wetland prices were very low for most of American history until the technology became available to develop them and the marginal benefits of drainage gradually exceeded the marginal costs (Vileisis 1997). These wetlands were rich in biodiversity while land prices were low, but became low in biodiversity as development proceeded and land prices increased. For example, some of the most expensive real estate in the United States may be found in Washington, DC, which was once a vast wetland and now contains scant ecological integrity (including native biodiversity).

Furthermore, biodiversity hotspots have typically been identified based upon numbers of species (Dobson *et al.* 1997), which are not equal representatives of biodiversity. Functional genome size, phylogenetic distinctiveness, and molecular clock speed should all be considered in prioritizing species for conservation (Czech and Krausman 1998). Based on these properties, one may argue that it is more important to conserve a large-bodied species (e.g, grizzly bear) by conserving lodgepole pine and other habitats than it is to conserve several small-bodied species by conserving a particular estuarine habitat.

This brief consideration of the relationship of biodiversity to land prices is sufficient to demonstrate that it is much more difficult to quantify conservation benefits than it is to quantify costs-particularly the monetary component of costs. The criteria for assessing the conservation benefits of a parcel are beyond the scope of this paper. Clearly, however, there is a relationship between the conservation value of a land acquisition and the cost of the acquisition, with lower price per acre generally associated with higher conservation value.

CONCLUSION

Economic growth proceeds at the competitive exclusion of biodiversity, including nonhuman species in the aggregate. Principles of economic geography indicate that urbanization will continue as a function of economic growth, while principles of conservation biology indicate that the most thorough competitive exclusion occurs in urban areas. The synthesis of these findings is that urbanization is somewhat of a red herring in the greater debate of economic growth vs. biodiversity conservation. Microeconomic and microecological approaches to biodiversity conservation in and around urban areas may be taken, but the results should be viewed as short-term compromises and perhaps an inefficient use of scarce conservation resources. As long as economic growth remains a primary policy goal, and to the extent such policy is effective, urbanization and biodiversity loss will continue. The only long-lasting approach to biodiversity conservation appears to be macroeconomic: i.e., the establishment of a steady state economy.

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