



Forest dynamics and ungulate herbivory: from leaf to landscape

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Abstract

Due primarily to anthropogenic influences such as land use change, exotic species introductions, livestock grazing, altered hunting regimes, and predator control, wild ungulate populations have undergone tremendous shifts in recent decades. Although the result has been endangerment or extirpation in some regions, ungulate numbers have increased to locally or regionally high levels in other areas, causing shifts in plant species composition, problems for forest regeneration, and conflict with humans and domestic livestock. Our ability to find solutions to these problems is limited because we lack sufficient understanding of how ungulate species interact with predators, habitat, forage, competing species, and humans at multiple scales from small foraging patches to large regions.

To bring together new findings in this area, encompassing various scales and foci of investigation, an international conference on “Forest Dynamics and Ungulate Herbivory” was held from 3 to 6 October 2001 in Davos, Switzerland. We provide a synthetic overview of the papers contained in this Special Issue, arising from that conference. A companion Special Issue of the *Journal for Nature Conservation* is devoted to the more management-oriented aspects of forest–ungulate interactions, entitled “Forest–Ungulate Interactions: Monitoring, Modeling and Management.”

From the papers in this issue, a number of important generalizations emerge to guide our understanding and further research. Our predictive understanding of foraging ecology needs to be generalized and scaled up, if it is to become useful for predicting the consequences of herbivory for broad-scale vegetation dynamics. Further, it is important to move beyond single-factor studies, to embrace the complexity of ungulate–vegetation interactions. The direction and magnitude of ungulate influences can be difficult to gauge because of complex interactions among species, structural units of vegetation or landscapes, ecosystem processes, and natural disturbances. Researchers need to look beyond the simplistic concept of “game damage”, and comprehensively address the direct and indirect effects of ungulates on communities, ecosystems and landscapes. This may require a more systems-oriented, and less species-oriented approach. Ungulate–vegetation interactions need to be better understood over multiple scales, and particularly at the coarser scales that are of interest to managers and policy-makers. Finally, a long-term view of ungulate–vegetation interactions, where past, present, and future effects are considered in their appropriate temporal context, is absolutely essential.

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1. Introduction

The articles in this special issue comprise a subset of papers presented at the International Conference on Forest Dynamics and Ungulate Herbivory, held at

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Davos, Switzerland on 3–6 October 2001. Additional conference papers, focusing more on management-related issues, are to be found in a special issue of *Journal for Nature Conservation*, “Forest–Ungulate Interactions: Monitoring, Modeling, and Management” (Weisberg and Bugmann, 2002). The compilation of papers included in this *Forest Ecology and Management* issue focuses on expressing the state of the art concerning the science of ungulate–vegetation interactions, rather than on management-related issues. However, generalities of relevance for forest and natural resource management emerge from many of the papers.

The Davos conference had two broad objectives. The first was simply to bring together researchers and natural resource managers concerned with the interactions between forest dynamics and ungulate herbivory. It seemed the time was ripe for such a meeting, since the last such international conference to address a similar theme (Conference on Ungulates in Temperate Forest Ecosystems) was held over 6 years earlier, in Wageningen, the Netherlands, in April 1995. We wanted to bring together the community of researchers, and to foster communication between them and the management community. Nearly 160 scientists and managers from 29 countries covering 5 continents attended the meeting.

A second objective was to summarize the current state of knowledge concerning forest–ungulate interactions at multiple spatial and temporal scales, and at different levels of ecological complexity. The contents of this Special Issue, and its companion issue in *Journal for Nature Conservation*, provide a test of whether this objective has been met.

Originally, our intention was to focus the conference on “forest ungulates” and “forest ecosystems.” Our conference, and subsequently this special issue, maintains that overall focus. However, it is telling that the distinction between forest and non-forest has been difficult to enforce, both with regard to ungulate species and vegetation type. Ungulate–vegetation interactions are best understood over multiple scales, from small to large. At certain scales, the mosaic of forested and non-forested patches becomes important, and one cannot isolate ungulate ecology within forests from that within meadows or woodland, when the same ungulate population makes use of both habitats. For that reason, this special issue also

includes papers that discuss aspects of ungulate–vegetation interactions for primarily non-forested systems such as subalpine meadows and woodlands (Mayer et al., 2003) or abandoned agricultural fields within a complex vegetation mosaic (Kuiters and Slim, 2003).

Wild ungulate habitat has become fragmented, concentrated and diminished throughout much of the world, due to anthropogenic influences such as land use change and livestock grazing. In combination with predator control or extirpation in many regions, this has resulted in situations of local overabundance, causing shifts in plant species composition (Husheer et al., 2003; Rooney and Waller, 2003; Schütz et al., 2003), problems for forest regeneration (Gill, 1992) or conflicts with domestic herbivores (Hobbs et al., 1996). Elsewhere, the result is endangerment or extirpation of the ungulate species. Our ability to find solutions to these problems is limited because we lack sufficient understanding of how ungulate species interact with predators, habitat, forage, competing species, and humans at multiple scales from small foraging patches to large regions. An intention of the Davos conference was to bring together new findings in this area, encompassing various scales and foci of investigation.

The purpose of this introductory article is to provide a brief overview of our state of knowledge as presented by the papers at the conference and in this special issue. We introduce the papers that follow, and attempt to provide a cohesive framework for integrating the knowledge included in the various subdisciplines represented. Where appropriate, we try to identify new questions raised by work presented at the Davos meeting, and new directions suggested for future research.

From the papers presented at the conference, and particularly those included in this Special Issue, the following general questions emerge that might help to guide ungulate–vegetation research:

1. How can our understanding of herbivore forage selection at fine scales be used to predict the consequences of herbivory for broad-scale vegetation dynamics?
2. How can we move beyond single-factor studies, to embrace the complexity of ungulate–vegetation interactions?

3. How can we better understand and integrate the indirect and direct effects exerted by ungulates on plant communities and ecosystems?
4. Which spatial interactions are important, and how can we better understand ungulate–vegetation interactions over multiple scales, and particularly for the coarser scales of interest to managers and policy-makers?
5. How can we take a long-term view of ungulate effects on forest dynamics, where we consider past, present and future effects in their appropriate temporal context?

2. Emergent generalizations

2.1. Linking foraging ecology to herbivore effects on vegetation

The process of herbivory lies at the core of the interaction between ungulates and vegetation. Ungulate herbivory affects plant processes at autecological, population, community and landscape levels, while plant responses to herbivory influence ungulate energetics, population dynamics, and distribution. Therefore we begin the special issue with several papers addressing ungulate foraging ecology, to form a foundation for the papers that follow, which focus more on ungulate effects on vegetation, or on ungulate–vegetation interactions at coarser spatial and temporal scales.

It is arguable that we understand more about the relationships between ungulates and vegetation at the level of individual bites within small foraging patches, than we do about such relationships at higher levels of organization. However, we still may not know enough to be able to derive the generalizations needed, to scale up to ungulate–vegetation interactions over multiple species and heterogeneous landscapes. Progress has been made toward generalizing the bite size selection of multiple ungulate species on the basis of allometric relationships with body size (Illius and Gordon, 1987; Shipley et al., 1994, 1999), as modified in predictable ways by plant chemistry and morphology (Shipley et al., 1998). In this issue, such relationships are described for a complex ungulate browser community in the South African thicket (Wilson and Kerley, 2003). These authors also address the relationship between bite size and forage quality, finding that

the larger bites cropped by larger browsers are relatively high in fiber, but low in protein, soluble ash, energy, condensed tannins and overall digestibility.

Gordon (2003) reviews the state of the art in foraging ecology, particularly addressing the question of what it is that differentiates functional guilds of species, such as browsers, grazers and intermediate feeders. He makes a strong call for more rigorous experimentation and hypothesis testing, which would control for confounding factors to explore differences in diet selection and forage intake. Gordon (2003) highlights recent research suggesting that the morphological and physiological distinctions presumed to drive this commonly used functional guild classification may not be as great as has been supposed, once allometric relationships with body mass and evolutionary history have been accounted for. Instead, it is proposed that differences in foraging behavior play a greater role. Foraging behavior is reviewed in the context of the functional response between resource abundance and the rate of consumption, herbivore responses to vegetation structure and the distribution of forage elements, and herbivore responses to the spatial distribution of resource patches.

Gordon (2003) reviews the functional response model introduced by Spalinger and Hobbs (1992) in the context of how well it distinguishes foraging behavior of browsers and grazers, and what experiments would be needed to test specific hypotheses concerning how the parameters of this mathematical model differ among these two feeding guilds. He makes the point that since a Type III functional response (Spalinger and Hobbs, 1992) appears to faithfully describe intake rates for a wide range of browsers and grazers spanning orders of magnitude of body size (Gross et al., 1993), bite size (the independent variable in the model) can fruitfully be considered the fundamental unit of forage intake. Therefore, “understanding the foraging behavior of herbivores requires us to describe the distribution of bites in the environment” (Gordon, 2003). It is hypothesized that the difference in distribution of bites (at a range of scales) in the landscape may be the determinant of differences in foraging behavior, social organization and impacts observed for ungulates that specialize in grass- or browse-based diets (see also Jarman, 1974).

When considering larger areas and longer time periods than can readily be accommodated by the

functional response models, the scale of forage selection becomes most important. Are herbivores responding to the distribution of bites, or to the distribution of clusters of bites, or simultaneously to multiple hierarchical levels of forage element clustering? Another paper in this issue uses a cafeteria experiment to demonstrate that red deer select for forage patches in close proximity to their shoulder height, and that contain internal structures of widely spaced forage elements (Renaud et al., 2003). Gordon (2003) summarizes a landmark paper by Danell et al. (1991) demonstrating that, for moose in Sweden, forage selection appears to operate on individual trees within stands, and not at the stand level. On the basis of this and other recent work, Gordon (2003) hypothesizes that browsers are more selective for individual plants according to their species-specific preferences, while grazers select at the level of grass–plant mixtures. There has been surprisingly little research concerning the scaling of forage selection under natural, non-experimental conditions, where plant responses to rebrowsing and greater patch heterogeneity become relevant. The point of Gordon (2003) is well-taken, that in order to scale up from our fine scale understanding of ungulate foraging behavior, where our predictive ability is relatively high, we need to better account for the spatial heterogeneity in forage resources over multiple spatial scales, from the perspective of the herbivore.

Even those models of ungulate–vegetation interactions that address landscape-level research problems (e.g. Moen et al., 1998; Weisberg et al., 2002) typically have at their core some conceptualization of the functional response. The functional response links the pool of available forage with the foraging behavior of the ungulate species, and so represents a major interface among plant and animal components of an integrated model. The methods for scaling the functional response to the landscape scale are, unfortunately, not well-developed. Scaling up explicitly (Bugmann et al., 2000) by simulating ungulate foraging simultaneously for many small forage patches, and then simply summing the patches over a large landscape, is difficult to implement even apart from computational issues associated with this “brute force” approach. Such an approach requires an accurate database of the spatial heterogeneity of available forage of varying quality, over the same fine scales as are modeled, which is

seldom available. It follows from Gordon (2003) that, even if we had this extremely fine scale map of landscape-level forage structure, we lack the understanding of how ungulates (of various species, in varying social positions, and during different seasons) select among forage patches over multiple scales, which likely involves higher-order processes not captured in the functional response models.

Therefore, the challenge remains how to use our knowledge of foraging ecology to predict effects on vegetation. Most foraging ecology studies are focused on implications for the animal side of the relationship (e.g. Bugalho and Milne, 2003; Mayer et al., 2003), and do not address plant responses. By the same token, studies of browsing or grazing effects on vegetation typically consider the level of biomass removed as a treatment level to be assessed empirically or used as model input, but do not consider the factors that influence the level of consumption. An integrated approach needs to more forcefully emerge, which considers the interactions among ungulates and vegetation as they unfold over sufficiently long time scales for manifestation of feedbacks and systems dynamics among the two components.

2.2. *Multiple factors and multiple influences*

It is perhaps in the nature of the reductionist scientific enterprise that most investigations address single or few factors, while relatively few studies explore interactions among multiple factors. This is especially a problem for ecology, where numerous interacting factors (e.g. individual species) combine with contingent effects of history and stochasticity (e.g. weather) to make difficult the formulation of general laws enabling useful prediction (Lawton, 1999). Such general, detectable patterns may be most likely to emerge at small or large scales, but not at the “meso” level of ecological communities. Lawton advocates that ecologists should place greater emphasis on large-scale macroecological research, where universal pattern–process relationships again emerge as we gloss over the details. Unfortunately, ungulate–vegetation research cannot readily retreat into this realm. Much of ungulate–vegetation research, based as it is upon interactions among species within and among trophic levels, is stuck in the mesoscale, where the world is complicated and generalities may be elusive. One feasible alternative to the search for

general laws could be the application of systems theory, focusing on the interactions among parts of a complex system, in order to understand and predict relationships and emergent properties (cf. Zeigler, 1976). Particularly, systems analysis approaches using agent-based modeling could be helpful for overcoming the weak signal-to-noise ratio that is characteristic of ungulate–vegetation systems.

A key generalization one can draw from many of the papers presented at the Davos conference is that interactions among multiple factors need to be considered, if we are to develop a useful, predictive understanding of ungulate–vegetation relationships (e.g. Danell et al., 2003; Kramer et al., 2003; Kuiters and Slim, 2003; Rooney and Waller, 2003; Sage et al., 2002a,b; White et al., 2003). While it is clear that forest ungulates can exert a profound influence on vegetation and ecosystem patterns and processes, the direction of such influences is not always certain because of often complex interactions among individual species or functional groups, structural units of forests or landscapes (e.g. forest overstory vs. understory), ecosystem processes, and landscape-level disturbances. Sustained, high-intensity browsing or grazing pressure may cause plant species richness to increase (Schütz et al., 2003) or decrease (Rooney and Waller, 2003). In one national park in the western US, ungulates increase the rate of nitrogen cycling; in another, they have a decelerating effect (Singer and Schoenecker, 2003). How ungulates influence vegetation and ecosystems involves strong interactions with numerous other processes. In the case of nitrogen cycling, effects may be contingent upon ungulate densities, vegetation type, spatial configuration of vegetation types on a landscape with regard to animal movement patterns, and plant community composition (including associated interspecific interactions) within each vegetation type (Singer and Schoenecker, 2003).

Ungulate effects on vegetation dynamics are also influenced by predation, considering both numerical and distributional influences. White et al. (2003) investigate aspen decline on multiple study areas in the Canadian Rocky Mountains, considering a 4-link trophic chain (humans–wolves–elk–aspen). Predation influences the form of the functional response for herbivory rate on aspen saplings, mainly through behavioral influences. Elk avoidance of dense aspen thickets, where predation risk is high, results in a Type

II response. It is significant that, while predator influences on plant–herbivore interactions are clearly important, this was our only conference contribution addressing this issue. In contrast to other fields of ecology such as limnology, top-down influences on producer–consumer interactions have been little investigated in terrestrial systems.

The result of this complexity is that it is difficult to arrive at broadly valid generalizations concerning ungulate effects. A systems approach is useful if we wish to develop the ability to make accurate forecasts. We need to embrace complexity in our studies, but in a rigorous manner that allows quantification of both the main factors and interactive effects. Studies of ungulate effects on vegetation would do well to take a multi-factor approach. For example, in their study of the relative role of deer for limiting eastern hemlock (*Tsuga canadensis*) and northern white-cedar (*Thuja occidentalis*) regeneration in Wisconsin, Rooney and Waller (2003) jointly consider light level, stand composition, leaf litter composition and depth, and local deer browsing pressure. Simulation models should provide a useful tool for integrating separate processes influencing the plant–herbivore system, in a way that provides information about likely emergent outcomes.

Kramer et al. (2003) use a spatially explicit simulation model, coupling vegetation with ungulate dynamics, to explore interactions among fire and ungulate grazing for a forest–heathland–grassland mosaic landscape in the Netherlands. Their model results suggest that fires may shift the producer–consumer system into a different stable state, and that ungulate grazing can help to maintain the system in its new state. However, ungulate grazing in the absence of fire does not push the vegetation into a different stable state. These results resonate with other studies of ungulates and multiple stable states, including the work of Dublin et al. (1990) on elephant–fire interactions in East Africa. Hobbs (1996) observed that while ungulate effects on vegetation structure may be subtle or minor during the long periods between episodic disturbances, their effects immediately following disturbance may act as a “switch” among alternative states, which may differ dramatically in structure and function. However, both Kramer et al. (2003) and Kuiters and Slim (2003) concur that, for similar Dutch landscapes including grasslands and abandoned agricultural land, ungulate grazing is likely

insufficient to maintain open land over the long-term, in the absence of fire. In any case, numerous studies around the world show that grazing and fire regimes interact to influence mosaic structures of forests and more open vegetation types, and that the one process cannot be meaningfully understood without the other.

2.3. *Direct and indirect effects*

Ungulates may exert a profound influence on ecosystem processes, including nutrient cycling, primary productivity and disturbance regimes (reviewed in Hobbs, 1996). Additionally, ungulates strongly influence plant population processes and vegetation dynamics in a variety of ways, and over a broad range of scales. The direct effects of ungulate herbivory on plants are certainly the most noticeable. Danell et al. (2003) present a careful review of the direct effects of forest ungulate browsing on plant population units, which they classify into two levels of organization, modules and genets. Modules represent individual growth units such as leaves, shoots or stems. Genets represent individuals developed from the original zygotes, originating from seed or other autonomous propagules. Module responses to herbivory (changes in number, size and chemical composition) have high variability and are influenced by tree species, tree age, module age, and the intensity, timing and seasonality of herbivory. Genet responses include influences on flowering, seed dispersal, the availability of suitable seed germination sites (through trampling effects), and the suppression of new age cohorts through influences on growth and mortality.

Danell et al. end their review of ungulate effects on woody plant species by discussing what Rooney and Waller (2003) term the “indirect effects” of ungulate herbivory—where the direct influences of herbivores on a given species are transmitted to additional “receiver species” through interspecific interactions such as competition, physical habitat modification, or trophic cascades. Rooney and Waller provide a useful review of such indirect effects, including food web interactions, mediation of plant–plant interactions, ungulates as predators or scavengers, habitat modification, and effects on plant-available nutrients. According to both review papers, selectivity is the main aspect of ungulate foraging that, coupled with differential plant responses to herbivory, leads to long-term vegetation change.

Shifts in plant community composition due to selective feeding may lead to major changes in ecosystem processes if, e.g. the tree species enhanced or diminished by ungulate herbivory have different biogeochemical characteristics, which in turn influence decomposition rates and nutrient availability. Vegetation shifts may also lead to larger-scale changes in landscape pattern, if plant types involved have greatly different morphological structures (e.g. trees vs. grass).

Interspecific interactions within the plant community may amplify the direct effects of ungulate herbivory, as relatively unpalatable species may out compete more palatable taxa through increased net shoot or root growth, leading to increased competitive ability for light or water. However, interspecific interactions may also dampen the ability of ungulate herbivory to influence vegetation dynamics. Kuiters and Slim (2003) study the efficacy of pony grazing as a management practice for maintaining open lands (formerly agricultural fields) on a Dutch nature reserve. They find that virtually all regeneration of saplings taller than 100 cm occurs within patches of bramble (*Rubus* spp.), which serves a protective “nurse shrub” function. On this landscape, the rate of ultimate establishment of oak forest depends, in large part, upon the rate of shrub encroachment onto grassland.

Much research has addressed the direct influences of ungulate herbivory on growth and mortality of individual plants, and on short-term changes in plant community structure. A preoccupation with direct effects of browsing and grazing may arise from an agricultural focus, out of which the research area of ungulate–vegetation interactions had originally emerged. But ungulate influences go well beyond the simplistic concept of “game damage.” Based on the findings of the papers presented in this Special Issue, we propose that further research is necessary in the areas of: (1) direct ungulate effects other than herbivory (e.g. trampling, antler-rubbing, seed dispersal) as well as (2) the indirect effects, or the ways in which ungulate influences cascade and feed back through interacting components of communities, ecosystems, and landscapes.

2.4. *Ungulates and spatial scale*

The concept of “scale” has transformed most ecological endeavors over the past 10–15 years (Kotliar and Wiens, 1990; Levin, 1992; Keitt et al., 1997). In

particular, there has been widespread recognition that ecologists need to address increasingly large spatial extents and long time scales, for their work to be relevant to natural resource management and policy-making (Van Gardingen et al., 1997; Hobbs, 1998). However, despite much apparent interest in scaling up ungulate–vegetation studies, most scientific efforts in this area still focus on relatively small areas (Hobbs, 2003). Hobbs identifies a likely reason for this dichotomy between “talking the talk and walking the walk”—the fundamentals of good study design lead researchers to develop studies with large sample sizes, freedom from bias, and maximal statistical power for hypothesis testing. For reasons discussed by Hobbs, nature seldom cooperates with our efforts to achieve good study design at coarse spatial scales, making such studies less attractive to researchers (and funding agencies). Ungulate researchers are urged to overthrow this preoccupation with statistical power (“the tyranny of power”), and to treat the ability to generalize results across scales as an additional, fundamental consideration for development and evaluation of study designs (Hobbs, 2003).

Several of the case studies reported in this issue consider multiple scales, or at least coarser scales. Didier and Porter (2003) investigate the regional-scale influence of white-tailed deer on sugar maple reproductive success in northern New York State. They question the correctness of directly extrapolating the observed effects of ungulates on tree regeneration taken from fine scale studies to regional scales. At local scales, using observational and exclosure studies, there is a clear effect of strong browsing impacts on sugar maple regeneration. At regional scales (10 km resolution, 42,000 km² extent), there is a lack of a spatial relationship between deer density and sugar maple reproductive success. They suggest that over coarse scales, other factors such as land use patterns and acidic deposition may play a greater role.

The studies of White et al. (2003) and Kuiters and Slim (2003) incorporate analyses over multiple spatial scales to consider influences of ungulates at the landscape level. Kuiters and Slim map five vegetation types within their 98 ha study area, and compare landscape-level vegetation patterns for three different time slices over a 30-year period. They combine this landscape-level analysis with observations of pony activity and tree regeneration surveys along transects,

to infer how the fine scale effects of pony grazing are likely to influence long-term, landscape-level vegetation change. White et al. investigate patterns of elk density and foraging on aspen over three spatial scales: regional scales, intermediate landscape scales allowing consideration of proximity to human and predator travel routes, and habitat patch scales. They find that at the landscape scale, human hunter and predator patterns are opposite of what they likely were historically, resulting in dramatically different patterns of elk impacts on aspen communities. Historically, predation risk from wolves and aboriginal hunters was greater in the valley bottoms, where animal movement is facilitated in these mountainous landscapes. Currently, elk may be attracted to valley bottom transportation routes where heavy human use deters wolves. The authors conclude that the results are historically unprecedented levels of elk browsing pressure on aspen stands in the valley bottoms.

2.5. *The long view of ungulate–vegetation interactions*

The concept of “the long now”, where current ecosystem states are understood in the context of their historical development, and in turn provide context for future ecosystem change, has been emphasized in a recent paper by Carpenter (2002). It is extremely difficult to look forward and make ecological predictions, without being able to trace the historical development of current situations and learn from the past. On the other hand, future conditions will differ from those of the past, so useful long-term prediction requires process-level understanding. Ungulate population dynamics and, especially, tree population dynamics fluctuate over long time scales relative to human perceptions and experience. It is therefore difficult to understand the significance of large herbivore impacts for long-term vegetation change, which is generally the interest of forest management. A long-term perspective is needed for both research and management. Such a perspective emerges from several of the papers included in this special issue, and various research methodologies for developing long-term perspectives are demonstrated or explored (Bradshaw et al., 2003; Husheer et al., 2003; Motta, 2003; Rooney and Waller, 2003; Schütz et al., 2003; Senn and Suter, 2003).

The perils of failing to take a long view are forcibly expressed by Senn and Suter (2003), emphasizing the case of European silver fir (*Abies alba* Mill.) in Switzerland. There, lack of regeneration over past decades has been attributed to browsing ungulates (red deer, roe deer and chamois). Based on the current scarcity of silver fir seedlings and saplings that escape browsing, many Swiss foresters predict widespread regeneration failure of this species, unless the situation is altered through management activities. However, as the authors point out, silver fir regeneration may naturally be a variable process in time and space, dependent on rare “windows of opportunity” (cf. Sage et al., 2002a,b). In the past, regeneration of this preferred forage species may have depended on strong fluctuations of ungulate populations, fluctuations which no longer occur on the same level due to careful management of deer populations. If we take the long view, is there a silver fir regeneration problem? Senn and Suter (2003) carefully review the evidence, and conclude that current browsing survey methods provide insufficient information for answering this question. Needed is a more mechanistic understanding of how forest ungulates influence tree population dynamics over time scales of decades to centuries. The module vs. genet classification proposed by Danell et al. (2003) may prove useful for this endeavor, as it separates module dynamics, operating over short time scales, from genet dynamics that unfold over much longer time periods. Senn and Suter suggest the use of forest dynamics models that address implications of natural variability in both browsing intensity and plant responses for long-term forest compositional dynamics.

In a similar vein, Motta (2003) points out the perils of relying solely upon browsing surveys to gauge the impact of ungulates upon forest vegetation. Browsing surveys clearly underestimate ungulate impacts where past browsing pressure has been so intense as to completely eliminate the most palatable species, as is observed for rowan (*Sorbus aucuparia*) in one of several study sites in the Italian Alps. This is a situation where knowledge of the site-specific history of forest–ungulate interactions is needed to understand the current situation. Motta demonstrates two complementary methods for studying ungulate effects on forest regeneration of the recent past: analysis of tree height structures, and dendroecological analysis of growth release dates. Such analyses facilitate scaling

up from ungulate effects on individual trees to long-term implications for forest dynamics, as Senn and Suter (2003) highlight the need for.

If we can reconstruct how ungulate herbivory influenced vegetation dynamics over long time periods in the past, we might be able to generalize current impacts to the future. The long view requires a historical context, which is lacking from browsing surveys as commonly implemented. A historical context can be gained from long-term studies involving remeasurements, dendroecological analysis, archival sources, or paleoecological studies. Several of the papers already discussed in the context of this special issue illustrate the first approach, where long-term studies involve repeated measurements over periods as long as several decades (Husheer et al., 2003; Rooney and Waller, 2003; Schütz et al., 2003).

In their study of pony grazing effects on woody tree regeneration in abandoned agricultural lands, Kuiters and Slim (2003) use historical air photos to quantify landscape change over the 27-year period since grazing was introduced. By combining vegetation mapping of the 98-ha reserve with tree regeneration surveys and observations of pony activity, these researchers were able to identify important legacy effects of past land use practices. Ponies prefer to graze the former agricultural fields, as opposed to areas that had formerly been natural grassland communities with heather (*Calluna vulgaris*). Since the ponies appear to be greatly slowing the rate of forest invasion on the former fields, this identifies a long-lasting effect of agricultural activity on vegetation pattern decades after land use practices had changed. The work of Schütz et al. (2003) tells a similar story for a nature reserve in the Swiss Alps that had formerly been heavily grazed. Even though it has been over 80 years since the founding of the Swiss National Park, the spatial foraging patterns of red deer are still greatly influenced by former agricultural use. Irrigation activities associated with livestock grazing have created phosphorus-rich patches that are now preferentially grazed by red deer. On these heavily grazed patches, grassland plant species composition has shifted toward unpalatable species, including annuals and low-growing grasses. For both case studies (Kuiters and Slim, 2003; Schütz et al., 2003), current grazing patterns and effects cannot be understood without a knowledge of past land use practices. It is unlikely that ecologists would have correctly predicted future ungulate–vegetation

interactions for these areas at the time of reserve establishment. Both then and now, a long view that incorporates a historical dimension is essential for accurate prediction and understanding.

Although ungulate effects on herbaceous communities may be readily quantified within a few decades (Rooney and Waller, 2003; Schütz et al., 2003), ungulate effects on forest dynamics may require a long time even to detect. For example, to study the effects of introduced deer on New Zealand's *Nothofagus* forests, Husheer et al. (2003) used data from permanent plots established 20 years apart. This proved an appropriate temporal resolution for detecting changes in understory plant community composition, which shifted from shrub-dominated toward browse-tolerant turf communities. However, no significant changes in forest overstory composition were detected. The authors observe that one cannot infer from this that deer do not have an effect on forest dynamics, since changes would be expected over longer time scales. Indeed, analysis of exclosure plots suggested that in the absence of deer, *Nothofagus* regeneration was more abundant. However, even 20 years of repeated observations proved not a long enough time period for making the connection between deer effects on plants and implications for long-term forest dynamics. Husheer et al. (2003) contend that conservation managers need to take action now, despite the uncertainties, because compositional shifts in plant communities may not readily be reversible.

The relationship between ungulate effects on individual plants and implications for long-term forest dynamics becomes more complex where high or strongly fluctuating ungulate densities greatly influence the ability of selected species to ultimately escape herbivory. In this situation, temporal variability and serial autocorrelation in climate, ungulate browsing intensity, rodent population levels, disturbance episodes, mast years, and silvicultural treatments interact to determine whether sufficient “windows of opportunity” occur for a natural or desired forest regeneration (Sage et al., 2002b; Senn and Suter, 2003). Such uncertainties concerning how contemporary ungulate effects translate into long-term vegetation dynamics highlight the importance of methodologies that allow us to further expand our temporal scales of inference, beyond even the contributions of long-term field studies. Two such methodologies include modeling approaches, and paleoecological reconstruction.

Modeling approaches for forecasting effects of herbivory on long-term vegetation dynamics have proven fruitful for a variety of research questions, geographical areas and ecosystem types (Jorritsma et al., 1999; Kienast et al., 1999; Seagle and Liang, 2001; Weisberg et al., 2002; Kramer et al., 2003). For example, Kramer et al. use the FORSPACE model to consider grazing–fire interactions (already discussed) and to demonstrate how, over a 100-year time period, grazing may be beneficial for certain species (pine and birch) at the expense of others (beech and oak). Weisberg et al. use a spatially explicit ecosystem model (SAVANNA) to estimate the carrying capacity for elk (*Cervus elaphus*) based on the supply of energy distributed over a spatially heterogeneous, temporally dynamic landscape. However, such modeling approaches have only recently begun to consider how ungulate distribution and foraging behavior are influenced by spatial heterogeneity in vegetation and environmental patterns, and to incorporate key feedbacks between ungulate and vegetation components. The “long view” requires such tools, for forecasting the future effects of extant pattern–process relationships.

Paleoecological reconstruction of ungulate–vegetation interactions is a relatively new field of study, exemplified in this volume by the review paper of Bradshaw et al. (2003). These authors discuss the uses and limitations of pollen, plant macrofossils, various other sedimentary analyses, and ungulate remains for reconstructing such interactions in the distant past. They review the body of evidence for two controversial hypotheses implicating large herbivores as playing a major role in pre-historical vegetation dynamics. The “mammoth-steppe” hypothesis suggests that the past vegetation of Beringia was significantly more diverse and productive than the tundra vegetation occurring in the region today, allowing a diverse fauna dominated by large grazers such as mammoth, bison and horse. Bradshaw et al. find that while ungulate populations were likely limited by available forage, a highly heterogeneous vegetation mosaic supported a diverse fauna. A second hypothesis reviewed in light of the paleoecological evidence is the “wood pasture” hypothesis put forth by Vera (2000). This hypothesis suggests that large herbivores of the early Holocene maintained large areas of open woodland and pasture throughout much of central and western Europe, quite unlike the dense temperate forests

found in modern-day nature reserves. Based on their review of the evidence, Bradshaw et al. suggest that past ungulate populations are only one of many disturbance factors, including fire and flooding, which influenced regional vegetation patterns. Past vegetation in Europe was likely quite heterogeneous, including elements of both dense forest and open areas. For properly evaluating either hypothesis, it is critical to obtain better estimates of past ungulate densities than are currently available (Bradshaw et al., 2003).

As mentioned by Bradshaw et al., the use of simulation modeling and paleoecological approaches in combination presents a potentially fruitful new research direction, where paleoecological data can be used to calibrate and validate historical model runs, and simulation models can be used to explore hypotheses about ungulate–vegetation interactions of long ago. For example, Moen et al. (1999) used a model of ungulate energetics to explore alternative explanations for Irish elk (*Megaloceros giganteus*) extinction more than 10,000 years ago. The authors propose that this species was unable to balance opposing selection pressures for larger antlers and larger body size (sexual selection), vs. pressures for smaller antlers and body size, imposed by more limited forage resources resulting from regional shifts in vegetation structure. This study shows the potential of combined modeling–paleoecological investigations, of which there have been few examples to date.

3. Conclusions

In their preface to the latest Special Issue in this journal addressing the topic of ungulate–forest interactions, Kuiters et al. (1996) observe a gradual shift from a species-oriented toward a system-oriented approach to research. The papers included in this issue, and in its companion issue in *Journal for Nature Conservation*, illustrate that this shift has continued, and even intensified over the past several years. Ungulate effects on forests cannot be generalized to spatial and temporal scales that are relevant for management if we do not understand them in the context of other important, interacting factors. Understanding the dynamics of such interacting effects requires a systems approach at various stages of the research process, including theoretical development, sampling

design, data collection, and model-assisted data analysis. The same holds for the various methodologies used to infer patterns from the natural world, including experimentation, observational studies, and simulation modeling. Perhaps it is most fruitful at this point to adopt more creative, integrative approaches that consider multiple processes and broad scales of inquiry—even if this means occasionally sacrificing a certain level of experimental rigor (Hobbs, 2003).

We are confident that the papers in these two special issues (this one and Weisberg and Bugmann, 2002) represent useful contributions to advancing our state of knowledge, but we still have a long way to go towards a predictive capability in the area of forest dynamics and ungulate herbivory. However, we do not believe that science in this field is hopelessly mired in the complexities inherent to the meso-scale (Lawton, 1999). Rather, we believe a number of important generalizations have emerged to date that are helpful for guiding our understanding and further research.

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