Legacies of Historical Human Activities in Arctic Woody Plant Dynamics

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Abstract
Recent changes in arctic vegetation might not be driven by climate change alone. Legacies of human activities have received little attention as a contributing factor. We examine the extent to which traditional human activities...
(hunting, herding, fire, wood extraction, and agriculture) have had lasting effects on arctic woody plant communities and therefore might continue to affect biome-wide responses to climate change. Evidence suggests that legacies are likely to be evident across meters to hundreds of kilometers and for decades, centuries, and millennia. The evidence, however, is currently sparse, and we highlight the potential to develop systematic assessments through a circumarctic collaboratory consisting of a network of interdisciplinary field sites, standardized protocols, participatory research, and new approaches. We suggest that human activities should be brought into consideration to increase our understanding of arctic vegetation dynamics in general and to assess woody plant responses to climate change in particular.

**Contents**

MOTIVATION ................................................................. 542
DISEQUILIBRIUM DYNAMICS, LEGACIES, AND THEIR
UNDERLYING FACTORS ..................................................... 543
SPATIAL AND TEMPORAL EXTENT OF HUMAN LEGACIES
IN ARCTIC WOODY PLANT DYNAMICS ................................... 546
Hunting .......................................................... 546
Herding .......................................................... 549
Fire Use ............................................................ 552
Wood Extraction ..................................................... 552
Agriculture ........................................................... 553
SUMMARY AND FUTURE DIRECTIONS .................................. 554
Circumarctic Interdisciplinary Collaboratory ......................... 555
Participatory Research .................................................. 555
Integrating Established and Novel Techniques ....................... 557

**MOTIVATION**

Anthropogenic pressures (e.g., land use and climate change) are rapidly transforming ecosystems and shifting the boundaries between biomes across the Earth. Assessing the relative importance of these pressures, including legacy effects, represents a major challenge for ecology and environmental management (1). At high altitudes and latitudes, one potential consequence attributed largely to climate change is the transformation of arctic and alpine ecosystems as shrub and tree vegetation expands upward and northward (2). However, climate change may provide an incomplete explanation since there is evidence for substantial local and regional variation in the growth and cover of woody plants (shrubification) (3–5). Observed changes in the abundance and distribution of woody plants in the Arctic do not always coincide with recent warming trends (6–10). In fact, the greening trend has been reversed in some regions in recent years, initiating substantial debate about multiple drivers of greening and browning in tundra regions (11). Furthermore, recent studies suggest that the distributions of arctic and boreal plant species are not in equilibrium with climate and may not have been so for thousands of years (12, 13). Therefore, the rate of expansion of woody plants within and into the Arctic might not necessarily be driven
by climate change alone. The observed variation in species responses to climate change across space and time may have several reasons, including unsuitable local environmental conditions, species interactions (e.g., herbivory or competition), dispersal limitation, or human disturbance (cf. 13). Although some insights have been gained into the role of environmental variation (3, 7, 14–16), our understanding of zoogenic and anthropogenic effects on arctic woody vegetation is currently limited. In particular, legacies of human activities have received little attention as a contributing factor in the Arctic. In response, we examine the degree to which past human activities may have had lasting effects on arctic woody plant communities. This knowledge is essential for forecasting and managing the response of tundra ecosystems to ongoing and future climate change.

Across the world, modification of the environment by humans produces important and dynamic ecological legacies and creates novel evolutionary pressures (17). Modern humans colonized the circumpolar North in the Late Pleistocene (18–24). These early migrants lived as hunter-gatherers, probably at relatively low population densities, and some arctic populations continue to do so (25). However, humans are likely to have acted as powerful ecosystem engineers, even prior to the Industrial Revolution, owing to the emergence and intensification of herding and agriculture (26). Grazing by large herbivores, associated with herding practices, can have long-term effects on vegetation by reducing cover and inhibiting the expansion of woody plants (27–29). In line with these effects, the gradual abandonment of transhumance activities in parts of northern Fennoscandia has resulted in the upward expansion of birch forest (30, 31). Anthropogenic legacies on arctic ecosystems have so far received little attention as a contributory factor to help explain variable rates of shrubification and the apparent disequilibrium of woody species to climate. We hypothesize that historical human activities likely had severe and lasting effects on arctic vegetation that will continue to affect biome-wide responses to climate change.

In this review, we lay out a road map toward a more holistic understanding of human legacies in arctic vegetation dynamics by describing how traditional human activities (hunting, herding, fire, wood extraction and agriculture) are likely to have affected and continue to affect vegetation within the arctic biome. First, we introduce a theoretical framework to describe the legacies of past events on vegetation dynamics, the related disequilibrium dynamics, ecological factors underlying the legacies, as well as their expected spatial and temporal extent. Thereafter, we provide examples of past human activities and empirical evidence for their effects on arctic vegetation structure and composition. We also discuss the potential temporal and spatial extent of these activities and their legacies. Finally, we outline future directions that could advance our understanding of human legacies on contemporary and future vegetation dynamics in the Arctic. Although we focus on arctic areas, we also include evidence from currently subarctic areas, as some human activities have occurred at the border between these biomes, which has shifted in concert with past climate change. We draw on literature from anthropology, archeology, socio-economics, and (paleo)ecology to understand how past human activities might affect current arctic vegetation, with a focus on woody plant species.

**DISEQUILIBRIUM DYNAMICS, LEGACIES, AND THEIR UNDERLYING FACTORS**

Past events such as natural disturbances, climate fluctuations, or human activities can cause disequilibrium dynamics that might leave either transient or lasting legacies in the vegetation (32). Disequilibrium might occur either when the vegetation is slow to respond to or regenerate following a perturbation or when it lags behind directional change in the environment caused by
climate change or continued human activity (33). Here we define, in a broad sense, any vegetation component to be in equilibrium with its environment when no directional changes caused by past human-driven activities would occur under natural conditions. In other words, a vegetation community is in equilibrium with its environment when all species (from a given regional species pool) that could occur in the community are present at a density, individual height, and biomass set by the current natural abiotic and biotic environment. This extends the equilibrium definition of Svenning & Sandel (34). Disequilibrium generally occurs when fewer species are present, the density is lower, individuals are smaller, or when the biomass is lower than under equilibrium conditions. However, disequilibrium might also occur when a site contains more species, the density is higher, individuals are taller, or when the biomass is higher than under equilibrium conditions. Such situations can arise, for example, when tall-growing, warm-demanding species persist as remnant populations under a cooling climate (35, 36) or when human activities lead to reduced herbivore pressure.

Legacies can be either transient or lasting. In the former case, after a time lag, the community will return to the initial equilibrium (Figure 1). In the latter case, the community will shift to a new equilibrium (also referred to as an alternative stable state) (37) (Figure 1), or it will remain in a disequilibrium condition (cf. 32). Here we discuss legacies arising from human activities that have either temporarily shifted the plant community away from the initial equilibrium or moved it to a new (dis-)equilibrium (Figure 1). Human activities can induce legacies in woody plant communities after the termination of single or repeated perturbations (Figure 1). Such perturbations may alter abiotic factors (i.e., the physical environmental conditions), biotic factors (i.e., species interactions), or the dispersal regime, all of which determine the structure and composition of plant communities (Figure 2). For example, human activities such as wood extraction not only alter interactions among species, but may also substantially change the abiotic environment (e.g., microclimatic conditions, nutrient availability, soil erosion) and the dispersal of seeds. Similarly, increasing herbivore pressure (e.g., reindeer herding) reduces biomass and thus alters species interactions, but it also results in nutrient displacement toward settlements, milking or resting places (38, 39). Herb movement may also affect the dispersal of seeds and other propagules.

Figure 1
Different scenarios for disequilibrium dynamics after human perturbations of varying frequency and duration (red bars) and their related transient or lasting legacies in the vegetation component (light gray lines). Transient legacies are indicated by lines ①, ②, and ③, whereas lasting legacies are indicated by lines ④ and ⑤. The equilibrium conditions are indicated at the start of the x-axis.
Human activity

Hunting
Herding
Fire
Extraction
Agriculture

Herbivores
Predators

Affected factors

Herbivore pressure
Dispersal
Nutrient availability
Soil erosion

Change in shrub community

Positive
Negative
Positive
Negative

Equilibrium

Structural changes

Compositional changes

Figure 2

Schematic illustration of the most likely pathways through which different human activities might create legacies in the structure and composition of arctic woody plant communities relative to an equilibrium state. Human activities either directly induce changes in woody plant communities (dashed gray lines) or indirectly induce changes by altering the physical environmental conditions (i.e., nutrient availability, blue lines, or soil erosion, brown lines), herbivore pressure (i.e., decreased pressure, light green lines, or increased pressure, dark green lines, through hunting of herbivores or hunting of predators and herding, respectively), or the dispersal regime (orange lines). Altered factors cause positive or negative changes in the structure or composition of a woody plant community. Structural changes relative to the equilibrium state generally occur through increase or decrease in height or density of woody plants, whereas changes in community composition occur by increase or decrease in the abundance or occurrence of woody plant species.

across the landscape. In addition to such immediate effects, human activities can introduce new selection pressures that change the frequency of particular ecotypes (40). The evolutionary-scale implications of human activities are beyond the scope of this review.

The spatial extent of a legacy should be positively related to the geographical extent of each human perturbation as well as its frequency and duration in space and time. The temporal scale of a legacy may be more difficult to determine as it depends on the frequency, duration, and magnitude of the perturbation, and the response time of the vegetation component to that perturbation. However, in general, repeated human activities cause cumulative effects and longer-lasting
vegetation legacies, and the duration of the outcomes thus differs from that of a single event of the same activity (Figure 1). Legacies are likely to be widespread in vegetation communities (41), and vegetation dynamics are generally slower in the Arctic than in other biomes, notably owing to the relatively short growing season and limited energy available for reproduction. Long time lags are often related to changes in abiotic factors, such as soil instability or disrupted nutrient cycles, rather than to biomass removal by humans or their domesticated animals (42, 43) (Figure 2). Structural changes with no compositional change might result in a relatively rapid return to equilibrium, whereas changes in the occurrence of species in the communities are expected to generate longer-term legacies. Likewise, compositional change resulting from altered dispersal patterns should create a stronger legacy effect. Lastly, some human activities might invoke multiple factors and result in changes to both vegetation structure and composition, possibly leading to more pronounced legacies (Figure 3).

**SPATIAL AND TEMPORAL EXTENT OF HUMAN LEGACIES IN ARCTIC WOODY PLANT DYNAMICS**

Using evidence from (paleo)ecology, anthropology, and archeology, we identify five traditional human activities in arctic and subarctic environments that can induce legacies in woody plant communities: hunting, herding, fire use, wood extraction and agricultural practice (Figure 2). In the following sections, we describe the history and extent of these activities, elaborate on the effects they can have on arctic plant communities (i.e., structure and composition), discuss whether their impacts are likely to have generated legacies in current vegetation patterns, and estimate the spatial and temporal extent of these legacies (Figure 3).

**Hunting**

Hunter-gatherers migrated into the Arctic as early as the Late Pleistocene, and hunting is still an important mode of subsistence for humans living at high latitudes (25, 44). By hunting herbivores and their predators, humans have changed herbivore pressure and thus are likely to have indirectly altered vegetation structure and composition, especially the balance between woody and non-woody plants (Figure 2). Here, we describe four main hunting-related events and their potential
imprints on current vegetation dynamics: (a) prehistoric hunting and its role in the extinction of megafauna, (b) intensive hunting and regional extirpation of extant herbivores, (c) (re)introductions of hunted species, and (d) hunting of predators.

Prehistoric hunting and extinction of megafauna. Prehistoric human hunting is likely to have contributed to the loss of a number of large herbivores from the Arctic or parts of it (45–49). Megaherbivores (herbivores weighing at least 1 ton) have become completely extinct: The last woolly mammoths (*Mammuthus primigenius*) survived on Wrangel Island and the Pribilof Islands until approximately 3,700 years before present (BP), and the last woolly rhinoceros (*Coelodonta antiquitatis*) survived until 14,000 or perhaps 10,000 years BP in Siberia (50–53). The extinction of these large herbivores is very likely to have had lasting vegetation impacts. It has been argued that megaherbivores promoted steppe-like vegetation at the expense of tundra (54, 55). There is also some indication that near-tree-line taiga vegetation in Siberia had a more mosaic structure, with open patches of low vegetation and greater representation of woody species, before the extinction of these megaherbivores (56). The relative roles of prehistoric hunting and climate change in the extinctions of arctic megafauna remain unknown (48, 57). Nonetheless, the extinction of megaherbivores is likely to have contributed to lower vegetation heterogeneity and a higher abundance of woody species. These changes may have generated lasting effects on plant community composition, with a temporal extent in the range of millennia and a spatial extent spanning the geographic range of the extinct species (i.e., up to several thousands of kilometers) (Figure 3).

Regional reduction and extirpation of extant herbivores. Extirpation of wild large herbivores or considerable reduction in their population size in different parts of the Arctic as a result of human hunting might have had similarly lasting effects on woody vegetation. Wild horses (*Equus ferus*) inhabited northeastern Siberia until 2,000 years BP. Muskoxen (*Ovibos moschatus*) survived in northern Siberia until approximately 3,000 years BP; they were subsequently restricted to North America until recent reintroductions to Eurasia (50). These losses are part of the broader Late Quaternary megafaunal extinctions and are therefore likely to have primarily been driven by humans. However, the detailed dynamics and causes of these specific losses are not well understood. Hunting appears to have been involved in the late regional extirpation of muskoxen in Alaska in the nineteenth century (58). Kay (45) suggests that aboriginal people were very effective hunters and proposes that aboriginal overkill led to moose (*Alces alces*) declines during past centuries. Furthermore, reindeer (caribou in North America; *Rangifer tarandus*) have been a keystone game species for human subsistence in the Arctic for tens of thousands of years, with specialized reindeer hunting evolving at various times and places (59–61). Evidence indicates that hunters constructed hunting guides and drive lanes (62), as well as corrals, since perhaps as early as 6,700–6,200 years BP (63) (Figure 4). Periods of low reindeer population size have been related to increased tree establishment (64). In general, the consequences of regional extirpation or declining population sizes of large herbivores are likely to have led to increased growth of woody plants with similar effects to the extinctions of arctic megafauna, although possibly with legacies of smaller temporal (i.e., centuries to a few millennia) and spatial (i.e., up to a few thousand kilometers) scales (Figure 3).

(Re)introductions. After their prehistoric and historic extirpation throughout arctic Eurasia and much of arctic North America (49), muskoxen have been successfully reintroduced to several of these areas or introduced beyond the native Holocene range. For example, after their extirpation muskoxen were reestablished in 1935 on Nunivak Island in Alaska with animals from eastern Greenland. Approximately 35 years later, further relocations to the mainland have led to
Figure 4
Examples of human activities and their impact on vegetation in arctic and subarctic environments: (a) drawing of prehistoric corral pecked into rock surface in Arctic Norway approximately 6700–6200 BP (drawing: Ernst Högtun, reprinted from Ref. 63); (b) muskox calves captured in Greenland and released in Svalbard in 1929 (photo: Hans Rekdal, Norwegian Polar Institute Photo Library); (c) soil erosion caused by the rounding of a reindeer herd (photo: Bruce Forbes); (d) transient Nenets campsite, where long-term grazing, trampling, and nutrient enrichment has shifted the vegetation from woody plants to graminoids (photo: Bruce Forbes) (166); (e) border fence between Norway and Finland with extensive (high albedo) fruticose lichen coverage in the north but nearly absent (low albedo) coverage in the south, where summer grazing and trampling by reindeer have occurred since the late 1950s (false color Ikonos-2 satellite image taken June 28, 2001, http://www.arcticbiodiversity.is/, CAFF, 2010, Arctic Biodiversity Trends: Selected indicators of change); (f) protected reindeer exclosure near the Finland-Norway border fence with approximately 15 years of erect willow growth, which reindeer graze almost to the ground each summer in the surrounding wetland (photo: Bruce Forbes); (g) woody plant extraction used as ground insulation in the tent (photo: Rane Willerslev); (h) grass-dominated vegetation in relation to the ruins of Hvalseys church from a Norse settlement in South Greenland (photo: Michael M. Hansen).

current population of more than 5,000 muskoxen in Alaska (65–67). In northwestern Siberia, muskoxen were present into the Holocene until at least 2,800 years BP. Reintroductions from Canada and Alaska in the mid-1970s of few muskoxen to northern Russia, and translocation from these areas, have led to more than 8,000 animals living in northern Russia today (68, 69). Captive releases from North to East Canada (70) and from East to West Greenland (71, 72) have also been very successful. For example, 27 muskoxen were initially introduced to Kangerlussuaq (Sondre Stromfjord, West Greenland) in the 1960s, and current estimates indicate a population of
10,000–25,000 animals (73). By contrast, attempts to establish muskox populations in Svalbard, Sweden, and Norway have been less successful (74–76).

In Canada, rapid population growth has not only been observed for muskoxen but also after introduction of caribou (77). Such an increase in number of herbivores is likely to have significant impacts on shrub vegetation. For example, exclusion of caribou and muskoxen for more than 8 years led to increased shrub cover and leaf area (78). Therefore, introductions in these areas are expected to lead to lower vegetation height and shrub dominance than under equilibrium conditions (Figure 2). The temporal extent of a legacy following an introduction is expected to be long lasting and at a spatial scale equal to the geographic range to which the population has spread. In contrast, in the case of only reintroductions, the vegetation might return to its initial equilibrium condition; i.e., there is no legacy, or the vegetation enters an alternative disequilibrium condition with a long-lasting effect (cf. 32). Estimating legacies after reintroductions remains a complex process.

Hunting of predators. By increasing herbivore densities, the hunting of predators can indirectly alter vegetation. Wolves (Canis lupus) are efficient predators, for example, annually killing 6–7% of caribou and 11–14% of moose populations in northern Alaska (79). European colonization and expansion released moose from hunting pressure by wolves and indigenous hunters, allowing moose populations to rise in the north (45). Severe hunting of large predators, like wolves in northern North America, appears to be linked mostly to European colonization (80). Historically, humans have killed large predators to protect their own food or to use the predators’ body parts such as the pelts (81). Hunting of predators for food seldom occurs, but was, for example, practiced by ancient Siberians, who hunted polar bears (82, 83). Nevertheless, the hunting of predators increased, mainly because of human safety considerations, as large predators were seen as competitors for game, or because of the threats such predators posed to semi-domesticated or domesticated animals (46, 84). Hunting of predators may have caused trophic cascades through local food webs and affected vegetation structure and composition, as documented through the exclusion or introduction of top predators into ecosystems. For example, exclusion of wolves in parts of northwestern Canada increased browsing by elk (Cervus elaphus) and decreased aspen recruitment and willow production (85), while the introduction of arctic foxes (Alopex lagopus) on some Aleutian Islands in the early nineteenth century led to the conversion of grasslands to shrub/forb-dominated tundra (86). Hence, hunting of predators could leave legacies at the temporal scale of decades to centuries and with a spatial extent equal to the area where herbivore pressure is substantially increased owing to reduced predator population size.

Herding

Herding affects vegetation structure and composition in three ways: (a) by altering herbivore pressure, (b) by changing the physical environment (e.g., nutrient displacement and soil erosion), and (c) by modifying dispersal patterns (Figure 2). Below, we first outline the history of herding in the Arctic and then discuss the effects of each of these factors and their possible related legacies.

History and geography of herding in the Arctic. Sheep (Ovis aries), goats (Capra aegagrus), cattle (Bos taurus), and horses have all been herded, but reindeer herding has been and remains the most common form of aggregated animal management in arctic and northern boreal regions. The transition from reindeer hunting to herding was probably gradual and many of the same technologies and economic strategies remain in use (87–89). Early forms of reindeer husbandry may date back to the Early Holocene or even the Late Glacial (90–92). Domestication may
have been developed independently in different areas by controlling or taming small groups of reindeer for easy access to meat and milk or for riding and transport, respectively (93, 94). The use of reindeer for transport radically expanded the area in which humans were able to settle and exploit the natural environment throughout the Euro-Asian North. From the seventeenth century onward, several indigenous groups in the Eurasian Arctic and subarctic established large-scale herds, sometimes numbering several thousand individuals (95). Today, the spatial extent of activities related to herding spans thousands of kilometers across the Siberian tundra (89, 96, 97). While herding activities have been and remain important and widespread across the Eurasian Arctic, historically they were largely absent from North America (98). Only in the past 100 years have domestic reindeer been introduced into North America, albeit sporadically and mostly without lasting success (99–101). Hence, the intensity and spatial extent of herding has varied substantially across the Arctic.

**Effects of herding-related changes in herbivore pressure.** Herding substantially increases herbivore pressure, and the associated reduction in vegetation biomass and height is likely to reduce the abundance of woody species and change plant community composition in favor of graminoid species (Figure 4). These effects are evident from changes in vegetation structure on the Finnish side of the Fennoscandian tundra zone, where a fence was built in the 1950s to prevent reindeer from crossing the state border. Higher herbivore pressure due to summer grazing reduced the height and abundance of willows in favor of graminoid species compared with the Norwegian side, where summer grazing was absent (28). Additional evidence from other sites in Fennoscandia indicates that grazing, by for instance reindeer, can prevent the advancement of shrubs and trees in periods of favorable climate and can thus override the effects of climate change, at least locally (29, 102–104). In some locations, higher forest limits and forest range expansion previously attributed to climate change are now considered to be the product of regrowth after abandonment by humans and their domestic livestock (e.g., sheep and cattle) (105, 106). However, exclosure experiments show varied responses to reduced herbivory. Excluding reindeer from summer grazing on the Finnish side of the border fence for four years led to only a moderate increase in shrub cover (28) (Figure 4). A similar result was obtained in northernmost Norway when semi-domesticated reindeer where excluded for a two-year period, although the exclusion of small rodents significantly increased shrub cover (107). Exclusion of reindeer and muskoxen in West Greenland over an eight-year period also led to strong increases in shrub cover (78), while exclusion of sheep for 28 years in South Greenland showed that the relative dominance of graminoids, woody plants, and forbs was not significantly affected by sheep grazing (8). Caribou exclusion in the low arctic tundra of Canada increased shrub leaf biomass substantially during a five-year experimental period (108). Hence, the effects of large herbivores on dwarf-shrub tundra seem site-specific, are controlled by a set of complex mechanisms, and depend on the particular characteristics of the shrub species, e.g., trampling tolerance, regrowth potential, or palatability (109, 110). Nevertheless, changes in shrub height and cover could emerge within a decade after abandonment of herding, indicating decadal-scale legacies (Figure 3).

Reindeer grazing can also drive changes in plant community composition, manifested as shifts in the relative abundance of representative shrubs, grasses and herbs. By combining observations of reindeer grazing behavior with ecological, palynological, and pedological analyses of favored grazing areas, Fredskild & Holt (39) showed that shrub cover (*Betula nana* and *Salix glauca*) decreased as the number of reindeer increased during the later twentieth century. Increased grazing was associated with a transition from dwarf birch heath to nonflowering grasslands comprising various herbs fertilized by urine and feces. By contrast, reduced grazing allowed profuse grass flowering prior to recolonization by shrubs. Similarly, in Eastern Siberia occupation by reindeer
herders led to a transition from taiga forest to meadows that were maintained through repeated use but returned to forest after abandonment (111). The temporal duration of vegetation imprints after herding is likely at the scale of decades to centuries, depending on the degree of structural versus compositional changes induced by the increased herbivore pressure (Figure 2). In addition, natural feedback interactions may result in permanent changes at the scale of several centuries, long after herding has ended, e.g., when established reindeer lawns continue to attract wild herbivores.

Effects of herding-related changes on the physical environment. Herding can lead to changes in environment conditions (e.g., nutrient displacement and soil erosion) that could affect the growth and distribution of plant species (Figure 2). Reindeer herding results in nutrient displacement toward settlements, milking (when practiced) and resting places (38, 39). Analyses around Sami reindeer herding settlements that were in use for approximately 300 years and abandoned approximately 100 years ago showed a shift toward early successional plant species and a threefold increase in soil microbial activity and nutrient availability close to the settlements, reflecting the concentration of nutrients (38). Ecological experiments over the past decade have demonstrated the speed with which graminoid-dominated “lawns” can replace shrub-dominated vegetation when reindeer activities (grazing, trampling, feces deposition) are concentrated in tundra areas (112, 113) (Figure 4). This shift in vegetation composition together with herbivore-induced changes in soil physical and chemical properties increases the soil nitrogen/phosphorus ratio (110). Such swards can develop under both zoogenic and anthropogenic disturbance regimes and on mesic to wet organic substrates. Interestingly, they might persist despite decades or even centuries of disuse, effectively functioning as alternative stable states (39, 114–116).

Soil disturbance associated with trampling, as well as exposure to wind erosion, can cause severe denudation, leading to the loss of soil and vegetation (117, 118) as well as changes in plant community composition (Figure 2). Anderson et al. (111) identified the development of plant communities that are characteristic of reindeer trampling in permafrost locations, as indicated by the appearance of pollen/spores of damp-loving plants, such as Sphagnum, and of plants adapted to drier habitats, such as B. nana and Caryophyllaceae. The yearly corral, which can measure several hundred meters in diameter, can produce some of the greatest impacts on shrub vegetation, as the reindeer are retained for days, leading to the death of all plants (Figure 4). Such sites are slow to recover and may remain unvegetated for more than 20 years (119). Another critical regime shift is associated with the trampling and grazing-driven disappearance of lichens across northern Fennoscandia on reindeer rangelands in recent decades (120, 121). Border fences constructed to support the reindeer husbandry prevent Finnish reindeer from crossing into Norway and restrict them to former winter rangelands during the summer. Reindeer trampling on the dry lichen pastures in summer, resulted in shattered lichen fragments that were blown and washed away over extensive areas in both tundra and forest zones (122). Legacies in vegetation composition due to herding-related changes in the physical environment are thus expected across hundreds of kilometers and might last from decades to centuries, especially when soils or key soil-forming taxa, such as lichens, are lost (111, 117).

Potential effects of herding on plant dispersal. The spread of seeds attached to the hooves and fur of animals might play a role in species occurrence in plant communities and could reduce lags in response to past climate change (cf. 123). Several studies from temperate Europe document the potential significance of historical herding practices for seed dispersal as well as plant community composition and richness (124, 125). To our knowledge, similar studies are absent from the Arctic, but the processes are likely to be similar (126). However, González et al. (127) showed that the century-long history of reindeer grazing in northern Norway depleted the seed bank, so that it
consisted mainly of small seeds without dispersal mechanisms and of seeds from graminoid species. Similarly, Cooper (128) found that reindeer on Svalbard depleted both the seed and the propagule banks.

**Fire Use**

Fire significantly changes ecosystems and their functioning and immediately initiates successional changes in the vegetation. Although it is unclear when humans started to deliberately manipulate the environment with fire, native communities all over the world have intentionally set fires to promote plant and animal productivity or to attract game animals (129–133). The degree to which humans have intentionally ignited fires in the Arctic is also controversial. Fires in shrub tundra and taiga forests were frequent during the Early Holocene. In Alaska, these fires were not humanly mediated (134), whereas in northern Europe it remains unclear whether these fires were ignited (either deliberately or accidentally) by humans or caused by climatic or other factors (135, 136). Succession after fire disturbances probably resulted in increased growth of various edible herbaceous plants and berries that serve as a food source for both hunter-gatherers and wild game, thus providing motivation for human-set fires (135).

Native communities in subarctic Alaska and Canada used fire to create and maintain open habitats and meadows and to promote the growth of shoreline roots and grasses facilitating access to game and providing food sources for wildlife (137–139). Thus, this rather patchy use of fire to create clearings or expand natural openings (e.g., along edges of streams or lakes) increased floral and faunal productivity for multiple decades (131, 133, 139, 140). In Iceland and Greenland, arriving agricultural communities may have used fire for initial shrub clearance, thereby stimulating grass growth and increasing pastoral productivity (141–143). However, at these high latitudes where wood is an important yet scarce resource, it seems unlikely that clearance by burning would have been a common practice, if used at all, and the paleoevidence for fire (increased levels of microcharcoal) could instead reflect the continuous use of domestic fires rather than isolated vegetation burnings (144, 145).

Therefore, legacies related to historical anthropogenic fires in the Arctic are expected to be rare and generally limited to the local or landscape scale (Figure 3). Regeneration of the different elements of vegetation could take a few years to a few decades in the tundra, which displays resiliency in recovery following fire (146–148). However, fires may be difficult to control, and catastrophic fires have swept through hundreds of thousands of square kilometers of the Eurasian Arctic forest-tundra (95).

**Wood Extraction**

Wood extraction directly affects vegetation structure and composition. It can also indirectly affect vegetation dynamics by altering the abiotic environment, for example, by changing microclimatic conditions, increasing wind exposure, promoting soil erosion in the shallow and fragile arctic soils, and by reducing or displacing soil nutrients through biomass removal and partial disruption of mycorrhizal nutrient control.

In addition to blubber, arctic hunters and herders have also used shrubs as fuel for fires, especially willow (*Salix*) and birch (*Betula*). For example, whenever contemporary Siberian herders establish a camp, which can remain for two or three days, the surrounding woody vegetation may be completely cut down to secure wood for cooking and heating. As insulation against permafrost, a thick carpet of fresh shrubs on top of which reindeer skins are laid is also used to cover the floors of large skin tents (Figure 4) (119). Herders also lay ritually killed reindeer carcasses on a bed of fresh
willow branches to keep the meat clean and to create a ritual bedding for the sacrificed reindeer (98, 149). Larger amounts of wood may also have been used for temporary corral fences (63).

Similar to the Siberian Arctic, Norse settlers also extracted wood for domestic fires in subarctic Greenland and Iceland. These agricultural communities cleared the woody vegetation to create meadows for sheep grazing, as indicated by a rise in grass (Poaceae) and sedge (Cyperaceae) pollen and a decline in the abundance of shrub pollen (150). Clearance was local but expanded through time; e.g., in South Greenland evidence suggests that woody species cover in upland areas persisted for at least a century longer than in lowland valleys (151). Following abandonment, vegetation response in South Greenland also showed recovery of shrubs within some decades (143, 152, 153). Thus, wood extraction around temporary or permanent human settlements in the Arctic can affect a few to several square kilometers. The expected duration of the legacies may range from less than a decade (for one-time extraction of species with a high regrowth potential) to hundreds of years (when repeated extractions have extirpated a species from a site or completely altered the vegetation composition).

Agriculture

Past agricultural practices in the Arctic have included all the above-described activities, as well as others (e.g., cultivation and manuring). Below, following a short introduction to the history of agriculture in the Arctic, we discuss the effects of these practices on nutrient availability and soil erosion.

History of agriculture in the Arctic. Despite considerable recent research (e.g., 154), the deep history of agriculture in the Arctic remains poorly understood. Husbandry of domesticated animals, has probably been present at high northern latitudes (above 60°N) since approximately 4,450–4,150 years BP, as evidenced by ruminant milk lipids in pottery and burnt sheep/goat bones in Finland (155, 156). Cultivation likely occurred at some Finnish sites from 3,450 years BP and seems thereafter to have advanced toward higher latitudes (154). Agricultural practices were brought to subarctic and arctic areas outside northern Europe (i.e., Greenland and Iceland) approximately 1080–965 years BP. According to Cramp et al. (155), however, there is no evidence of agricultural practices at high northern latitudes in North America or Siberia prior to European colonization. Climatic and environmental conditions are and were unsuitable for reliable crop yields in large parts of the Arctic, and fully agricultural economies probably only ever attained a tenuous foothold and only during periods of warmer climate. Historical records clearly indicate that even slight alterations in temperature and precipitation caused widespread crop failure, with its attendant demographic and social consequences (157).

Effects of agriculture. Soil alterations around Norse settlements in Iceland and Greenland included manuring and irrigation to increase nutrient pools and plant productivity (158, 159). Shrub removal, grazing, and cultivation (e.g., hay and cereals) by farmers caused soil destabilization, erosion, and degradation in quality (160–163). The impact and legacies of these human activities may differ between sites within regions and between Iceland and Greenland. In Iceland agricultural activities have continued from settlement to the present, whereas in Greenland Norse abandonment led to the recovery of shrub vegetation and reductions in soil erosion (162). Cooling climate near the end of the time of the Norse settlement in Greenland likely amplified the land degradation caused by Norse agricultural practices, which are thought to have contributed to the heavily eroded landscapes present in Greenland today (118). Furthermore, nutrient enrichment through manuring in some areas (158) probably had persistent
post-abandonment effects on nutrient content and species composition. The post-settlement era was marked by an increase in Cyperaceae, indicating the expansion of subarctic steppe communities, and by some delay or reduced recovery of birch in contrast to willow, possibly because of its reduced tolerance to the colder conditions (i.e., Little Ice Age) during the post-settlement period (145). However, the difference between pre- and post-settlement conditions and the recovery of shrub species might be subtle, site specific, and challenging to infer from paleoecological records (164). Nonetheless, paleoecological evidence from settlements in the Scandinavian mountains indicates floristic legacies of several centuries, lasting until today, in relation to nutrient addition in alpine heath and extraction of *Betula pubescens* below the tree line (116). Hence, agricultural practices in the Arctic, which include the combined and possibly additive effects of wood extraction, grazing, soil erosion, nutrient addition, and their complex interactions, have created centennial legacies at the landscape scale (Figure 3).

**SUMMARY AND FUTURE DIRECTIONS**

Theoretical perspectives and modeling efforts strongly suggest that long-term ecological legacies of past events, such as human activities, should be visible in the Arctic (e.g., 13, 32, 34). Although data are still sparse, we provide evidence suggesting that legacies of past human activities in the Arctic are likely to exist at the spatial scale of meters to hundreds of kilometers and at temporal scales ranging from decades to centuries, or even millennia (Figure 3). The evidence provided here suggests that most of the examined human activities (i.e., herding, hunting of predators, introductions of herbivores, fire, wood extraction, and agricultural practices) have resulted in a shift toward lower and less dense woody plant vegetation and/or grass-dominated vegetation (Figure 2). In contrast, legacies of herbivore hunting may have left some arctic areas with a higher current dominance of woody plants than under equilibrium conditions, potentially with the largest effects arising from local extirpation of herbivores or megafauna extinctions (Figure 2). These long-lasting effects on arctic vegetation may influence the perceived/observed responses of arctic woody vegetation to climate change in two ways, depending on the type of legacy (transient or lasting). First, when a legacy is transient the directional change in response to past human activity may act in concert with climate change or may be mistaken as a response to climate change, for example, the northward expansion of forest in northern Fennoscandia as a result of gradual decrease in human activity (105, 106). Second, when a legacy has become lasting, e.g., after megafauna extinction, climate change responses of woody vegetation are expected to differ from those of areas not harboring such human legacy. Hence, an observed response will not reflect natural dynamics, thus making biome-wide predictions of climate change challenging. Furthermore, if a lasting legacy is overcome (e.g., by re-immigration or reintroduction), the system could switch back if associated environmental conditions remain unchanged, which in turn may further complicate any predictions of future dynamics. Across the Arctic, the responses of woody plant species to recent climate change vary with macroclimate and local environmental conditions. (e.g., 3, 7, 14–16). Evidence presented here suggests that legacies of human activities have likely contributed to the observed variation in climate change responses of arctic woody vegetation.

We have concentrated on describing the effects of human activities which occurred in the past and have a long tradition in the respective regions, i.e., hunting, herding, fire, wood extraction, and agriculture. Of these, some activities are ongoing and others have diminished, but they are all expected potentially to affect the observed variation in responses to climate change across the region. Additional impacts and legacies which lie beyond the scope of our review and are also likely to affect vegetation include local nutrient enrichment in relation to Inuit settlements, huts of European trappers, and whaling stations as well as the indirect effect of the hunting of herbivores.
and predators. Furthermore, we have not considered recent and growing human activities in the Arctic, e.g., oil extraction, mining, shipping, and large-scale suppression of natural fires. These more recent influences are expected to cause additional legacies in future vegetation patterns, and we may anticipate stronger and potentially novel ecological impacts, particularly in combination with climate change.

In summary, legacies after historical human activities on arctic vegetation are likely to affect our understanding and predictions of biome-wide responses to climate change. However, there are many unanswered questions, and we are far from having a full understanding of the degree to which human legacies affect climate change responses in the Arctic. We lack directly comparable circumpolar data with a high spatial and temporal resolution and thus the ability to explicitly link human activities with environmental and vegetation responses in space and time. Fully integrated studies that aim to elucidate human impacts on arctic environments and their feedback on human communities are uncommon and have focused on relatively small areas, yet they have also provided evidence for culturally and geographically diverse patterns (165–168). As a result, making generalizations is difficult. In part, the lack of studies may be the result of disciplinary boundaries and the differing epistemologies and domains of interest among the relevant research fields (169). We here propose an integrative approach to arctic human-environmental dynamics that includes three elements: (a) a circumarctic interdisciplinary collaboratory, (b) participatory research, and (c) new methodologies.

Circumarctic Interdisciplinary Collaboratory

One way to promote interdisciplinary synthesis is to establish a collaboratory, i.e., an organizational entity facilitating collaboration among researchers from different institutions and/or disciplines who are focused on a common research agenda; agree on norms, principles, and values; and share infrastructure, data, and standardized protocols (170–172). Gathering under the label of environmental humanities, a range of social science and humanities disciplines (e.g., environmental archeology, historical ecology and environmental history) are now interested in interdisciplinary research with a focus on the interaction between humans and their environment (173, 174), thus providing an excellent platform for interdisciplinary engagement. Furthermore, both social and natural scientists recognize the necessity of integrating the archeological record into long-term studies of ecological processes (175). Last, paleoecologists, historians, and social scientists have an increasing interest in using an experimental study design and quantitative statistical analyses when the goal is to strengthen causal inferences (176–179).

In our view, a productive avenue for empirically addressing the ecological legacies of human activities in the Arctic is to use a natural experimental study design to establish a circumarctic collaboratory consisting of a network of field sites and a cyberinfrastructure for data sharing through which social and natural scientists collaborate to investigate the role of human-environmental interactions through time and space. Such coordination could provide the basis for generalizations of the impact of human activities on arctic vegetation dynamics by controlling for cultural and environmental differences across time and space. Furthermore, we argue that establishing long-term monitoring at these sites would provide valuable information for understanding the influence of past and ongoing human activities on arctic vegetation dynamics. Networks of experimental sites have proven very valuable for monitoring the responses of arctic vegetation to climate change (14, 15), and recently a collaboration has been established to stimulate the integration of atmospheric research in the Arctic (172). A prerequisite for inferences from a network of field sites is comparability of observations and measurements. Hence, the development of standardized protocols with the aim of parallel inference on human activities and vegetation dynamics through time and
space is needed both within disciplines (e.g., ecology, paleoecology, archeology, anthropology) and to compare and integrate knowledge production across disciplines. Within the natural sciences, the formulation of standardized protocols is already a valuable tool, e.g., for the study of global variation in plant functional traits (180).

There are several sites with historical human activities that could be important parts of a circumarctic collaboratory, e.g., hunter-gatherer and Norse settlements, abandoned whaling stations, or milking sites for reindeer herders. Examples of such sites, which could contribute to our understanding of how vegetation responses differ along gradients of climate and legacies after human activities, include (a) the Western and Eastern Norse settlements in Greenland, of which the more northerly Western Settlement today is beyond the limits of cultivation (181). (b) Sites in Scandinavia, Siberia, North Kamchatka, and North America have different histories of reindeer-related activities. In Scandinavia and Siberia reindeer herding predominates, whereas in North America reindeer hunting predominates. North Kamchatka had no reindeer before the end of the nineteenth century and could serve as an area for comparison with other sites in Far-East Siberia. (c) The subarctic areas of Iceland and the inhabited coastal areas of Greenland provide a useful comparison for understanding the relative influence of herbivores, people, soil processes, and climate on shrub dynamics. No mammalian herbivores were present in Iceland prior to the settlement 1,080 years BP, so pre-settlement vegetation dynamics are useful for assessing the impacts of sheep and reindeer grazing within comparable biomes. Similarly, records from Greenland allow the nature and detectability of native reindeer and muskox impacts to be assessed before the arrival of the Norse agricultural communities from 965 years BP.

**Participatory Research**

A collaboratory for environmental research conducted by social and natural scientists can benefit from a link to participatory and educational components. Tackling a task as complex as understanding human legacies on arctic vegetation and envisioning trajectories of future vegetation dynamics under the rapid expansion of modern human activities and climate change calls for a strong participatory approach. There has arguably been little technological change during the transition from hunting to herding among arctic indigenous people (87, 88). Therefore, indigenous people who actively engaged in herding, hunting, fishing, and gathering in modern mixed and subsistence economies can contribute substantially to the interpretation of human legacies. Even local people who have spent many years on the land involved in extractive industries may hold highly relevant knowledge pertaining to vegetation and permafrost dynamics (182).

Co-management of natural resources in the Arctic has its roots in the North American land claim processes of the 1970s, whereas indigenous people of Fennoscandia (Sámi) and northwest Russia (e.g., Komi, Nenets) have no history of formalized cooperation and shared responsibility for the production or coproduction of knowledge (183). However, recent and ongoing projects in northern Fennoscandia and Russia provide useful insight into how co-management partnerships between locals and scientists can be facilitated (e.g., 166). Unfortunately, project lifetimes are typically fewer than five years. In the social sciences, it can take many years to develop the levels of trust necessary to tackle sensitive issues like overgrazing, yet that is exactly where research on human legacies begins. Integrating a circumarctic collaboratory and participatory research provides an option for bridging thematically similar research in space and time. National borders and linguistic barriers provide a challenge for such initiatives. However, contemporary funding instruments now encourage international and interdisciplinary linkages as well as partnerships with local populations that have a stake in applied research topics. Attracting funding for truly long-term research efforts remains challenging nonetheless.
Integrating Established and Novel Techniques

Understanding the temporal and spatial scale of human legacies requires detailed and simultaneous documentation of variation in the environment, vegetation responses, and human activities across geographic space and time. Developing a spatially and temporally representative sample is challenging. One of the big challenges is to identify control sites with no past human activity as well as sites with past human activities that have left no legacy in the contemporary vegetation.

Four approaches may help when tackling these challenges. First, long-term records from paleoecology and archeology can help identify areas where past human activities have been minor or had little discernible effect on contemporary vegetation. This is important where natural dynamics create contemporary vegetation patterns similar to those created by human activities, e.g., where wild reindeer gatherings create grass-dominated “lawns” even in the absence of humans (39).

Second, the application of space-for-time substitutions where spatially distributed observations at landscape to regional scales could help identify sites with similar environmental conditions but with no or different past human activities. Distributing these observations in a paired or stratified random design may provide the best basis for generalization of the findings. Third, any repeated human perturbation has the potential to mask earlier impacts. Hence, investigations toward the periphery of human resource areas, where repeated human perturbations may be rare, could be important for detecting the effects of single events and subtler impacts. Fourth, participatory research may, as outlined above, be highly valuable because local knowledge can help in interpreting patterns of past and present activities and their legacies.

Simultaneous and detailed documentation of the presence or absence of human activities, their effect on abiotic and biotic factors, and the related vegetation responses (Figure 2) is likewise challenging. This challenge is related to the difficulty of disentangling the effects of natural and human-mediated effects through time and the fact that absence of evidence is not evidence of absence. Thus, multiproxy and interdisciplinary efforts and integration of less common and novel techniques are strongly needed.

Climate is a strong determinant of vegetation patterns and their dynamics. Therefore, past climatic changes may have acted in synchrony with or have overwritten the imprints of human activities on the vegetation. To shed light on the complex interactions of past natural and human activities, and thus to disentangle natural, anthropogenic, and zoogenic legacies, we need to combine well-dated and independent records of paleoclimate, palynology (e.g., pollen and coprophilic fungal spores), and archeology. Temperature and moisture-sensitive proxies can be derived from biomarkers, such as alkenone-based paleo-temperature reconstruction from lake sediment cores (184). In addition, for recent centuries, dendrochronological analysis of several-hundred-year-old shrubs may contribute to past climate reconstructions (185).

In terms of the vegetation responses, there are a number of methodological considerations that affect how readily we can distinguish these past processes using paleoecological evidence. Arctic floral and faunal complexity is lower than in temperate zones, including a limited number of plant taxa with overlapping climatic tolerances and an invertebrate fauna dominated by generalists (186). These features mean that it can be difficult to differentiate between small or subtle differences in community composition using paleoecological indicators, like pollen, which cannot always be determined to the species level (39, 187). Techniques that allow more quantitative assessment of vegetation will become more important in determining how different arctic plant communities can be identified and differentiated using their pollen signatures (117, 164, 188, 189). Accordingly, advances in extraction and amplification of ancient DNA from sediments along with more routine use of coprophilic fungal spore analysis and fecal biomarkers would help increase the potential for understanding faunal-vegetation interactions by providing information on past
biodiversity (55, 117, 190–192). Paleoecological data provide only limited insight into changes in plant biomass, height, demography, or ecotypes, but progress is being made toward a more nuanced understanding of tree and grass biomass from pollen accumulation rates (143, 151, 193).

Remote sensing has proven very valuable for detecting and mapping the contemporary spatial patterns of archeological sites and past human activities at the landscape to regional scale (e.g., 194–196) and thus for analyzing human-environment interactions (197). Within the Arctic, satellite-, air-, and drone-borne images have been used to detect potential archeological sites from hunter-gathers in Alaska (198), features from Inuit hunter-gathers in Canada (199), and prehistoric wooden houses in Alaska (200). Combining spatially explicit patterns of human activities with remotely sensed patterns of contemporary variation in environmental conditions and plant communities provides the option of generating valuable space-for-time substitution and analyses of human-environment interactions and the extent of human legacies.

In summary, we have outlined how multiproxy interference through the integration of less common and novel techniques is expected to provide a better understanding of the influence of past human activities and their related legacies on arctic vegetation dynamics. There is still theoretical and practical work to be done to align information from different techniques and proxies in space and time. This alignment could be a first step toward the development of an interdisciplinary research agenda for a future circumarctic collaboratory to investigate these effects.

SUMMARY POINTS
1. Key traditional human activities are likely to have affected and continue to affect the structure and composition of woody plant communities within the arctic biome.
2. Legacies of historical human activities in the Arctic are evident at the spatial scale of meters to hundreds of kilometers and at a temporal scale of decades, centuries, and millennia.
3. Evidence for the spatial and temporal extent of human legacies is sparse. Future insight on human-environment interactions could be obtained through a circumarctic collaboratory, standardized protocols, participatory research, and new methodological approaches.
4. To understand and predict the ongoing and future arctic vegetation dynamics, legacies related to historical human activities need to be brought into consideration.

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Contents

I. Integrative Themes and Emerging Concerns

Plastic as a Persistent Marine Pollutant
   Boris Worm, Heike K. Lotze, Isabelle Jubinville, Chris Wilcox, and Jenna Jambeck ...... 1

African Environmental Change from the Pleistocene to the Anthropocene
   Colin Hoag and Jens-Christian Svenning ......................................................... 27

The Intergovernmental Panel on Climate Change: Challenges and Opportunities
   Mark Vardy, Michael Oppenheimer, Navroz K. Dubash, Jessica O’Reilly, and Dale Jamieson ................................................................. 55

The Concept of the Anthropocene
   Yadvinder Malhi .................................................................................................. 77

Marked for Life: Epigenetic Effects of Endocrine Disrupting Chemicals
   Miriam N. Jacobs, Emma L. Marczylo, Carlos Guerrero-Bosagna, and Joëlle Ruegg .......................................................... 105

II. Earth’s Life Support Systems

Degradation and Recovery in Changing Forest Landscapes: A Multiscale Conceptual Framework
   Jaboury Ghazoul and Robin Chazdon .............................................................. 161

III. Human Use of the Environment and Resources

Drivers of Human Stress on the Environment in the Twenty-First Century
   Thomas Dietz ....................................................................................................... 189

Linking Urbanization and the Environment: Conceptual and Empirical Advances
   Xuemei Bai, Timon McPhearson, Helen Cleugh, Harini Nagendra, Xin Tong, Tong Zhu, and Yong-Guan Zhu .............................................. 215
Debating Unconventional Energy: Social, Political, and Economic Implications
Kate J. Neville, Jennifer Baka, Shanti Gamper-Rabindran, Karen Bakker, Stefan Andreasson, Avner Vengosh, Alvin Lin, Jewellord Nem Singh, and Erika Weinthal ............................................. 241

Emerging Technologies for Higher Fuel Economy
Automobile Standards
Timothy E. Lipman .................................................................................................................. 267

The Future of Low-Carbon Electricity
Jeffery B. Greenblatt, Nicholas R. Brown, Rachel Slaybaugh, Theresa Wilks, Emma Stewart, and Sean T. McCoy .......................................................... 289

Organic and Conventional Agriculture: A Useful Framing?
Carol Shennan, Timothy J. Krupnik, Graeme Baird, Hamutahl Cohen, Kelsey Forbush, Robin J. Lovell, and Elissa M. Olimpi ........................................................................ 317

Smallholder Agriculture and Climate Change
Avery S. Cohn, Peter Newton, Juliana D.B. Gil, Laura Kuhl, Leab Samberg, Vincent Ricciardi, Jessica R. Manly, and Sarah Northrop ........................................... 347

The Future Promise of Vehicle-to-Grid (V2G) Integration:
A Sociotechnical Review and Research Agenda
Benjamin K. Sovacool, Jonn Axsen, and Willett Kempton .................................................. 377

Technology and Engineering of the Water-Energy Nexus
Prakash Rao, Robert Kostecki, Larry Dale, and Ashok Gadgil ............................................. 407

IV. Management and Governance of Resources and Environment

Landscape Approaches: A State-of-the-Art Review
Bas Arts, Marleen Butzer, Lamina Horlings, Verina Ingram, Cora van Oosten, and Paul Opdam ......................................................................................... 439

Foreign Direct Investment and the Environment
Matthew A. Cole, Robert J.R. Elliott, and Liyun Zhang ....................................................... 465

Land Tenure Transitions in the Global South: Trends, Drivers, and Policy Implications
Thomas K. Rudel and Monica Hernandez ........................................................................... 489

Ecosystem Services from Transborder Migratory Species: Implications for Conservation Governance
Laura López-Hoffman, Charles C. Chester, Darius J. Semmens, Wayne E. Thogmartin, M. Sofia Rodriguez-McGoffin, Robert Merideth, and Jay E. Diffendorfer ....................................................................... 509
V. Methods and Indicators

Legacies of Historical Human Activities in Arctic Woody Plant Dynamics
  Signe Normand, Toke T. Høye, Bruce C. Forbes, Joseph J. Bowden,
  Althea L. Davies, Bent V. Odgaard, Felix Riede, Jens-Christian Svenning,
  Urs A. Treier, Rane Willerslev, and Juliane Wischnewski ........................................ 541

Toward the Next Generation of Assessment
  Katharine J. Mach and Christopher B. Field ................................................................. 569

Sustainability Transitions Research: Transforming Science and Practice for Societal Change
  Derk Loorbach, Niki Frantzeskaki, and Flor Avelino .................................................... 599

Attribution of Weather and Climate Events
  Friederike E.L. Otto ............................................................................................................. 627

Material Flow Accounting: Measuring Global Material Use for Sustainable Development
  Fridolin Krausmann, Heinz Schandl, Nina Eisenmenger, Stefan Giljum,
  and Tim Jackson ................................................................................................................ 647

The Impact of Systematic Conservation Planning
  Emma J. McIntosh, Robert L. Pressey, Samuel Lloyd, Robert J. Smith,
  and Richard Grenyer ......................................................................................................... 677

Indexes

Cumulative Index of Contributing Authors, Volumes 33–42 .............................................. 699
Cumulative Index of Article Titles, Volumes 33–42 ............................................................ 705

Errata

An online log of corrections to *Annual Review of Environment and Resources* articles may be found at http://www.annualreviews.org/errata/environ