A FRAMEWORK AND METHODS FOR SIMPLIFYING COMPLEX LANDSCAPES TO REDUCE UNCERTAINTY IN PREDICTIONS

Debra P.C. Peters[1]*, Jin Yao[1], Laura F. Huenneke[2], Robert P. Gibbens[1], Kris M. Havstad[1], Jeffrey E. Herrick[1], Albert Rango[1], and William H. Schlesinger[3]

[1] USDA ARS, Jornada Experimental Range, Las Cruces, NM, USA 88003-0003

[2] Department of Biology, New Mexico State University, Las Cruces, NM, USA 88003

[3] Nicholas School of the Environment and Earth Sciences, Duke University, Durham NC, USA.

* Author for correspondence: debpeter@nmsu.edu; voice 505 646 2777; FAX 505 646 5889

Abstract

Extrapolation of information from sites to landscapes or regions is especially problematic in spatially and temporally heterogeneous ecosystems. Although linear extrapolations are the easiest and most cost-effective, other approaches are necessary when spatial location and contagious or neighborhood processes are important. Because landscapes and regions consist of a mosaic of sites differing in spatial heterogeneity and degree of connectivity, we expect that a combination of scaling approaches is needed to characterize these areas. Nonspatial extrapolations may be most appropriate for areas that are relatively homogeneous and can be described by a relatively small number of units that repeat across a landscape or region. Spatially implicit or explicit approaches are expected to be necessary for those parts in which functionally similar, repeating units do not exist because of the importance of multiple interacting internal factors (spatially implicit) or connectivity with neighboring sites (spatially explicit). Our goal was to develop a conceptual framework to simplifying complex landscapes in order to minimize uncertainty in predictions. We illustrate our framework for arid and semiarid landscapes where determining spatial variation in carbon dynamics, and, in particular, aboveground net primary production (ANPP), is a timely and important problem.

Keywords: ANPP, carbon dynamics, Chihuahuan Desert, nonspatial, spatially explicit, spatially implicit,

I. Introduction and background

Many of our most pressing ecological problems, such as the conservation of biodiversity, spread of invasive species, patterns in carbon sequestration, and impacts of disturbances (e.g., fire) must be addressed at the landscape scale (Hansen et al. 1993; Solomon et al. 1993; Dale et al. 1994; Pitelka et al. 1997; Turner et al. 1997; Aronson and Plotnick 1998; Bender et al. 1998; Stohlgren et al. 1999; Bachelet et al. 2001; Heyerdahl et al. 2001; Groffman et al. chapter 2 this volume; Law et al. Chapter 7 this volume; Urban et al. Chapter 14 this volume). However, much of our information about these problems comes from plot-scale studies that must be extrapolated to the landscape. Because landscapes are complex, this extrapolation is not always straightforward or easy to accomplish (Turner et al. 1989a). Landscape complexity results from the processes, factors, and their interactions that occur across a range of spatial and temporal scales. The problem is further complicated by the presence of contagious or neighborhood processes that connect different parts of a landscape. Dispersal of seeds by wind or animals, fire, and erosion and deposition of soil and nutrients by wind and water are examples of spatial or contagious processes that influence ecosystem dynamics. Landscape complexity makes it difficult to understand and predict ecosystem dynamics across spatial scales with high levels of confidence or certainty. Our goal is to develop a conceptual framework and operational approach to simplifying complex landscapes in order to minimize both prediction errors and costs associated with measurement, analysis, and prediction.

A number of methods are available to extrapolate information that differ in the key processes involved (King 1991; Jarvis 1995). There are three main classes of extrapolation methods: (1)

nonspatial, (2) spatially implicit, and (3) spatially explicit (Peters et al. submitted). These methods differ in the amount of spatial information required to carry out the analysis. In most cases, the objective of the extrapolation is to obtain a single estimate for an entire landscape.

Nonspatial methods are the simplest and contain the fewest parameters. These methods include linear extrapolation where fine-scale information is extrapolated to broad-scales using weighted averages based on the area covered by each type of landscape unit. The classic example is the extrapolation of net primary production from sampled plots to biomes (Leith and Whittaker 1975). Other extrapolation techniques are possible (King 1991). In each case, it is assumed that spatial location on a map and quantification of contagious processes are not needed for the extrapolation.

Spatially implicit methods include the importance of spatial location in both the input and response variables. For example, gap models that simulate grassland or forest successional dynamics (Peters 2002; Keane et al. 2001; Symstad et al. 2003), nutrient cycling models (e.g., Burke et al. 1991, 1997), and most biogeographic models currently used to predict vegetation types at regional to global scales (e.g., Neilson and Running 1996; Melillo et al. 1995) are spatially implicit methods. These models typically simulate grid cells that differ in properties such as soil texture, precipitation, and temperature. Simulations are conducted for each grid cell containing a unique combination of parameters. Spatial location is important to the extrapolation because location is used to determine the value of some parameters, but it is assumed that the important processes occur within a grid cell; thus connections among grid cells are assumed to be negligible.

Spatially explicit or interactive methods are the most complex in that they require information on spatial location as well as on neighborhood processes. Familiar examples of spatially explicit models include cellular automata (Green et al. 1983; Hogeweg 1988), dispersal models that compute dispersal likelihood in terms of the distance between the target and source sites (Coffin and Lauenroth 1989, 1992; Clark et al. 1998, 1999; Rastetter et al. 2003), and models of contagious disturbances such as fire and disease (Turner et al. 1989b; Miller and Urban 1999). In each case, simulations are conducted for grid cells that differ in properties such as soil texture and climate. Furthermore, both processes within and among grid cells are important to ecosystem dynamics. Parameter values of a grid cell may depend upon either the identity of its neighboring cells, or specific exchanges of material or individuals among neighboring cells may be modeled explicitly.

Each of the three classes of scaling methods has tradeoffs in errors associated with uncertainty. Studies of model error have shown that simple models are often optimal when information is imprecise (O'Neill 1979; Reynolds and Acock 1985). However, more complicated models may be better when dynamics are complex and extensive data are available; yet these data may be expensive to collect and contain a number of small errors that accumulate to produce disproportionately large uncertainties in predictions (Gardner et al. 1980; Li and Wu Chapter 9 this volume). Thus, there are relative trade-offs between errors of omission (high in simple models, low in complex models) and errors of commission (high in complex models, low in simple models) for each method. In general, one should select the simplest method possible that represents the key processes influencing system dynamics in order to minimize both types of error (Peters et al. submitted).

Typically, researchers select one method for an entire landscape that depends on the question being addressed. However, the use of one method likely results in high errors of omission for some parts of a landscape, and high errors of commission for other parts. For example, a nonspatial extrapolation will result in high errors of omission for the areas on the landscape where contagious processes are particularly important, such as topographic lows where water accumulates and production is higher than the landscape average. Similarly, using a spatially explicit method for an entire landscape will result in high errors of commission associated with including unnecessary and poorly estimated parameters for those areas where spatial location and contagious processes are relatively unimportant, such as level uplands where dynamics are best explained by precipitation and soil texture. Because each parameter has an associated uncertainty in its estimate, including unnecessary parameters increases the overall uncertainty of the prediction (Peters et al. submitted).

Because landscapes consist of a mosaic of sites differing in spatial heterogeneity and degree of connectedness, we expect that a combination of scaling methods is needed to simplify complex landscapes in order to minimize errors of prediction. This general approach is similar to hierarchical scaling strategies (Wu 1999). Linear extrapolations may be most appropriate for the parts of a landscape that are relatively homogeneous. Spatially implicit or explicit approaches are expected to be necessary for those parts with high spatial heterogeneity or connectedness with neighboring sites (Peters et al. submitted).

We focus on the important and timely problem of scaling patterns in carbon sequestration and dynamics across semiarid and arid ecosystems to illustrate our approach of combining these methods to simplify landscapes. Recent estimates suggest that the carbon sink in grasslands and shrublands in the coterminous U.S. from 1980-1990 may be similar to that in forests (Pacala et al. 2001). In particular, shrub-dominated ecosystems are important contributors to carbon sinks due both to their extensive area (44% of the total land area of the U.S.) and to their high potential sequestration rates (Hibbard et al. 2001). The area dominated by shrubs and other woody plants has increased worldwide over the past century because of complex interactions among a number of factors, including effects of large and small animals, drought, fire, climate change, and changes in soil properties (Humphrey 1958; Schlesinger at al. 1990; Allred 1996; Van Auken 2000). Increases in above- and belowground carbon storage as well as increases in emissions of NO_x and non-methane hydrocarbons (e.g., terpenes, isoprene, and other aromatics) have resulted from the replacement of grasses by shrubs (Archer et al. 2001; Hartley and Schlesinger 2001; Jackson et al. 2002).

Estimates for carbon sinks and losses in areas encroached upon by woody plants have a high degree of uncertainty because of landscape-scale variation in edaphic and topographic factors (Pacala et al. 2001; Hurtt et al. 2002). Furthermore, spatial patterns in carbon and other soil nutrients may be complex because of processes such as wind and water erosion, and animal redistribution of plant material and nutrients (Schlesinger and Pilmanis 1998). Our specific objectives were: 1) to illustrate the use of each of the three scaling methods for extrapolating estimates of carbon dynamics based on aboveground net primary production (ANPP) for arid and semiarid landscapes, 2) to examine the key processes and factors leading to heterogeneity in carbon dynamics at the landscape scale, and 3) to develop a framework to identify the landscape locations where each scaling method is most appropriate.

II. System description

The study was conducted using data collected from the Jornada Basin Long Term Ecological Research site (JRN) located in southern New Mexico (32.5^{o}N, 106.8^{o}W). The Jornada consists of the Jornada Experimental Range, a 78,266-ha area administered by the USDA Agricultural Research Service, and the adjacent Chihuahuan Desert Rangeland Research Center, a 25,900-ha area administered by New Mexico State University. The JRN is characteristic of the northern Chihuahuan Desert with long term (80 y) mean annual precipitation of 248 mm/y (S.D. = 87) and mean monthly temperatures ranging from 3.8^{o}C in January to 26.1^{o}C in July. Elevation ranges from 1200m in the basin to > 2500 m in the mountains.

Similar to many other arid and semiarid ecosystems, a key characteristic of the JRN is that much of the area has changed from perennial grasslands to shrublands within the past 100 years (Buffington and Herbel 1965; Gibbens and Beck 1988; Fredrickson et al. 1998). In many areas within the JRN basin, black grama (*Bouteloua eriopoda*) dominated grasslands have been replaced by one of three shrub species (honey mesquite [*Prosopis glandulosa*], creosote bush [*Larrea tridentata*], and tarbush [*Fluorensia cernua*]). Grasslands dominated by tobosa (*Hilaria mutica*) commonly occur in low-lying areas. Currently at the JRN, communities dominated by these five species occur on >90% of the study area (Gibbens et al. in prep). Subdominant plants include annual and other perennial grasses, forbs, subshrubs, and other shrubs.

III. Extrapolation of ANPP from plots to a landscape

We used aboveground net primary productivity (ANPP) sampled seasonally in three exclosures in each of the five major vegetation types as our plot-level estimates of changes in carbon storage (Huenneke et al. 2001, 2002). Within each vegetation type, exclosures were selected to represent the range of variability in production of that type rather than as replicates of average conditions. Each exclosure was sampled using 49 1-m^2 quadrats. Methods of sampling are described in detail in Huenneke et al. (2001; 2002). Annual values of ANPP from 1990-1998 were averaged across exclosures and years to obtain a long term estimate for each vegetation type (http://jornada-www.nmsu.edu). We then used one of three methods (nonspatial, spatially implicit, spatially explicit; Peters et. al. submitted) to illustrate how to extrapolate these plot-level estimates to the entire Jornada landscape.

a. Nonspatial

The average plot-based estimate of ANPP for each of the five vegetation types was extrapolated nonspatially to the landscape scale using a weighted-averaging method (Table 1). Average ANPP from plot-scale estimates ranged from 91 g/m^2/y in a shrub-dominated area (tarbush) to 222 g/m^2/y in an upland perennial grassland (black grama). These ANPP values for each vegetation type were weighted by the area associated with that type using an eight-ha resolution map generated from field surveys conducted in 1998 (Gibbens et al. in prep). Most of the area (90%) is dominated by one of two shrubs (creosotebush, honey mesquite). Only 2% of the area is currently dominated by the perennial grass, black grama, a species that historically dominated much of the area. Using this weighted averaging method, the average ANPP for the JRN is 130 g/m^2/y during the period of sampling (1990 to 1998).

Nonspatial extrapolation of ecosystem variables from plots to larger areas is useful for coarse-scale comparisons where heterogeneity within landscape units is less important than large-scale patterns. For example, comparisons of biomes often use nonspatial extrapolations (Lieth and Whittaker 1975; Webb et al. 1978; Knapp and Smith 2001). Tabular estimates of ANPP for each vegetation type also allow comparisons with similar types of vegetation within the region as well as with other types of grasslands and shrublands (Lauenroth 1979; Le Houérou et al. 1988). However, nonspatial methods have limited utility when dealing with specific parts of a heterogeneous landscape where variation in ANPP is high (Huenneke et al. 2001, 2002). For example, grazing management that assumes a constant, uniform estimate of ANPP for an entire landscape will result in over-use in areas with below-average ANPP and under-use in areas with high ANPP.

b. Spatially implicit

Spatially implicit methods combine plot-scale estimates of carbon with spatial databases in a geographic information system. For the JRN, we extrapolated the ANPP estimate for each vegetation type (Table 1) using the vegetation map of 1998 (Fig. 1; Gibbens et al. in prep). This spatially implicit map shows the spatial distribution of ANPP across the JRN (Fig. 2). Although total ANPP is the same as for the nonspatial approach, large-scale patterns are evident that cannot be discerned from a tabular format (Table 1). For example, remnant grassland areas dominated by black grama are located primarily in the west and south whereas tobosa grasslands are located along a previous channel of the Rio Grande that went through the center of the JRN from northwest to southeast ca. 1.6 million years ago (Mack et al. 1996). Low productivity tarbush sites are mostly located in the southeast.

Another spatially implicit method could be used that includes spatial variation in environmental factors in the extrapolation. Plot-scale measures of soil texture, elevation, and precipitation could be used with ANPP estimates to develop a regression equation for each vegetation type. Spatial maps of these same variables (soil texture, elevation, and precipitation) could then be used with the regression equations to extrapolate ANPP across the landscape (Fig. 3). Although we have not conducted this analysis, this spatially implicit approach would provide a more spatially resolved map than the previous example (Fig. 2), and would account for potential variation in ANPP as related to variation in environmental factors.

Spatially implicit methods have been used frequently in arid and semiarid landscapes where environmental heterogeneity is often recognized as important. Spatial variation in ANPP has been documented because of variation in elevation and soil properties that likely affect water availability, although the redistribution of water was not actually measured (Ludwig 1986, 1987). Patterns in other properties of vegetation have been found associated with landforms, microtopography, and soils (Stein and Ludwig 1979; Wieranga et al. 1987; Wondzell et al. 1990, 1996; Wondzell and Ludwig 1995). Soil properties, including carbon, are often extrapolated from soil pits and field surveys selected to represent characteristic locations on a landscape (Gile et al. 1981). Although many of these earlier efforts did not publish maps, all of the sampling methods were spatially implicit in that the design was stratified by the environmental variation and the results were extrapolated to similar locations on the landscape.

Spatially implicit methods of extrapolation are increasingly used as the availability of spatial databases and geographic information systems analyses increases. Recent examples include the extrapolation of above- and belowground carbon pools across the JRN landscape from 1858 to present using maps of soils and precipitation as inputs to the CENTURY simulation model (Mitchell et al. 2002). Spatial variation in field estimates of carbon pools have also been extrapolated to the landscape scale using maps of soils and landforms (Monger et al. submitted). Spatial variation in shrub invasion and loss of perennial grasses with implications for changes in biomass quantity and vertical distribution through time have also been related to maps of soil texture, precipitation, elevation, and other factors (Yao et al. 2002). Identification of landscape locations where shrub invasion has occurred most rapidly allows management efforts to focus on these sensitive areas.

c. Spatially explicit

Spatially explicit approaches include landscape location as well as neighborhood or contagious processes, such as seed dispersal or wind and water redistribution of soil particles. These approaches require information on the movement or transfer of materials, energy or information within and among spatial units on a landscape. Because these transfers are difficult and costly to measure for large areas, field experiments typically focus on specific areas of interest rather than attempting to instrument an entire landscape. For example, Schlesinger and Jones (1984) related patterns in plant biomass to localized runoff and run-on areas in the Mojave Desert. Recent experiments at the JRN have also documented the importance of water redistribution to patterns in vegetation (Wainwright et al. 2000; 2002).

Alternatively, spatially explicit simulation models can be used to represent large areas if sufficient information is known for model parameterization and validation. Peters and Herrick (1999) used a spatially explicit simulation model to examine the importance of seed dispersal to the recovery of perennial grasses following shrub invasion on sites with different vegetation and soil properties. Plot-scale parameters were combined with spatial maps of soil texture and precipitation as well as the movement of seeds among plots to extrapolate model results to a landscape. Spatially explicit simulation models can also be combined with regression models to simulate ecosystem dynamics (Reynolds Chapter 13).

In general, spatially explicit models are becoming increasing popular in ecology as computer limitations decrease and the quality and quantity of spatial information increases (e.g., Dunning et al. 1995; Schimel et al. 1997; He and Mladenoff 1999). However, complex models that require a large number of parameters that are difficult to estimate, and thus, have greater errors associated with them and are more difficult to validate than simple models (Oreskes et al. 1994; Rykiel 1996).

IV. What makes a landscape complex?

Landscapes are complex because of interactions among contagious or neighboring processes and spatial variation in the physical template and disturbance regime. Contagious processes are related to three main vectors of dispersal (water, wind, animals) that redistribute seeds, nutrients, soil particles, and water. The physical template includes factors such as soil properties (texture, depth), precipitation, temperature, and elevation. The disturbance regime includes both natural (e.g., fire) and management-related disturbances (cultivation, roads, herbicide). Landscapes are complex because the importance of these processes, environmental factors, and disturbances varies for different sites. On some sites, spatial heterogeneity in soil texture can be the most important factor for explaining ecosystem dynamics whereas the redistribution of water may be more important on other sites. Furthermore, more than one contagious process or environmental factor may be important for some sites such that complex interactions among processes determine ecosystem dynamics.

In arid and semiarid ecosystems, patterns in ecosystem dynamics and ANPP are complex at the landscape scale because of a number of processes that are also variable at the landscape scale. Spatial variation in water redistribution at the landscape scale is most important along elevational gradients where channels and arroyos move water from upslope to downslope (Fig. 4). Spatial variability in soil properties interacts with variability in water redistribution to generate complex patterns in ANPP. The result is that upper alluvial fans or bajadas dominated by creosotebush with thin, rocky soils have higher runoff, less available water, and lower ANPP than downslope positions. The extreme situation occurs when water accumulates in playas on soils with high water holding capacity and high plant production (Huenneke et al. 2002). Because water is an important dispersal agent for seeds as well as soil particles, plant litter, and nutrients, these materials are also expected to be heterogeneously distributed across the landscape.

Wind redistribution of particles is also unevenly distributed at the landscape scale with important consequences for patterns in ANPP (Fig. 4). Sandy soils dominated by honey mesquite are more susceptible to wind erosion than other soil-plant community combinations (Gibbens et al. 1983;

Gillette and Chen 2001). Soil particles eroded from interdune areas in mesquite-dominated systems are deposited both locally in dunes and at large distances in vegetation types located downwind.

The effects of animals on ecosystem dynamics and ANPP are also non-uniformly distributed across a landscape (Fig. 4). Both small and large animals are effective dispersal agents of seeds and nutrients. Densities of small animals are often related to soil properties and vegetation type (Kerley and Whitford 2000). Furthermore, small animals, such as ants and rodents, are selective in the seeds collected with differential effects on seed availability and plant species dynamics (Inouye et al. 1980). Large animals, such as cattle, are effective dispersal agents of mesquite seeds, and likely played an important role in the expansion of this shrub into perennial grasslands. Spatial heterogeneity in ANPP also results from non-uniform grazing patterns by cattle (Paulsen and Ares 1962; Valentine 1970). Areas currently excluded from cattle often have higher plant production than adjacent grazed areas. Low plant production also occurs near watering holes where grazing and trampling are intense (Fusco et al. 1995; de Soyza et al. 1997; Nash et al. 1999).

Spatial heterogeneity in ANPP also occurs as a result of spatial variation in disturbances. Fire occurs most frequently in grassland systems with high production and continuous fuel load. Although low production occurs immediately following a fire, high production is possible later in the season if rainfall is high (Drewa et al. 2001). By contrast, low production can be maintained if fire occurs during or before a drought. Other types of disturbances, such as herbicide treatments, cultivation, road and building construction are also heterogeneously distributed across a landscape (Fig. 4). These disturbances affect patterns in ANPP both locally on the disturbed area as well as in adjacent areas through modifications to wind and water erosion.

V. Simplifying complex landscapes: a new conceptual framework

In our conceptual framework, landscapes consist of a mosaic of sites where spatial variation in the environment and contagious processes may or may not be important in understanding and predicting ecosystem dynamics. Our approach to simplifying complex landscapes is to determine the locations on a landscape where spatial information and contagious processes must be known in order for predictions to be accurate. Predictions for the remainder of the landscape can be obtained using estimates from representative sites that are extrapolated to similar areas using either nonspatial or spatially implicit methods (Peters et al. submitted). One approach to identifying these locations and to determining the important spatial processes is to combine remotely sensed images with field data and spatial databases residing in a geographic information system.

For example, remotely sensed images combined with field estimates of ANPP can be used both to determine the most appropriate vegetation spectral index for each of the major ecosystem types, and to identify the locations ("hot spots") with extremely low and high ANPP values for each ecosystem type compared with the rest of the landscape. Spatial databases can be used to provide insight into the key processes operating to generate these extremely low or high values. For example, digital elevation models can be used to determine the locations where water is expected to runoff as a result of steep slopes or where water accumulates when the slopes are shallower than the surrounding locations. Spatial databases of animal distribution can be generated using average stocking densities combined with the location of exclosures (no animal activity) and water sources (locations of intense animal activity). Correlating vegetation indices from the remotely sensed images with the spatial databases can confirm the greater importance of spatial processes at these key locations compared with the rest of the landscape. Uncertainty analyses can then be conducted to identify the major sources of uncertainty, and to explore the effects of reducing the uncertainty in predictions by including spatial databases. Identifying these locations and key processes is the first step in simplifying complex landscapes in order to prioritize management decisions and to guide research questions and experimental designs.

VI. Summary and Conclusions

Complex landscapes pose a critical challenge to ecologists. Addressing problems at the landscape scale requires the extrapolation of information from plot-scale studies. Three general classes of extrapolation methods exist that differ in the amount of spatial information required. For a given problem, ecologists typically use one method for all parts of a landscape. However, the use of one method likely results in high errors of omission for some parts of a landscape, and high errors of commission for other parts, thus resulting in high uncertainty in predictions for the entire landscape. An alternative approach was developed that simplifies complex landscapes into different parts where each extrapolation method is most appropriately used. This approach reduces the uncertainty in predictions at the landscape scale, and provides guidance to ecologists and land managers interested in the key parts of the landscape where spatial variation and contagious processes have the greatest impact on ecosystem dynamics. This approach is expected to also be useful for other ecosystems where complexity in landscape structure and spatial processes are important.

VII. Literature cited

Allred, K. W. 1996. Vegetative changes in New Mexico rangelands. Pages 168-231 in E. A. Herrera and L. F. Huenneke, editors. New Mexico's Natural Heritage: Biological diversity in the land of enchantment. New Mexico Journal of Science 36. New Mexico Academy of Science, Albuquerque, NM, USA.

Archer, S, T. W. Boutton, and K. A. Hibbard. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. Pages 115-137 In: Global biogeochemical cycles in the climate system (E-D Schulze, SP Harrison, M Heimann, EA Holland, J Lloyd, IC Prentice, D Schimel, eds.). Academic Press, San Diego, CA, USA.

Aronson, R. B., and R. E. Plotnick. 1998. Scale-independent interpretations of macroevolutionary dynamics. Pages 430-450 *in* M. L. McKinney and J. A. Drake, editors. Biodiversity dynamics: Turnover of populations, taxa, and communities. Columbia University Press, New York., USA.

Bachelet, D., R. P. Neilson, J. M. Lenihan, and R. J. Drapek. 2001. Climate change effects on vegetation distribution and carbon budget in the United States. Ecosystems 4:164-185.

Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79:517-533.

Burke, I. C., T. G. F. Kittel, W. K. Lauenroth, P. Snook, C. M. Yonker, and W. J. Parton. 1991. Regional analysis of the Central Great Plains. BioScience 41:685-692.

Burke, I. C., W. K. Lauenroth, and W. J. Parton. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. Ecology 78:1330-1340.

Buffington, L. C., and C. H. Herbel. 1965. Vegetational change on a semidesert grassland range from 1858 to 1963. Ecological Monographs 35: 139-164.

Clark, J. S., S. R. Carpenter, M. Barber, S. Collins, A. Dobson, J. A. Foley, D. M. Lodge, M. Pascual, R. Pielke, W. Pizer, C. Pringle, W. V. Reid, K. A. Rose, O. Sala, W. H. Schlesinger, D. H. Wall, and D. Wear. 2001. Ecological forecasts: An emerging imperative. Science 293:657-660.

Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. Ecological Monographs 68:213-235.

Coffin, D. P., and W. K. Lauenroth. 1989. Disturbances and gap dynamics in a semiarid grassland: A landscape-level approach. Landscape Ecology 3:19-27.

Coffin, D. P., and W. K. Lauenroth. 1990. A gap dynamics simulation model of succession in the shortgrass steppe. Ecological Modelling 49:229-266.

Dale, V. H., S. M. Pearson , H. L. Offerman, and R. V. O'Neill. 1994. Relating patterns of land-use change to faunal biodiversity in the central Amazon. Conservation Biology 8:1027-1036.

de Soyza, A. G., W. G. Whitford, and J. E. Herrick. 1997. Sensitivity testing of indicators of ecosystem health. Ecosystem Health 3:44-53.

Drewa, P. B., D.P.C. Peters, and K.M. Havstad. 2001. Fire, grazing, and shrub invasion in the Chihuahuan Desert. Pages 31-39 in T. P. Wilson and K. E. M. Galley (eds.). Proceedings of the Invasive Species Workshop: The role of fire in the control and spread of invasive species. Fire Conference 2000: the National Congress on Fire Ecology, Prevention, and Management. Misc. Pub. No. 11, Tall Timbers Research Station, Tallahassee, FL.

Dunning, J. B. Jr., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. Ecological Applications 5:3-11.

Fredrickson, E., K. M. Havstad, R. Estell, P. Hyder. 1998. Perspectives on desertification: south-western United States. Journal Arid Environments 39:191-207.

Fusco, M., J. Holechek, A. Tembo, A. Daniel, and M. Cardenas. 1995. Grazing influences on watering point vegetation in the Chihuahuan Desert. Journal Range Management 48:32-38.

Gardner, R. H., R. V. O'Neill, J. B. Mankin, and D. Kumar. 1980. Comparative error analysis of six predator-prey models. Ecology 61:323-332.

Gibbens, R. P., and R. F. Beck. 1988. Changes in grass basal area and forb densities over a 64-year period on grassland types of the Jornada Experimental Range. Journal Range Management 41:186-192.

Gibbens, R. P., R. P. McNeely, K. M. Havstad, R. F. Beck, and B. Nolen. Vegetation change in the Jornada Basin from 1858 to 1998. Journal Arid Environments (to be submitted).

Gibbens, R. P., J. M. Tromble, J. T. Hennessy, and M. Cardenas. 1983. Soil movement in mesquite dunelands and former grasslands of southern New Mexico from 1933 to 1980. Journal Range Management 36: 145-148.

Gile, L. H., J. W. Hawley, and R. B. Grossman. 1981. Soils and geomorphology in the basin and range area of southern New Mexico: guidebook to the Desert Project. New Mexico Bureau of Mines and Mineral Resources, Socorro, New Mexico, USA.

Gillette, D. A., and W. Chen. 2001. Particle production and aeolian transport from a "supply-limited" source area in the Chihuahuan desert, New Mexico, United States. Journal of Geophysical Research 106: 5267-5278.

Green, D. G., A. M. Gill, and I. R. Noble. 1983. Fire shapes and the adequacy of fire-spread models. Ecological Modelling 20:33-45.

Groffman, P. M., R. T. Venterea, L. V. Verchot, and C. S. Potter. Landscape and regional scale studies of nitrogen gas fluxes. .Pages 000-000 IN J. Wu, B. Jones, H. Li, and O. Loucks, editors. Scaling and uncertainty analysis in ecology: methods and application. Columbia University Press, New York, USA.

Hansen, A. J., S. L. Garman, B. Marks, and D. L. Urban. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. Ecological Applications 3:481-496.

Hartley, A. E., and W. H. Schlesinger. 2000. Environmental controls on nitric oxide emission from northern Chihuahuan desert soils. Biogeochemistry 50:279-300.

He, H. S., and D. J. Mladenoff. 1999. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. Ecology 80:81-99.

Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2001. Spatial controls of historical fire regimes: A multiscale example from the interior west, USA. Ecology 82:660-678.

Hibbard, K. A., S. Archer, D. S. Schimel, and D. W. Valentine. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. Ecology 82:1999-2011.

Hogeweg, P. 1988. Cellular automata as a paradigm for ecological modeling. Applications in Mathematics and Computation 27:81-100.

Huenneke, L. F., J. P. Anderson, M. Remmenga, and W. H. Schlesinger. 2002. Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. Global Change Biology 8: 247-264.

Huenneke, L. F., D. Clason, and E. Muldavin. 2001. Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. Journal of Arid Environments 47: 257-70.

Humphrey, R. R. 1958. The desert grassland: a history of vegetational change and an analysis of causes. Botanical Review 24: 193-252.

Hurtt, G. C., S. W. Pacala, P. R. Moorcroft, J. Casperson, E. Shevliakova, R. A. Houghton, and B. Moore III. 2002. Projecting the future of the U.S. carbon sink. Proceedings National Academy of Sciences 99(3): 1389-1394.

Inouye, R.S., G. S. Byers, and J.H. Brown. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. Ecology 6: 1344-1351.

Jackson, R. B., J. L. Banner, E. G. Jobbagy, W. T. Pockman, and D. H. Wall. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418: 623-626.

Jarvis, P.G. 1995. Scaling processes and problems. Plant, Cell and Environment 18: 1079-1089.

Keane, R. E., M. Austin, R. Dahlman, C. Field, A. Huth, M. Lexer, D. Peters, A. Solomon, and P. Wyckoff. 2001. Plant mortality in gap models. Journal of Climate Change 51: 509-540.

Kerley, G. H., and W. Whitford. 2000. Impact of grazing and desertification in the Chihuahuan Desert: plant communities, granivores, and granivory. American Midland Naturalist 144: 78-91.

King, A. 1991. Translating models across scales in the landscape. Pages 479-517 *in* M. G. Turner and R. H. Gardner, editors. Quantitative methods in landscape ecology. Springer-Verlag, New York, NY, USA.

Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of above-ground primary production. Science 291:481-484.

Lauenroth, W. K. 1979. Grassland primary production: North American grasslands in perspective. In N. R. French, ed. Perspectives in grassland ecology. Springer-Verlag, New York.

Le Houérou, H. N., R. L. Bingham, and W. Skerbek. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. Journal Arid Environments 15: 1-18.

Li, H., and J. Wu. Uncertainty and error analysis in ecological studies: an overview. Pages 000-000 IN J. Wu, B. Jones, H. Li, and O. Loucks, editors. Scaling and uncertainty analysis in ecology: methods and application. Columbia University Press, New York, USA.

Law, B. E., D. Turner, M. Lefsky, M. Guzy, O. Sun, S. Van Tuyl, and W. Cohen. Carbon fluxes across regions: observational constraints at multiple scales. Pages 000-000 IN J. Wu, B. Jones, H. Li, and O. Loucks, editors. Scaling and uncertainty analysis in ecology: methods and application. Columbia University Press, New York, USA.

Lieth, H., and R. H. Whittaker, eds. 1975. The primary productivity of the biosphere. Springer, New York, NY, USA.

Ludwig, J. A. 1986. Primary production variability in desert ecosystems. Pages 5-17 In W. G. Whitford, ed. Patterns and process in desert ecosystems. University of New Mexico Press, Albuquerque, NM, USA.

Ludwig, J. A. 1987. Primary productivity in arid lands: myth and realities. Journal Arid Environments 13: 1-7.

Mack, G.H., W.C. McIntosh, M.R. Leeder, and H.C. Monger. 1996. Plio-Pleistocene pumice floods in the ancestral Rio Grande, southern Rio Grande rift, USA. Sedimentary Geology 103:1-8.

Melillo, J. M., J. Borchers, J. Chaney, H. Fisher, S. Fox, A. Haxeltine, A. Janetos, D. W. Kicklighter, T. G. F. Kittel, A. D. McGuire, R. McKeown, R. Neilson, R. Nemani, D. S. Ojima, T. Painter, Y. Pan, W. J. Parton, L. Pierce, L. Pitelka, C. Prentice, B. Rizzo, N. A. Rosenbloom, S. Running, D. S. Schimel, S. Sitch, T. Smith, and I. Woodward. 1995. Vegetation Ecosystem Modeling and Analysis Project - Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate-change and CO_2 doubling. Global Biogeochemical Cycles 9:407-437.

Miller, C., and D. L. Urban. 1999. Interactions between forest heterogeneity and surface fire regimes in the southern Sierra Nevada. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 29:202-212.

Mitchell, K. A., D. P. C. Peters, J. E. Herrick, and H. C. Monger. 2002. Long term changes in carbon pools accompanying shrub invasion of a desert grassland: the Jornada Experimental Range 1850 – today. Bulletin Ecological Society America 83:215.

Monger, H. C., J. Martinez-Rios, and B. Nolen. Regional setting of the Jornada Basin. Pages 000-000 in L. F. Huenneke, W. H. Schlesinger, and K. M. Havstad, editors. Long term research in the Jornada Basin. Oxford University Press.

Nash, M. S., W. G. Whitford, A. G. deSoyza AG, J. W. VanZee, and K. M. Havstad. 1999. Livestock activity and Chihuahuan Desert annual-plant communities: Boundary analysis of disturbance gradients. Ecological Applications 9: 814-823.

Neilson, R.P., and S.W. Running. 1996. Global dynamic vegetation modelling: coupling biogeochemistry and biogeography models. Pages 451-465 *in* B. Walker and W. Steffen, editors. Global Change and Terrestrial Ecosystems. Cambridge University Press, Cambridge, UK.

O'Neill, R. V. 1979. Natural variability as a source of error in model predictions. Pages 23-32 *in* G. S. Innis and R. V. O'Neill, editors. Systems analysis of ecosystems. International Co-operative, Fairland, Maryland, USA.

Oreskes, N., K. Shrader-Frechette, and K. Belitz. 1994. Verification, validation, and confirmation of numerical models in the earth sciences. Science 263:641-646.

Pacala, S. W., G. C. Hurtt, D. Baker, P. Peylin, R. A. Houghton, R. A. Birdsey, L. Heath, E. T. Sundquist, R. F. Stallard, P. Ciais, P. Moorcroft, J. P. Caspersen, E. Shevliakova, B. Moore, G. Kohlmaier, E. Holland, M. Gloor, M. E. Harmon, S.-M. Fan, J. L. Sarmiento, C. L. Goodale, D. Schimel, and C. B. Field. 2001. Consistent land- and atmosphere-based U.S. carbon sink estimates. Science 292: 2316-2320.

Paulsen, H. A. Jr., and F. N. Ares 1962. Grazing values and management of black gram and tobosa grasslands and associated shrub ranges of the Southwest. USDA Forest Service Bulletin 1270.

Peters, D.P.C. 2002. Plant species dominance at a grassland-shrubland ecotone: an individual-based gap dynamics model of herbaceous and woody species. Ecological Modelling 152:5-32.

Peters, D. P. C., and J. E. Herrick. 1999. Vegetation-soil feedbacks and sensitivity of Chihuahuan desert ecosystems to climate change. Bulletin of the Ecological Society of America 80:69.

Peters, D. P. C., D. L. Urban, R. H. Gardner, D. D. Breshears, and J. E. Herrick. Strategies for ecological extrapolation. Oikos (submitted).

Pitelka, L. F., R. H. Gardner, J. Ash, S. Berry, H. Gitay, I. R. Noble, A. Saunders, R. H. W. Bradshaw, L. Brubaker, J. S. Clark, M. B. Davis, S. Sugita, J. M. Dyer, R. Hengeveld, G.

Hope, B. Huntley, G. A. King, S. Lavorel, R. N. Mack, G. P. Malanson, M. McGlone, I. C. Prentice, and M. Rejmanek. 1997. Plant migration and climate change. American Scientist 85:464-473.

Rastetter, E. B., J. D. Aber, D. P. C. Peters, D. S. Ojima, and I. C. Burke. 2003. Using mechanistic models to scale ecological processes across space and time. BioScience 53: 1-9.

Reynolds, J. F. Scale-related uncertainties in landscape dynamics of the Jornada during the past 100 years. Pages 000-000 IN J. Wu, B. Jones, H. Li, and O. Loucks, editors. Scaling and uncertainty analysis in ecology: methods and application. Columbia University Press, New York, USA.

Reynolds, J. F., and B. Acock. 1985. Predicting the response of plants to increasing carbon dioxide: a critique of plant growth models. Ecological Modelling 29:107-129.

Rykiel, E. J. Jr. 1996. Testing ecological models: the meaning of validation. Ecological Modelling 90:229-244.

Schimel, D., VEMAP participants, and B. Braswell. 1997. Continental scale variability in ecosystem processes: models, data, and the role of disturbance. Ecological Monographs 67:251-271.

Schlesinger, W. H., and A. M. Pilmanis. 1998. Plant-soil interactions in deserts. Biogeochemistry 42:169-187.

Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. Science 247:1043-1048.

Schlesinger, W. H., and C. S. Jones. 1984. The comparative importance of overland runoff and mean annual rainfall to shrub communities of the Mojave Desert. Botanical Gazette 145: 116-124.

Solomon, A. M., I. C. Prentice, R. Leemans, and W. P. Cramer. 1993. The interaction of climate and land-use in future terrestrial carbon storage and release. Water Air and Soil Pollution 70:595-614.

Stein, R. A., and J. A. Ludwig. 1979. Vegetation and soil patterns on a Chihuahuan Desert bajada. The American Midland Naturalist 101:28-37.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69:25-46.

Symstad, A. J. F. S. Chapin, D. H. Wall, K. L. Gross, L. F. Huenneke, G. G. Mittlebach, D. P. C. Peters, and G. D. Tilman. 2003. Long-term perspectives on biodiversity-ecosystem function relationships. BioScience 53: 89-98.

Turner, M. G., V. H. Dale, and R. H. Gardner. 1989a. Predicting across scales: theory development and testing. Landscape Ecology 3: 245-252.

Turner, M.G., R.H. Gardner, V.H. Dale, and R.V. O'Neill. 1989b. Predicting the spread of disturbance across heterogeneous landscapes. Oikos 55:121-129.

Turner, M. G., W. H. Romme, R. H. Gardner and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs 67:411-433.

Urban, D. L., R. I. McDonald, E. S. Minor, and E. A. Treml. Causes and consequences of land use change in the North Carolina Piedmont: the scope of uncertainty. Pages 000-000 IN

J. Wu, B. Jones, H. Li, and O. Loucks, editors. Scaling and uncertainty analysis in ecology: methods and application. Columbia University Press, New York, USA.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review Ecology Systematics 31: 197-215.

Valentine K. A. 1970. Influences of grazing intensity on improvement of deteriorated black grama range. NMSU Agricultural Experiment Station Bulletin 553.

Wainwright, J., A. J. Parson, and A. D. Abrahams. 2000. Plot-scale studies of vegetation, overland flow and erosion interactions: case studies from Arizona and New Mexico. Hydrological Processes 14: 2921-2943.

Wainwright, J., A. J. Parson, W. H. Schlesinger, and A. D. Abrahams. 2002. Hydrology-vegetation interactions in areas with discontinuous flow on a semi-arid bajada, southern New Mexico. Journal Arid Environments 51:219-258.

Webb, W. L., S. R. Szarek, W. K. Lauenroth, R. S. Kinerson, and M. H. Smith. 1978. Primary productivity and water-use in native forest, grassland and desert ecosystems. Ecology 59: 1239-1247.

Wieranga, P. J., J. M. H. Hendrickx, M. H. Nash, J. A. Ludwig, and L. A. Daugherty. 1987. Variation of soil and vegetation with distance along a transect in the Chihuahuan Desert. Journal Arid Environments 13: 53-63.

Wondzell, S. M., J. M. Cornelius, and G. L. Cunningham. 1990. Vegetation patterns, microtopography, and soils on a Chihuahuan Desert playa. Journal Vegetation Science 1:403-410.

Wondzell, S. M., G. L. Cunningham, and D. Bachelet. 1996. Relationships between landforms, geomorphic processes, and plant communities on a watershed in the northern Chihuahuan Desert. Landscape Ecology 11:351-362.

Wondzell, S. M., and J. A. Ludwig. 1995. Community dynamics of desert grasslands: influences of climate, landforms, and soils. Journal of Vegetation Science 6:377-390.

Wu, J. 1999. Hierarchy and scaling: extrapolating information along a scaling ladder. Canadian Journal Remote Sensing 25: 367-380.

Yao, J., D. P. C. Peters, R. P. Gibbens, and K. M. Havstad. 2002. Response of perennial grasses to precipitation in the northern Chihuahuan Desert: implications for grassland restoration. Bulletin Ecological Society America 83: 302.

Table 1. Vegetation type by ANPP (g/m2 from Huenneke et al. 2002) and area to obtain weighted average for the JRN. ANPP is long-term average and standard deviation of all dates and years. Area extent (ha) obtained from Gibbens et al. (in prep). Areas not dominated by these vegetation types (others) were excluded from the analysis.

Vegetation type	Mean ANPP (g/m2/y) [standard deviation]	Areal extent (ha)
Black grama grasslands	229 [114]	699
Creosotebush shrublands	139 [51]	14,485
Honey mesquite shrublands	140 [60]	34,387
Tarbush shrublands	96 [20]	3,826
Tobosa playa grasslands	194 [214]	844
Weighted average	143	

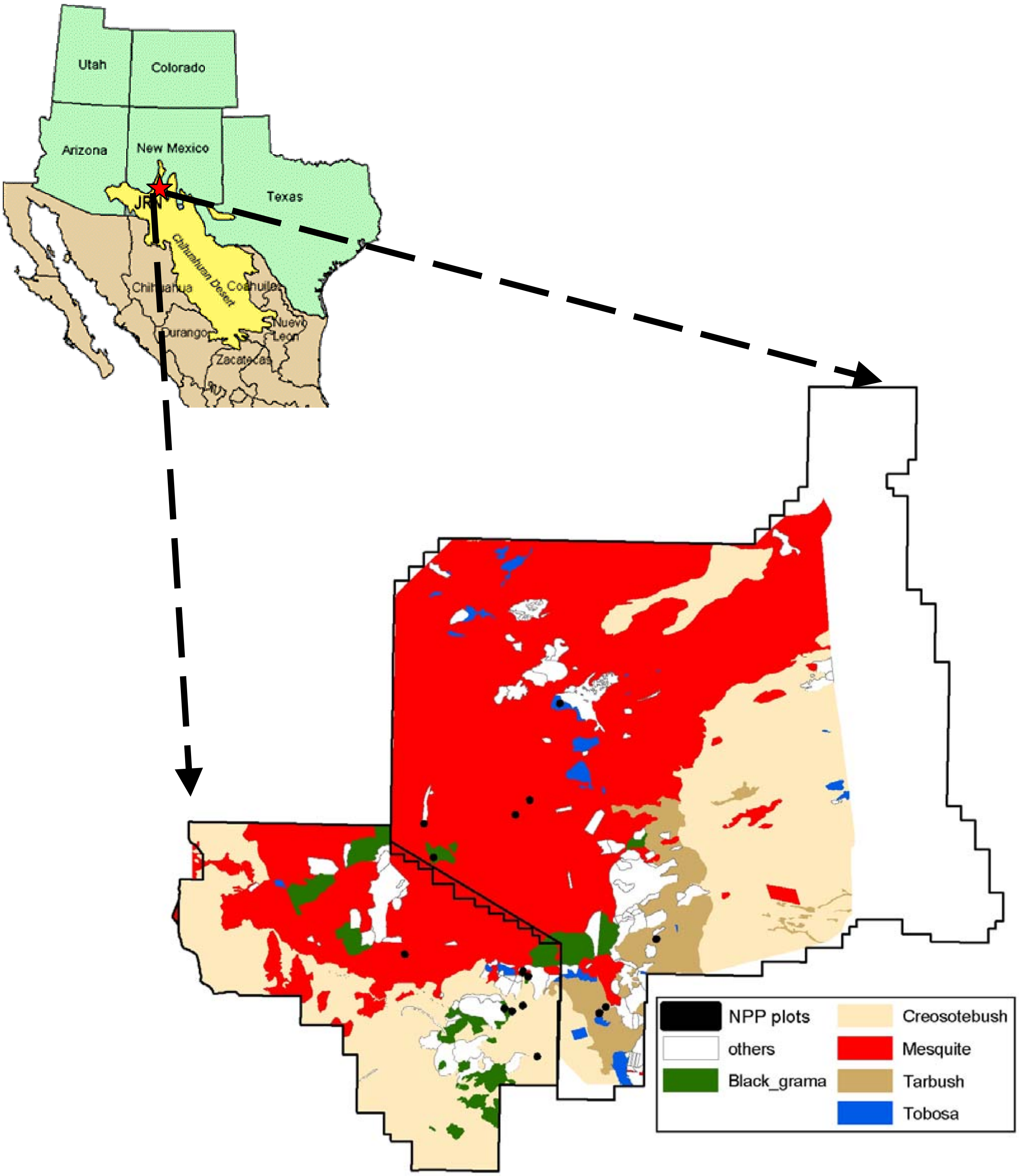
VIII. Figure legends

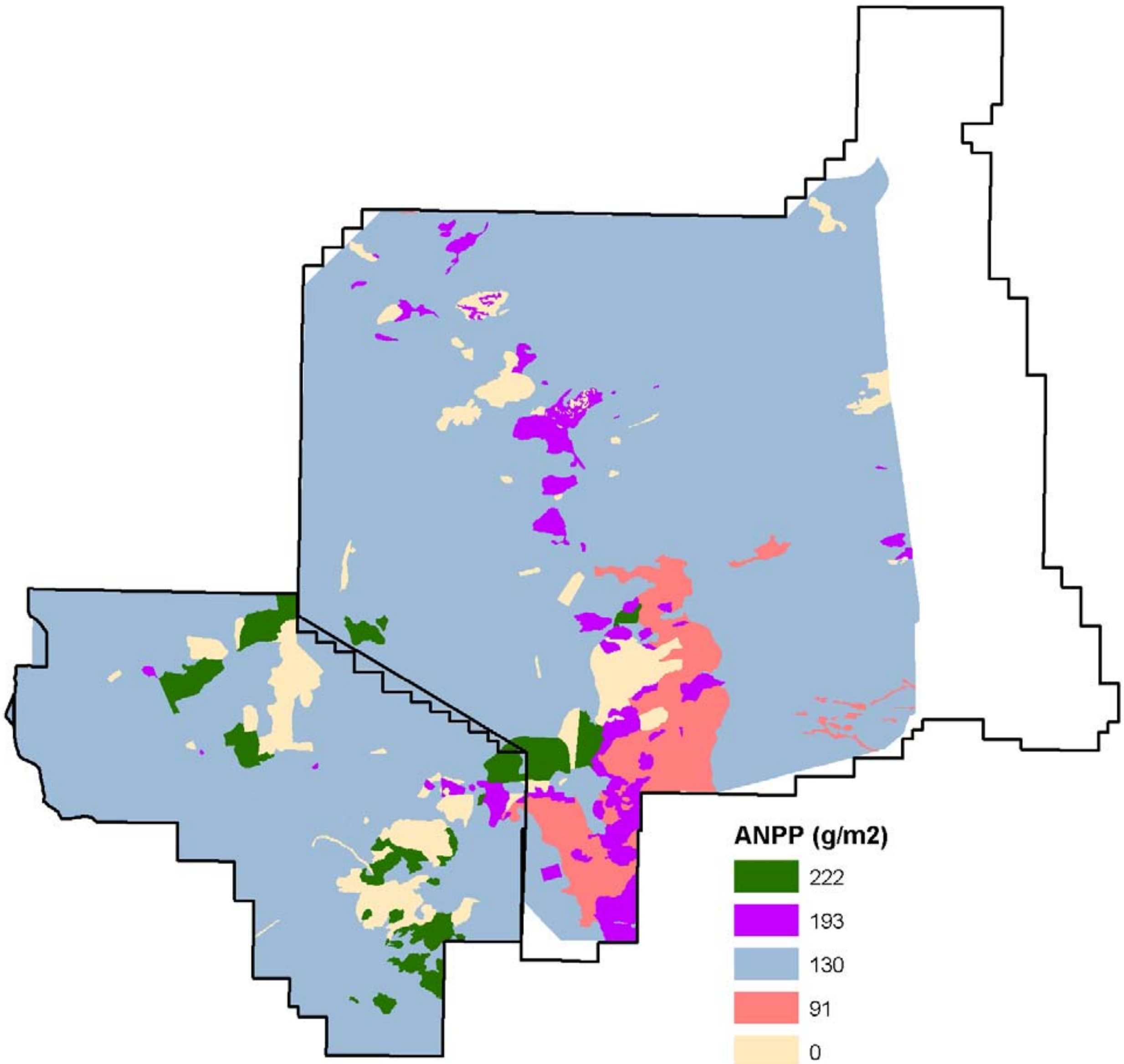
Fig. 1. Site map showing location of Jornada LTER within New Mexico and the U.S. Study site insert shows location of the 15 areas sampled for ANPP.

Fig. 2. Spatially implicit extrapolation of ANPP to the JRN landscape using the vegetation map and plot-based estimates. Both creosotebush and mesquite have the same average ANPP (130 g/m^2) and are shown in the same color.

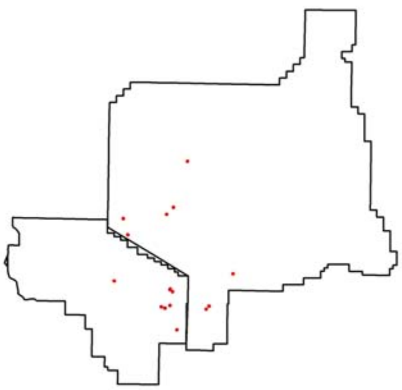
Fig. 3. Spatially implicit extrapolation of ANPP to the JRN landscape using a regression equation between plot-based measures of ANPP, soil texture, average precipitation, and elevation. The regression equation is then used to predict ANPP for the entire landscape using maps of the explanatory variables.

Fig. 4. Aerial photo showing complex landscapes at the JRN. Some areas near the mountains are dominated by water erosion as shown by the arroyos. Other areas on sandy soils are dominated by wind erosion as shown by dunes. Effects of animals on low plant production occur near water sources (wells). Human-caused disturbances are also non-uniformly distributed across the landscape. Areas with homogeneous vegetation and soils also occur.


Utah
Colorado
Arizona
New Mexico
Texas
JRN
Chihuahuan Desert
Chihuahua
Coahuila
Durango
Nuevo Leon
Zacatecas
NPP plots
others
Black_grama
Creosotebush
Mesquite
Tarbush
Tobosa


ANPP (g/m2)
222
193
130
91
0

Step 1. Develop regression equation using plot-based measures

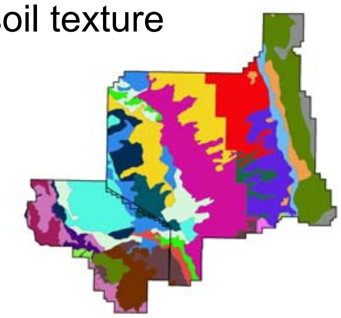


site	ANPP (g/m2/y) (1990-1998)	soil texture class	elevation (meters a.s.l.)	annual precipitation (mm/y) (1979-1997)
Creosote				
CCALI	91	gravelly fine sandy loam	1374	288.0
CGRAV	189	gravelly fine sandy loam	1377	289.6
CSAND		gravelly fine sandy loam	1355	277.8
Black grama				
GBASN	171	fine sandy loam	1316	247.9
GIBPE	194	loamy sand, fine sandy loam, fine sand	1323	245.3
GSUMM	322	loamy sand, fine sandy loam, fine sand	1387	291.2
Mesquite				
MNORT	184	loamy fine sand	1329	275.1
MRABB	115	loamy fine sand	1325	276.9
MWELL	122	loamy sand, fine sandy loam, fine sand	1323	247.4
Playa grass				
PCOLL	224	clay loam	1312	248.0
PSMAL	266	fine sandy loam, loamy fine sand, sandy loam	1326	255.8
PTOBO	92	fine sandy loam, loam	1312	274.3
Tarbush				
TEAST	107	fine sandy loam, loam	1314	246.9

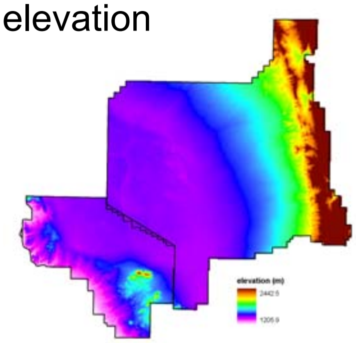
ANPP = f(SOIL, PRECIPITATION, ELEVATION)

Step 2. Use regression equation and maps of explanatory variables to predict spatial patterns in ANPP

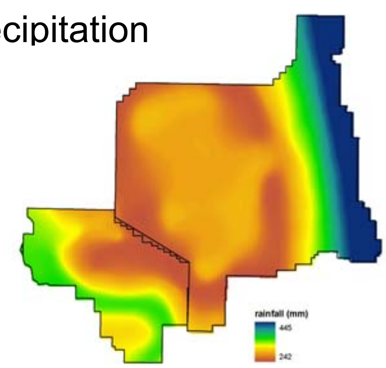
soil texture



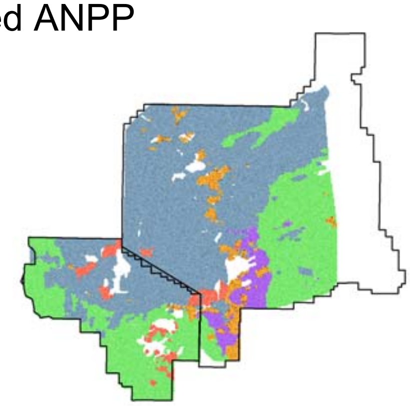
elevation

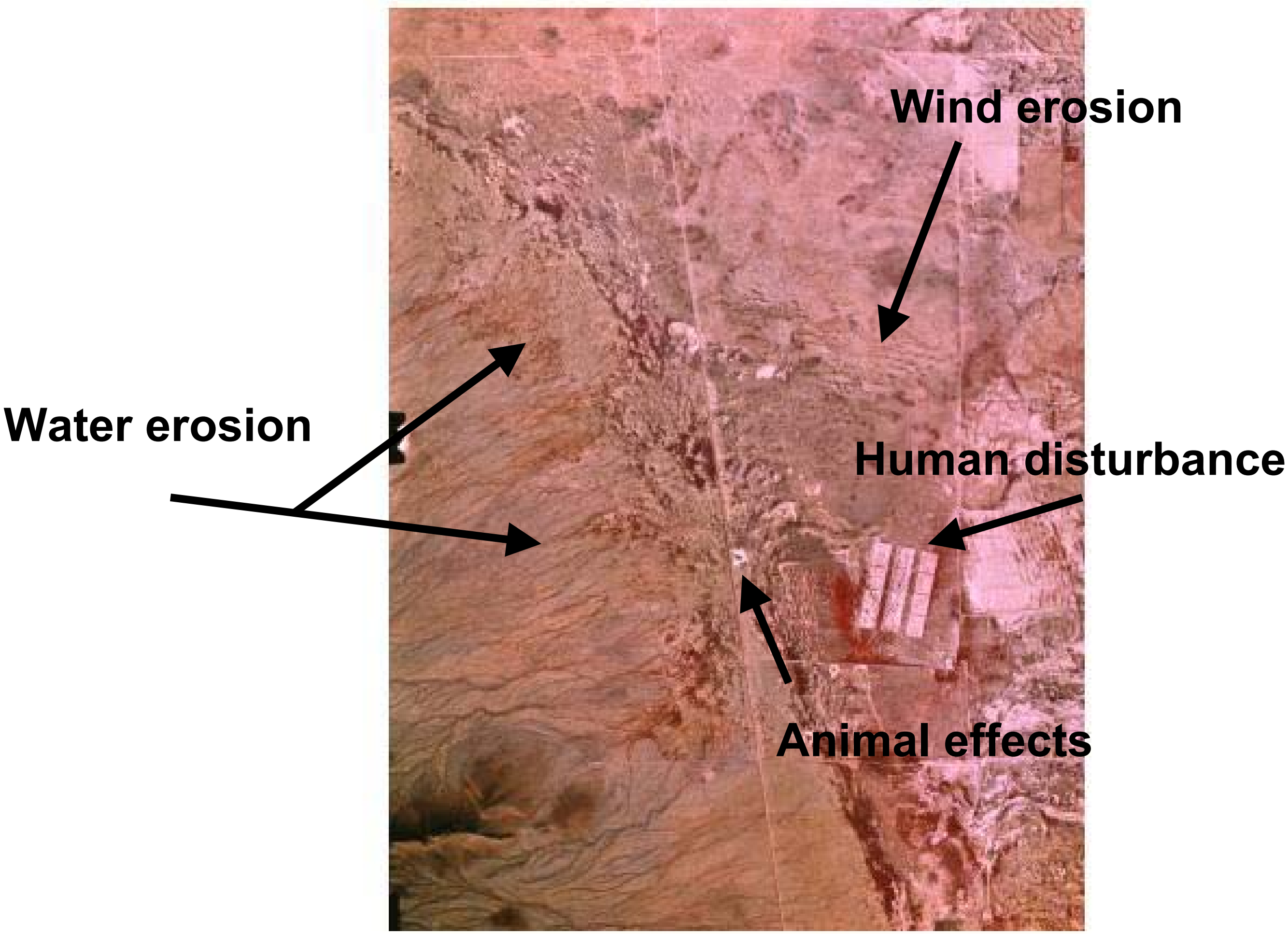


precipitation



Predicted ANPP




Wind erosion
Water erosion
Human disturbance
Animal effects