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Herbivory Network: An international, collaborative effort to study herbivory in Arctic and alpine ecosystems

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A B S T R A C T

Plant-herbivore interactions are central to the functioning of tundra ecosystems, but their outcomes vary over space and time. Accurate forecasting of ecosystem responses to ongoing environmental changes requires a better understanding of the processes responsible for this heterogeneity. To effectively address this complexity at a global scale, coordinated research efforts, including multi-site comparisons within and across disciplines, are needed. The Herbivory Network was established as a forum for researchers from Arctic and alpine regions to collaboratively investigate the multifunctional role of herbivores in these changing ecosystems. One of the priorities is to integrate sites, methodologies, and metrics used in previous work, to develop a set of common protocols and design long-term geographically-balanced, coordinated experiments. The implementation of these collaborative research efforts will also improve our understanding of traditional human-managed systems that encompass significant portions of the sub-Arctic and alpine areas worldwide. A deeper understanding of the role of herbivory in these systems under ongoing environmental changes will guide appropriate adaptive strategies to preserve their natural values and related ecosystem services.

1. Introduction

Arctic and alpine environments are changing rapidly (IPCC, 2013). A variety of ecological responses have been reported, from phenological mismatches between interacting organisms (Kerby and Post, 2013) to changes in the structure and composition of biotic communities (Myers-Smith et al., 2011). These responses vary across sites and seem to depend on a number of interrelated factors, including biotic interactions (Post, 2013b). For instance, herbivory may counteract some of the responses of tundra ecosystems to global changes (Post and Pedersen, 2008; Olofsson et al., 2009), but the magnitude and direction of these responses often depend on interactions with a number of environmental factors. Such environmental contingency limits our ability to predict ecosystem responses to global changes (Borer et al., 2014) and calls for the use of coordinated experiments, standardized data collection and long-term observations (Sternberg and Yakir, 2015).

A workshop organized during the Arctic Science Summit Week 2014 (Bueno et al., 2014) laid the foundations of an international research network to investigate the role of herbivory in changing tundra ecosystems (Herbivory Network; http://herbivory.biology.ualberta.ca). The network currently has over 100 members from 17 countries, and involves researchers in different stages of their research careers. Some results of the first year of development of this international initiative were presented at ASSW 2015 in Toyama. In this paper we briefly review our current understanding of plant-herbivore interactions in Arctic and alpine ecosystems and how they vary across the tundra biome, provide an overview of the activities of the Herbivory Network and propose a roadmap for developing a distributed collaborative experiment to address the role of herbivory in tundra ecosystems and its variability at broad spatial and temporal scales.

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2. Plant-herbivore interactions in Arctic and alpine ecosystems

Plant-herbivore interactions are central to the functioning of tundra ecosystems, through their effects on biodiversity, energy flows and nutrient cycling, and the role of herbivory in structuring these ecosystems is increasingly being recognized. For example, a search in SCOPUS on 21 October 2015 using as search terms herbivor* AND (tundra OR *Arctic OR alpine) retrieved 1221 results (Fig. 1), 40.2% of them (491) from the last 5 years. Since 2010, 67% also included some aspect of climate change (restricted search by including ("climate change" OR warming OR "environmental change") as additional search terms).

Albeit their low annual primary productivity, most northern terrestrial ecosystems are dominated by plant-herbivore interactions (Oksanen et al., 1981; Aunapuu et al., 2008; Hoset et al., 2014). Through direct consumption, herbivores can affect the structure and composition of tundra plant communities (Grellmann, 2002; Olofsson et al., 2004a; Pajunen et al., 2012), by altering competitive interactions between plants (Jónsdóttir, 1991; Olofsson et al., 2002). Herbivores also influence nutrient cycling, either through direct fertilization (Hik and Jefferies, 1990; Van der Wal et al., 2004; Kaukonen et al., 2013; Barthelemy et al., 2015; Stark et al., 2015) or indirectly, changing plant chemistry and litter decomposition rates (Olofsson and Oksanen, 2002; Stark et al., 2007) or enhancing microbial decomposition processes through increased soil temperatures (Van der Wal et al., 2001; Olofsson et al., 2004b).

The role of plant-herbivore interactions in tundra ecosystems is further highlighted by recent studies investigating the impacts of environmental changes. Herbivory by large ungulates may buffer the destabilizing effects of warming on tundra plant communities (Post, 2013a) and increase the resilience of tundra ecosystems (Olsen and Klanderud, 2014; Kaarlejärvi et al., 2015), preventing the expansion of low-elevation species into higher elevations (Speed et al., 2012; Kaarlejärvi et al., 2013; Kaarlejärvi and Olofsson, 2014) or the encroachment of woody species onto tundra (Olofsson et al., 2009; Hofgaard et al., 2010; Pajunen et al., 2012; Speed et al., 2013; Christie et al., 2015). Through their effects on canopy structure, plant species composition and vegetation productivity, herbivores can affect global carbon (C) dynamics counteracting the predicted net C sequestration associated with the 'greening' of the Arctic under warming scenarios (Van Der Wal et al., 2007; Cahoon et al., 2012; Väisänen et al., 2014; Falk et al., 2015). Under some circumstances selective herbivory may also promote aboveground C stocks in unpalatable plants (Ylänne et al., 2015). The impacts of herbivory on climate feedbacks and energy budgets of tundra ecosystems are also starting to be recognized (Cohen et al., 2013; Biuw et al., 2014). Summer grazing by reindeer affects yearly energy balance by delaying snowmelt date, increasing surface albedo and decreasing ground heating through changes in shrub cover and vegetation structure (Cohen et al., 2013). Therefore, grazing management might be regarded as a strategy to moderate some of the effects of warming on tundra ecosystems (Biuw et al., 2014). This is particularly important in northern ecosystems that are changing at unprecedented rates, with climate warming being one of the major causes of biodiversity loss in the Arctic (Post et al., 2009).

These effects have been mostly reported for large mammalian herbivores through their impacts on shrub encroachment, but are likely widespread and relevant to other herbivores and plant communities as well (Barrio et al., 2016). For example, small mammals (voles and lemmings) may consume more plant biomass per year than larger herbivores in Fennoscandia (Olofsson et al., 2012; Olofsson et al., 2013). Similarly, invertebrate herbivores can cause dramatic losses of plant biomass during outbreaks in the forest-tundra ecotone (Jepsen et al., 2008; Bjerke et al., 2014), but their wider impacts in tundra ecosystems have yet to be investigated (Kozlov et al., 2015).

3. Variability in the outcomes of plant-herbivore interactions

The effects of herbivores on plant communities and the functioning of tundra ecosystems tend to vary regionally and locally (Mulder, 1999; Bryant et al., 2014), but the causes of this variation are poorly understood. It seems that the role of herbivory is modified by ecosystem-specific ecological conditions, including human management (Kitti et al., 2009; Aune et al., 2011; Biuw et al., 2014), cryosphere feedbacks (Plante et al., 2014), the co-evolutionary history between plants and herbivores (Bryant et al., 2014), or by variations in geology (Bråthen et al., 2007), soil conditions (Saccone et al., 2014) and soil processes (Väisänen et al., 2014), topography (Bauer, 1990) or in herbivore populations (Ravolainen et al., 2011, 2014). In turn, these conditions are modulated by (or can mediate the responses to) major external drivers of tundra ecosystems. Consequently, to accurately forecast the responses of tundra ecosystems to ongoing environmental changes we need to understand the drivers of the spatial variation

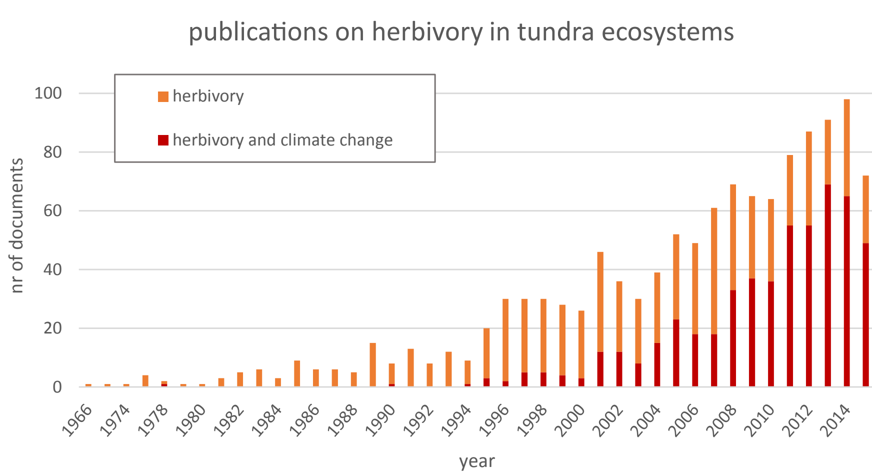

Fig. 1. Number of publications on herbivory in tundra ecosystems since 1966. Studies including some aspect of climate change are indicated in red. The search was conducted in SCOPUS in October 2015, using as search terms: herbivor* AND (tundra OR *arctic OR alpine).

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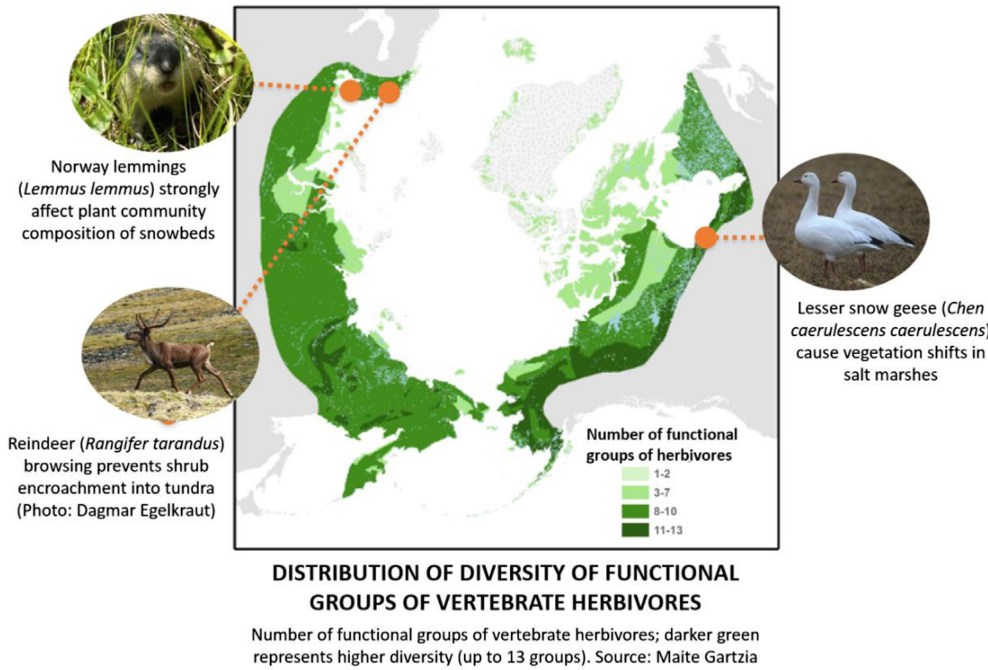

Fig. 2. Given the different herbivores and plants present in a given location, as well as the differences in abiotic conditions, the outcomes of plant-herbivore interactions may not be directly comparable across the Arctic. Novel collaborative studies using functional approaches that take advantage of the presence of similar herbivore guilds and comparable vegetation attributes (at the level of species, plant traits or functional groups) and environmental conditions represent an opportunity to understand inherently local ecological processes across broad geographical ranges. For example, Eurasian reindeer are large semi-domestic herbivores, lesser snow geese are medium-sized migratory herbivores, and Norwegian lemmings are small herbivores with cyclic dynamics. Their differences in body size, diet and population dynamics allow grouping them into three different guilds of vertebrate herbivores in tundra ecosystems, whose impacts on vegetation can be considered separately and in combination.

that influence the outcomes of plant-herbivore interactions.

The frequency, extent and intensity of herbivory can play a main role in the outcome of plant-herbivore interactions (Olofsson et al., 2004b). Productivity seems to play a key role in the responses of plant communities (Bråthen et al., 2007), with more productive sites responding more strongly to herbivory (Gough et al., 2007; Virtanen et al., 2010; Pajunen et al., 2012) although the opposite has also been found (Olofsson et al., 2002). Timing of herbivory can also influence the impacts of herbivores on plants. For example, summer grazing by reindeer may accelerate nutrient cycling rates because nutrient input through faeces deposition is coincident with rapid plant nutrient uptake during the growing season (Olofsson et al., 2004b; Stark et al., 2007); on the contrary, winter herbivory has the opposite effect because faeces and urea deposited in winter probably leach out of the system, decelerating nutrient cycling rates (Stark and Grellmann, 2002). Even within the same growing season, herbivory can have different outcomes. Early season herbivory can affect the ability of plants to recover from the effects of grazing (Hik and Jefferies, 1990), and can affect food quality to subsequent herbivores (Den Herder et al., 2004; Barrio et al., 2013).

Finally, the impacts of herbivory will depend on the identity and abundance of the herbivores involved, i.e., the composition of herbivore communities. For example, large and small mammalian tundra herbivores can have complementary effects on vegetation (Olofsson et al., 2004a; Ravolainen et al., 2014) with each targeting different plant species, life stages or plant parts (Soininen et al., 2013). Most studies on the role of herbivory in tundra ecosystems however, have focused on one (or a few) species of herbivores, overlooking the relative importance of different herbivores or their combined effects. Given the different species of plants and herbivores that engage in plant-herbivore interactions, it seems unrealistic to draw general conclusions about the impacts of herbivores across the tundra biome. However, adopting a functional approach that investigates the impacts of different herbivore guilds on plants or vegetation types that share common traits may prove fruitful to understand which outcomes of herbivory are local and context-specific and which may represent broader patterns of general ecological processes. For example, reindeer/caribou, geese and small rodents are important herbivores in terms of their broad geographic distribution (across bioclimatic sub-zones and longitudinal eco-regions) and their strong impact on vegetation (CAFF, 2013, Fig. 2). These herbivores are, however, also fundamentally different in their modes of herbivory (food preferences and foraging behaviour, i.e. grazing, browsing or grubbing), mobility (migratory or resident) and population dynamics (including sensitivity to predation and climatic variability), so they can be seen as representing three different guilds of vertebrate herbivores in tundra ecosystems, whose impacts on vegetation can be considered separately and in combination.

4. Designing new studies to address these questions

Variability in plant-herbivore interactions in Arctic and alpine environments precludes generalizations about the responses of tundra ecosystems to ongoing environmental changes. This variability calls for coordinated research efforts and highlights the need for common, standardized protocols to address these questions at a global scale, through the use of coordinated distributed experiments and observations, and established priorities for future collaborative research.

One of the priorities for the Herbivory Network is to integrate sites, methodologies, and metrics used in previous work, to develop a set of common protocols and design a coordinated experiment that is balanced geographically and with respect to the main environmental factors. The use of coordinated distributed experiments is increasingly being recognized in ecology and has been successfully applied to some ecological questions (Fraser et al.,

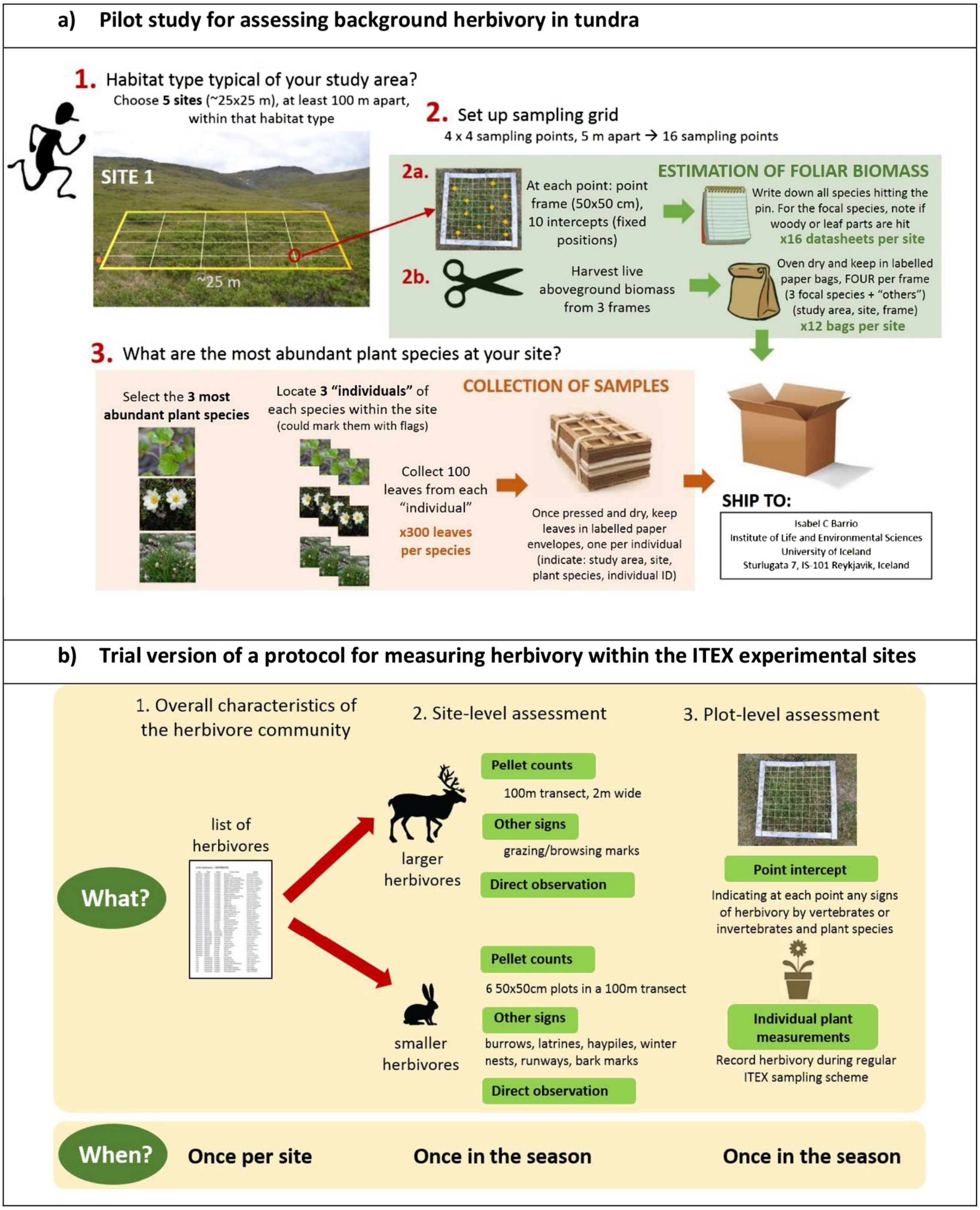

Fig. 3. Protocol for the 2015 pilot study aimed at evaluating levels of background invertebrate herbivory (a), and trial version of a protocol to quantify the variation in herbivory across sites and following experimental warming (b) proposed by the Herbivory Network. These protocols, and others, will be extended to other sites and monitoring programs in the future (http://herbivory.biology.ualberta.ca).

2013; Sternberg and Yakir, 2015). In Arctic and alpine regions, the International Tundra Experiment (ITEX; Henry and Molau, 1997), established in 1990, has enhanced our understanding of the effects of warming on tundra plant communities through the use of a simple experimental design replicated at many sites. Replicated experimental sites across a broad geographical range and a set of selected environmental conditions, are necessary to encompass the potential sources of variation in plant-herbivore interactions that have been identified by studies conducted at single sites. From this point of view, hierarchical study designs that include the use of several spatial information layers can help in teasing apart causalities at different spatial scales (Bråthen and Ravolainen, 2015).

A critical aspect of coordinated experiments is the need to use standardized protocols that allow comparisons across sites, including detailed recommendations on how to measure the variables of interest, as well as guidelines for study design. For example, one of the research priorities identified by a recent synthesis on the impacts of caribou/reindeer grazing in the circumpolar Arctic was the need to develop common protocols to quantify grazing impacts in a standardized way (Bernes et al., 2015).

One of the main activities of the Herbivory Network in its first year has been to begin the process of designing common protocols to evaluate invertebrate and vertebrate herbivory and the impacts of herbivores on soils, in order to allow for comparative studies. In several cases, pilot studies aimed at providing specific information to design the protocols are being conducted in the field; for others, first versions of these measurement protocols are already available. For example, the development of robust sampling protocols to measure herbivory by invertebrates requires a better understanding of the average intensity and the spatial extent at which invertebrate herbivory occurs in tundra. During summer 2015 participants in the network (N = 15 principal investigators, at 22 study sites) contributed to a pilot study to collect this essential baseline information (Fig. 3a). Similarly, a protocol for assessment of the occurrence and intensity of invertebrate herbivory within ITEX plots (Open Top Chambers vs controls) and among study sites (controls at different sites) was initiated in summer 2014 and continued in 2015 (Fig. 3b). Eventually, after robust validation, these protocols will be updated and published so that they can serve as a basis for future coordinated research (e.g. Henry et al., 2013) and be implemented by monitoring programmes such as the Circumpolar Biodiversity Monitoring Program (CBMP; http://www.caff.is/monitoring). Importantly, any protocol to be implemented by a large group of users across an area as heterogeneous as the Arctic, needs to be easy to use, cost-efficient (mainly in terms of time investment), minimize observer bias, and be applicable across a range of habitats and environmental conditions, while still providing valuable data.

As well, long-term observations are essential for detecting trajectories of change in slowly responding tundra plant communities. However, the short- and long-term responses of plants to herbivory may differ (Saccone and Virtanen, 2016), and this variability needs to be taken into account when combining data from sites with treatments with different ages. Synthesizing evidence from different sites with different study designs and experimental manipulations may prove particularly challenging. For example, some studies address plant-herbivore interactions by excluding a main herbivore (Kaarlejärvi et al., 2015) or selectively exclude different herbivores (Ravolainen et al., 2014), while others manipulate their densities using enclosures (Speed et al., 2013) or simulate herbivory by clipping (Ylänne et al., 2015). We can learn from ongoing efforts within the wider Arctic research and observing community (http://www.arcticobserving.org) to design and optimize observing systems (ADI, 2012). By identifying and prioritizing research questions that focus on processes for which mechanisms are already well understood we anticipate being able to determine the causes of spatial and temporal variation more efficiently.

5. Concluding remarks

Given the pervasive effects of herbivory in tundra ecosystems and the context-specificity of its outcomes, it is timely to harmonise research efforts and adopt approaches that allow for generalization across sites and plant-herbivore systems. For instance, functional approaches that identify guilds of herbivores and vegetation attributes could represent a first step forward. Coordinated experiments and standardized data collection for long-term observations can help address these questions effectively at a global scale, but require careful planning and coordination. Such an undertaking can only be effectively addressed by an international research network like the Herbivory Network. The implementation of these collaborative research efforts will improve our understanding of systems that are traditionally managed by humans in Arctic and alpine areas across the globe (CAFF, 2013). For example, herbivory is relevant to many local communities in the Arctic, as the main herbivores are herded (e.g. reindeer) or hunted (e.g. caribou, geese and ptarmigan). In the face of the rapid changes occurring in these regions, a better understanding of the role of herbivory is warranted to inform adaptive management strategies aimed at the preservation of their natural values.

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