# The emergence of land change science for global environmental change and sustainability

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Land change science has emerged as a fundamental component of global environmental change and sustainability research. This interdisciplinary field seeks to understand the dynamics of land cover and land use as a coupled human–environment system to address theory, concepts, models, and applications relevant to environmental and societal problems, including the intersection of the two. The major components and advances in land change are addressed: observation and monitoring; understanding the coupled system—causes, impacts, and consequences; modeling; and synthesis issues. The six articles of the special feature are introduced and situated within these components of study.

#### Land Change and Its Science

uman-driven changes in the terrestrial surface of the earth hold wide-ranging significance for the structure and function of ecosystems to the earth system, with equally far-reaching consequences for human well-being (1). The antiquity of the unintended impacts of these changes is well documented for locales and regions (2, 3), and those linked to megafauna losses obtained a global reach by 10,000 B.P. (4–6).

Deforestation and irrigation were the largest sources of human-released greenhouse gasses to the atmosphere until the advent of industrial era fossil-fuel burning, and as much as 35% of the human-induced CO<sub>2</sub> equivalents in the atmosphere today can be traced to the totality of landuse/cover changes (7, 8). These land-based changes currently support over 6 billion people with food, fiber, water, and other benefits, and they support the highest global average per capita consumption ever known. This unprecedented level of land production, however, has been matched by unparalleled impacts on the earth system, especially since the latter part of the twentieth century.

Today, as much as 50% of the earth's ice-free land surface has been transformed (9, 10), and virtually all land has been affected in some way by such processes as coadapted landscapes, climate change, and tropospheric pollution (11-14).<sup>¶</sup> Much of this change is a direct consequence of land uses:  $\approx 40\%$  of land surface is in agriculture (including improved pasture and coadapted grassland), which accounts for nearly 85% of annual water withdrawals globally (8) and surpasses nature as the principal source of nitrogen emissions (15, 16); 3.3 billion ruminants graze rangelands, producing methane (17); and land uses take up 10– 50% of terrestrial net primary productivity (18).<sup>||</sup> In the face of these global dimensions, local to regional land changes remain important. For example, the largescale replacement of natural land cover by urban and agricultural land uses in southern Florida has reduced precipitation there (19), consistent with land change– regional climate impacts found elsewhere (20). Even more dramatically, massive irrigated agricultural projects triggered the collapse of the Aral Sea and its fishing industry, with feedbacks that include wind-dispersed deposition of surface salts from the dry sea bed on adjacent agricultural lands and even on the glacial sources of rivers feeding the sea (21).

Changes in land and ecosystems and their implications for global environmental change and sustainability are a major research challenge for the humanenvironmental sciences (22-24). This research is undertaken by various communities, including remote sensing, political ecology, resource economics, institution governance, landscape ecology, biogeography, and integrated assessment, among others. Its most comprehensive form, however, joins the human, environmental, and geographical information-remote sensing sciences in an interdisciplinary effort increasingly referred to as land change (or land system) science (LCS) (25, 26). This emergent research community seeks to improve: (i) observation and monitoring of land changes underway throughout the world, (ii) understanding of these changes as a coupled humanenvironment system, (iii) spatially explicit modeling of land change, and (iv) assessments of system outcomes, such as vulnerability, resilience, or sustainability (Fig. 1) (27). This agenda is made more complex by treating the environment in terms of its array of ecosystem (environmental) goods and services, rather than individual resources (22, 28). Decisions to use land affect these goods and services, with consequences for the structure and function of ecosystems (and ultimately, the earth

system) as well as the human system bevond the immediate land use.

The daunting objectives of LCS (8, 25, 27) are treated in this introductory paper. For each of the four main components of LCS research, we briefly review the research progress underway, discuss some of the major implications for global environmental change and sustainability themes, and outline some of the major challenges remaining. Finally, the six research papers that compose this special feature are set within the structure of the overall LCS effort.

#### The Dimensions of LCS: Advances, Implications, and Challenges

**Observation, Monitoring, and Land Characterization.** The number of and improvements in air- and space-borne sensors over the past two decades have fundamentally altered the capacity to observe

""Land transformation" refers to radical changes in land use and cover, usually over the long term, such as forest to row crop cultivation, or wetlands to urban settlement. The various estimates of these changes differ owing to the use of different metrics and measures and the uncertainties involved. Regardless, transformations are sizable as proportion of the ice-free land surface. If lands altered by human activity—lands retaining their base land cover but configured differently than in the "wildland" state-are included, a much larger estimate would result. Examples include degraded arid lands, pasture and grasslands invaded by or planted to exotic flora, and coadapted forests and grassland. Coadapted land covers are shaped and maintained by prolonged and repeated human activity, such as burning, that enlarges land use or land production: for example, annual burning that expands savanna grasses relative to woody species and enlarges food stocks for livestock and native grazers.

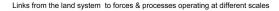
As with estimates of land transformations and alterations, there is little doubt that human activity usurps a large proportion of terrestrial net primary productivity, but the uncertainty in the estimates remains large (16).

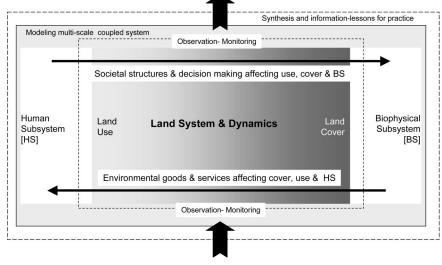
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Links from forces & processes operating at different scales to the land system

Fig. 1. The base phenomena and processes examined in and base research components of land change science.

and monitor land change. Seamless global data of land cover or its attributes (29–31) permit global assessments of changes in net primary productivity, flora, carbon sources and sinks, and biodiversity, among other categories of study, the results of which serve climate and other global environmental models and reveal such markers of climate warming as phenological changes in northern latitudes (32). Local to regional emphases have generated detailed land classifications (33) of use for both social and environmental problem solving, and land change assessments are increasingly "targeted" to specific problems. Examples include the role of stocking strategies versus climate flux in pasture degradation in the Karoo of South Africa (34), the ecological consequences of selective logging in tropical forests (35, 36), the loss of prime agricultural lands to peri-urban growth in southern China (37), and the relative susceptibility of forest loss versus agricultural intensification to market signals in Amazonia (38). The sheer volume of such work and the absence of a universal landuse/cover taxonomy have given rise to metaclassifications of land use/cover (39) and translations between different classification schemes (40, 41) to compare case studies and aggregate their findings. Confidence in detection and monitoring, given the use of standard land characterizations, is sufficient that the European Union employs imagery assessment as an accounting mechanism for tracking environmental performances across different governing units (42). Finally, new metrics have been developed to deal with coupled system dynamics, such as the "roadless volume,"

a measure of the amount and location of potential human activities on the landscape owing to encroachment by roads (43).

Observation and monitoring reveal a terrestrial surface increasingly dominated by humankind and serve as the empirical foundation for most claims about trajectories of land-use/cover change, supplanting observations made from ground-based surveys. The results inform us that, from 2000 to 2005, temperate forests registered a net gain globally, despite substantial logging in North America and Siberia. The world's humid tropical forests, in contrast, lost 5.8  $\pm$  1.4 million ha/yr between 1990 and 1997 but gained  $1.0 \pm 0.32$  million ha/vr of regrowth, resulting in a net annual loss of 0.43% (44). These figures do not include the affects of selective logging and burning, which are estimated by some to match the area of tropical forest conversion, at least in Amazonia (35, 36), nor do all calculations include uncertainty estimates (32). The global areas of cropland and pasture in 2000 were estimated to be 15.1 million km<sup>2</sup> and 28.3 million km<sup>2</sup>, respectively (45). Surprisingly, perhaps, the greatest density of cropland is in Eastern Europe, whereas pasture area is most common in Asia and Africa. Urban expansion is estimated to consume 1 to 2 million ha/yr of cropland in the developing world (46), much of it prime agricultural real estate.

Several challenges confront this category of research. The first is to maintain continuous time series of data to generate uninterrupted times series for analyses. This need is and will continue to be impeded by the malfunction of Landsat 7, given that the Landsat system, with its spatiotemporal resolution (900 m<sup>2</sup>; every 16 days) and relatively low costs, has been the "workhorse" database for so much of LCS (47). Research has also moved toward such land changes as "cryptic" deforestation (e.g., due to selective logging; 36), soil erosion, pest impacts on land cover, and shifts in land management practices. These subtle changes pose a series of challenges because they require the detection of trends in biophysical attributes of the land surface within landcover categories, independent of interannual variability in such attributes largely climate driven. Finally, mechanisms by which monitoring systems can integrate information at multiple spatiotemporal resolutions and from different instruments must be improved.

Land Change as a Coupled System. Causes of land-use change. Mimicking debates in social science, no facet of land change research has been more contested than that of cause. Empirical linkages between proposed causal variables and land change have been documented, but these commonly involve the more proximate factors to the land-outcome end of complex explanatory connections, such as immigrant, subsistence farmers and deforestation or locally configured common property resource regimes and land degradation (48, 49). The distal factors that shape the proximate ones, such as urban poverty or national policies, tend to be difficult to connect empirically to land outcomes, typically owing to the number and complexity of the linkages involved. Attention to proximate causes elevates the potential to commit errors of omission that lead to such errors as "blaming the victim" in cases of tropical deforestation by impoverished farmers.

Demonstrated empirical linkages in land change vary substantially by the spatiotemporal scale of analysis, impeded by difficulties in obtaining and matching socioeconomic, environmental, and remotesensing data by scale (50). Globally and historically (coarse grain), however, land dynamics appear to track well with the population, affluence, and technology (PAT) variables of the IPAT (I = environmental impact) identity because they capture, if coarsely, the demand for land and resources and the means by which they are supplied (51). These relationships are commonly lost at descending scales of analysis, however, a situation amplified by the spatial disconnect between sources of consumption and production in a global economy, as in the case of industrial deforestation in Borneo or Siberia (52). Comparative and metaanalyses of placebased land change studies have demonstrated the roles of such factors as

markets (53), policy (54), transportation (55), governance (56), and household life cycles (57, 58) on different types of land covers (e.g., tropical deforestation). To date, other than climate change, biophysical variables have received less attention as causal factors (but see refs. 59-61); rather they tend to be used as ambient conditions in which human or social factors operate. The major exception involves semiarid land degradation, often called desertification. This process examined in Sahel, for example, has demonstrated the synergy between land management practices, whatever their origins, and prolonged climatic drought in triggering land degradation (62).

For any locale (fine grain) composed of multiple land uses and covers, suites of factors tend to operate in chain-linked or nested ways (27, 48, 63, 64), and their specific configuration and interaction may lead to dissimilar outcomes. For example, the same international regulations and markets, operating through similar, cascading tiers of national institutions and local conditions, potentially yield dissimilar land-use/cover outcomes. Unpacking this complexity and rebuilding it to move beyond the variance of place remains a central challenge. If single-sector analyses of land change provide incomplete understanding but insights about general causes (65), place-based analyses provide more complete understanding but are often void of linkages to the general. Much attention needs to be directed to the reformulation of the sector-based concepts by place-based outcomes.

Biophysical impacts and feedbacks. The LCS community seeks to emphasize the totality of ecosystem goods and services involved in land change (22, 28); thus much attention is given to the structure and function of the biophysical subsystem. This ideal has proven difficult to implement for a number of reasons, including the complexity and costs involved in addressing goods and services holistically. It is more common for research to examine sets of goods and services or parts of ecosystems (66, 67). Examples include the impacts of landscape fragmentation on keystone species and the consequences for other biota and landscape functioning (52, 68, 69); the spread of invasive species as a consequence of land use; land-change consequences for water and food supply and amenity values (70-72); various consequences of increased area of forest edges, from the loss of biota to the opening of corridors for disease vectors (73); and the impacts of changing crop-fallow practices on tropical forest succession and nutrient dynamics (74). This focus on specific goods and services or subsystems dominates research at most scales of analysis, such as that directed to global land-cover

consequences for atmospheric greenhouse gasses, albedo, or the hydrologic cycle (75, 76).

Research on biophysical feedbacks on land uses and human well-being has been constrained similarly to that on impacts (above). Examples include local-toregional scale changes in precipitation and temperature or watershed flooding rendered by land-cover changes (19, 77), as well as the regional reach of "urban heat island" effects (78). Various pollutants from urban-industrial areas reduce crop yields, often at large spatial scales and interacting with nitrous oxide released from fertilizer (12, 14, 15, 79). Serious pressure on the environment has been noted in pig-producing regions of Germany, The Netherlands, Denmark, and Switzerland, where ammonia deposition exceeds the critical loads of nitrogen of sensitive ecosystems (80). Climate change, itself partially linked to changes in the terrestrial surface of the earth, interacts with land-cover change to threaten ecosystems worldwide (81, 82) as well as land uses, foremost agriculture (83). In addition, ecosystem transformation modifies habitat suitability for vectors of diseases and for animal hosts of zoonotic diseases, and land-use change may increase human exposure to these diseases, therefore affecting human health (8, 84).

These focused approaches (above) notwithstanding, various lines of research and modeling are becoming more inclusive and complex, attempting to incorporate more dimensions of the coupled system. For instance, research on the ignition, propagation, and impacts of forest fires has linked the interactions among climate, vegetation structure, and land use on local to regional scales to address impacts on biodiversity and such ecosystem services as carbon sequestration, soil fertility, and grazing and touristic value, and hence land-use change (85). Additionally, modeling assessments of Europe have singled out the Mediterranean region as increasingly confronting water shortages with climate change, owing to changes in snowcover dynamics, including the timing of runoff, and higher water extractions for irrigation and tourism (86).

The challenges for research on biophysical consequences and feedbacks are numerous and detailed in other fora (87). They include the identification of causal links between ecosystem processes and ecosystem services and their dependence on biodiversity, and the identification of tipping points beyond which the resilience of different environmental systems is lost. These and other challenges, of course, require improvements in dealing with complexity of the "complete" coupled land system (see *Synthesis and Assessment*). Modeling. Land change models are complex, owing to their coupling of human and environmental dynamics and to their need to be spatially (geographically) explicit (88-92). The spatial configuration of land uses and covers affects and is affected by the processes in question. The prevalent use in LCS of data derived from satellite imagery makes the scale of the pixel, which ranges in size from less than a meter to several kilometers, the finest grain of spatially specificity in the model (93, 94). These complexities notwithstanding, a range of econometric, ecological, and agent-based models have been explored to meet land management needs to better assess and project the future role of land-use/cover change in the functioning of the earth system, or simply to gain insights into a land system from various perspectives (95-97). Land-use change models allow testing of the stability of linked human-environment systems through scenario building. These models tend either to apply advanced statistical modeling tools to spatially explicit datasets or to simulate human-environment systems based on a set of idealized rules of behavior, although combinations of these approaches also exist. Statistical models rely on the assumption that landuse change processes are stationary, whereas process-based models represent changes in processes through time related to a change in system properties. Such shifts in system behavior can take place once some threshold is passed or can be triggered by single events, whether they are biophysical (e.g., drought, hurricanes, soil degradation) or socioeconomic (e.g., technological innovation, war, economic crisis) in kind.

Land-use change models have been designed either at the scale of humanenvironment systems as a whole [e.g., IMAGE (Integrated Model to Assess the Global Environment), CLUE (Conversion of Land Use Change and its Effects), and SALU (SAhelian Land-Use)] or at the scale of agents that represent individual units of decision making, interacting among themselves and with their environment (92). In the latter vein, statistical modeling has given rise to a growing body of research linking people to pixels, such as household survey data to land-cover data derived by remote sensing at a fine spatial resolution (97, 98). Simulation models at the level of agents are also gaining traction. Environmental change is simulated as an emergent property of interactions between agents (94, 96). Differences between the relevant spatial units for biophysical processes and decision making by actors is one of the methodological difficulties confronting the coupling of subsystems in these models (50).

Numerous challenges confront the

modeling of land change (50). A solid framework for a systematic validation of land-change projections is an essential component of this research field (99), but it remains particularly challenging in the case of multiagent simulations, given the need for validation data on decisionmaking processes and interactions between actors. It is also essential to understand how the scale of analysis affects modeling results (100). Whereas some models are focused on predicting the rates or quantities of change, others put more emphasis on spatial patterns. Moreover, land-use change models need to account for the endogeneity of variables, such as land management technologies, infrastructures, or land-use policies. Finally, land modeling confronts the need to couple the dynamics of the human and biophysical subsystems with outputs that are useful for land-use/cover assessments. This coupling is conceived in the context of hierarchy theory, allowing for multilevel interactions and feedbacks. The representation of many potential feedbacks generates numerical instability in models (90) that create levels of uncertainties impeding their use for decision making.

Synthesis and Assessment. The coupling of the human and environmental subsystems, commonly through the use of models, typifies synthesis and assessment research in LCS, much of which is devoted to sustainability themes. Holistic assessments that address sustainability, broadly interpreted, consistent with the objectives of LCS are few in number (64, 101) but are increasing across a wide spectrum of issues. Examples include research that informs practice about such issues as carbon offsets and tropical deforestation (102) and combating land degradation in arid lands (62). Headway has been made on such themes as the resilience-vulnerability of coupled human-environment systems (103-105) as well as attempts to identify the characteristics of sustainable and unsustainable land systems, ranging from syndromes of degradation to land practice outcomes by rules of governance to linking ecosystem and human well-being (56, 66, 101, 106). In concert with global environmental change and sustainability, increasing attention has been given to the delivery of information that facilitates decision making (62).

Of the many synthesis issues under study, none has received more attention than land transitions and parks/reserves. Land transitions refer to common sequences of land uses and covers resulting from sustained development and occupation. In the most generic model, ascending levels of socioeconomic development are associated with increasing intensities of land uses that capture "natural" ecosystems and attempts to micromanage the physical world. The results are transitions from presettlement wildlands to urban settlement and managed reserve lands (8). The most developed and tested of these models-the forest transition-shares striking similarities to that of the demographic transition: forest cover decreases with economic development until the economy industrializes (or obtains industrial levels of wealth), in which case forest cover regenerates, although never to its former extent and often with an altered composition and structure (107).\*\* This thesis has been supported by several quantitative assessments based on country-level comparisons, including the contemporary tropical world (109-111), although an alternative pathway may exist in which forest cover is related to the need for forest products (e.g., plantations). Shortterm, reverse transitions are common in economic frontier zones, and long-term reversals not associated with high-end development phases have been documented, such as the reforesting of the Maya lowlands beginning about 1000 B.P. and maintained until recently (112).

Parks and reserves established to preserve and conserve biodiversity have drawn special attention in regard to the land dynamics in which they exist and the nature of their boundaries. More often than not, the first line of research demonstrates that land practices, pressures, and changes outside the reserve affect the biota within it (113). For example, the development of commercial grain farms in the breeding lands of wildebeest in Kenya affect the number of this keystone species in the Masai-Mara Nature Reserve (69), while exurban development surrounding Yellowstone National Park in the United States triggers a complex suite of biodiversity responses, such as the loss of riparian habitat, elk winter range, and migration corridors (114, 115). In many cases, the establishment of reserves affects the subsistence practices of people living within or adjacent to them, with implications for human well-being and reserve ecosystems (116). For example, the collection of wood fuel and expansion of agricultural lands in the Wolong Nature Reserve of China was reducing the area of giant panda habitat and the connectivity of these habitats within and beyond the reserve up to 2001. Subsequently, new economic opportunities for residents beyond the reserve helped to reduce habitat loss there and stabilize habitat connectivity with the reserve, while increasing household income (117, 118). Such work demonstrates the need for a more expansive assessment of landuse dynamics to assess and monitor reserves as well as consideration of park boundaries and rules of access and resource use as they affect human– environment relationships in and around reserves (119, 120).

The coupling of the human-environment subsystems and assessments of their spatially explicit outcomes leads to a number of major challenges for LCS, perhaps none more important than the search for sustainable land architecture. This search is directed to the overarching mission of sustainability scienceprovisioning humankind while reducing the threats to the earth system (121)—and is captured within the land-ecosystem communities under the rubric of "win-win" solutions (122), or those in which the human subsystem maintains the delivery of ecosystem services that society values from the environmental subsystem. These solutions involve a complex suite of coupled system outcomes that, more often than not, are processed and delivered throughout the landscape in spatially incongruent ways. The complete array of ecosystem goods and services for a landscape or region can rarely be supplied by setting aside one piece of land, no matter how large, and lands optimal for human uses, more often than not, coincide with those most critical for providing certain goods and services. Thus attempts to reach solutions that provision the array and level of services wanted by society require complex patterns of land uses/ covers specified for the area in question (66). These patterns constitute architecture in that most lands, including wildlands, are governed, and thus their use is designed, de facto or de jure. A sustainable land architecture for one place, however, need not render similar results if duplicated across different locales or expanded to large units of assessment, such as biomes or continents (123, 124). The aggregation of the local solutions could lead to threats to both parts of the coupled system at ascending scales of analysis. In a world fast approaching governance and *de facto* planning of the entire terrestrial surface, the question of deriving a sustainable land architecture constitutes a grand challenge.

## Case Study Illustrations of the Dimensions of LCS

The five research articles that constitute this special feature provide a glimpse of the advances underway in each category of LCS (above) as they map onto Fig. 1, and were selected, in part, to demonstrate the international and interdisciplinary reach of the land change community.

Irwin and Bockstael (125) illustrate how data drawn from land monitoring efforts

<sup>\*\*</sup>Attempts are also underway to address land transitions for semi-arid lands (108).

can be directed to questions anchored in the core of the social sciences. They demonstrate that low-density or sub-/exurban housing in the state of Maryland, partially within the northeastern metropolitan corridor, has resulted in a substantial increase in undeveloped land fragmentation relative to development infill as measured by edge or land fragmentation metrics. Various factors associated with the expansion of exurbia and its increasing fragmentation pattern are also explored. They find that fragmentation is significantly higher in areas with more open space and significantly lower within proximity to Chesapeake Bay, suggesting that the pull of natural landscape amenities is an important determinant of these patterns.

Biophysical impacts and feedbacks are addressed in two case studies. In the first, Díaz, Lavorel, and colleagues (126) provide a framework that permits assessments of the indirect effects of functional diversity on ecosystem properties and services, and they illustrate it through a case study of grassland systems in the French Alps. These indirect effects have, heretofore, generated considerable uncertainty in understanding land-change impacts on ecosystem services. Application of the framework indicates that community-level averages often explain much about ecosystem properties, and it helps elucidate the role of other factors and the conditions in which uncertainty cannot be reduced. Importantly, this study reveals that the relationships among abiotic factors, different components of functional diversity, and ecosystem services can be addressed systematically. The procedure thus allows a formal incorporation of biodiversity as a driving factor in the sensitivity of ecosystem services to environmental change.

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In the second example, Lawrence and associates (127) examine the impacts of slash and burn cultivation on soil phosphorus (P) in the tropical dry forest of southern Yucatán. They demonstrate a marked decline in readily available soil P with the increased number of crop-fallow cycles undertaken, such that by the third cycle available soil P is insufficient to support mature forest. Successional forest, in turn, captures less P from the atmosphere, creating a positive feedback that degrades the ecosystem with implications for both forests and farmers. The linkages to farmers can be made because this research is part of a larger land change study treating the coupled human-environment system.

A virtual explosion in land modeling is illustrated by the work of Manson and Evans (128). They integrate agent-based models with other methods to examine household decision making in southcentral Indiana and the southern Yucatán. The Indiana case links data from multiple sources, including interviews and laboratory-based experiments, to examine the role of uncertainty, preferences, demographics, and changing experience. The Yucatán case uses evolutionary programming to represent bounded rationality in agriculturalist households to identify simple rules of thumb and broader social and environmental factors in decision making. This integrated modeling supports the concept of land managers as boundedly rational actors in both deforesting (Yucatán) and reforesting (Indiana) systems. The models also demonstrate the heterogeneity of land management strategies used by local actors and highlight the utility of models to provide insight into complex land change systems.

Finally, McKeon and associates (129) provide a synthetic assessment of land

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change in the coupled and coevolving, multiscalar land system of the "outback" of Australia, using the principles of the Drylands Development Paradigm (62) to understand these dynamics. They examine the vagaries of drought and livestock markets on land management, and the consequent impacts on the ecological and human subsystems, linked to learning at the property, state, and national scales. Lessons drawn that link LCS to application include not planning based on average conditions in either subsystem, and the need for knowledge systems beyond the managers themselves.

#### **Concluding Comments**

Approaching two decades of concerted international and interdisciplinary efforts to address land-use/cover change as a coupled system, LCS appears to have moved beyond an adolescence phase but has not yet fully matured. It has proven difficult to achieve a theory of coupled land systems. Complex systems concepts point to attributes of this coupling that are conceptually appealing but difficult to translate into useful land-change outcomes (130). Subsystem concepts and associated theory, in contrast, have proven useful in understanding specific outcomes and interactions of parts of the coupled system (27), providing substantial insights for decision making. The achievements made across the various dimensions of LCS, only a few of which could be illustrated in the six case studies that follow, suggest an increasingly rewarding and significant research future.

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### Correction

DN A C

**PERSPECTIVE.** For the article "Land Change Science Special Feature: The emergence of land change science for global environmental change and sustainability," by B. L. Turner II, Eric F. Lambin, and Anette Reenberg, which appeared in issue 52, December 26, 2007, of *Proc Natl Acad Sci USA* (104:20666–20671; first published December 19, 2007; 10.1073/pnas.0704119104), the authors note that, due to a printer's error, refs. 125–129 appeared incorrectly in part. For each reference, the volume number 105 should instead appear as 104. The online version has been corrected. The corrected references appear below.

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