

What does it mean to put caribou knowledge into an ecosystem context?

Fred H. Harrington

Mt. St. Vincent University, Halifax, Nova Scotia, Canada B3M 2J6 (fred.harrington@msvu.ca).

Abstract: Ecosystems are envisioned as integrated, complex systems with both living and non-living components, that are linked through processes of energy flow and nutrient cycling (Bowen, 1971; Ricklefs, 1979). The ecosystem approach seeks to describe the components of this system, the pathways through which energy and nutrients move, and the processes that govern that movement. The goal is a better understanding of the role or effect of each component (abiotic or biotic) within the system. Theoretically, the more we know, the better we can predict the future behaviour of the ecosystem and therefore manage the system on whatever sustainable basis we deem appropriate. Caribou (*Rangifer tarandus*) presently inhabit two ecosystems, tundra (arctic and alpine) and taiga (or boreal forest), both characterized by relatively low productivity and diversity (Bowen, 1971; Bliss, 1981; Bonan, 1992a). As increased anthropogenic impacts are expected in these ecosystems through the next century, our ability to ensure the continued survival of caribou requires that we pay increasing attention to the processes that drive these systems. In this endeavour, an awareness of the effects of both spatial and temporal scale, in both ecosystem processes and our research programs to understand those processes, is critical.

Key words: climate, succession, wildfire, Pleistocene, boreal forest, taiga, tundra, conservation, *Rangifer tarandus*.

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The principal defining feature of an ecosystem approach is scale, which can vary along several dimensions. Spatially, an ecosystem can range from a single organism (i.e., a tropical forest tree with its associated epiphytic flora and fauna) to the entire earth (i.e., the Gaia hypothesis) (Usher, 1973). In general, however, ecosystems are described at intermediate scales, defined by their dominant plant communities: desert, scrub, grassland, shrubland, woodland, and forest (Caughley & Sinclair, 1994). Each of these can be subdivided into increasingly similar floras (i.e., forests in general into tropical, temperate and boreal forests) and these in turn can be further divided. The boundaries between neighbouring ecosystems, at whatever level of analysis, represent relative rather than absolute divisions of the natural world.

Ecosystems also vary temporally, representing the continuity of time from yesterday to today and Tertiary to Quaternary. As the time frame lengthens, change shifts from stochastic to evolutionary processes. Year to year changes in species' abun-

dance due to vagaries in rainfall give way to longer term successional changes which in turn yield to evolutionary changes as some species become extinct and others are modified by natural selection. Thus change of a dynamic nature, and not stasis, is expected in an ecosystem approach.

Subordinate features of scale in ecosystems include diversity, productivity and stability. As human activities have increasing impacts on a variety of ecological processes at all levels of scale throughout the earth's ecosystems, incorporating an ecosystem outlook into caribou science means keeping an awareness of these aspects of scale, periodically reassessing our current focus to avoid losing sight of important ecological processes that may be operating on another level of scale.

Spatial scale

The vegetation communities that distinguish ecosystems are products of five factors: parent material (substrate), topography (especially elevation, aspect

and slope), climate, the biota, and time (Viereck *et al.*, 1986). The first three factors set the basic spatial boundaries of the ecosystem, influencing the biotic possibilities within a specific area. These factors, in essence, set the stage that is later "fleshed out" by the biota over time (Kimmings & Wein, 1986). As the stage changes, opportunities for the biota also change.

Boundaries between adjacent ecosystems are relative rather than absolute, with one replacing another through a transition of intermediate habitats (Payette, 1983; Sirois, 1992). Even ecosystems that seem relatively well defined, such as the terrestrial, aquatic and marine ecosystems of arctic tundra biomes may have unexpected interconnections. Power & Barton (1987) proposed that caribou may have a significant impact on arctic char (*Salvelinus alpinus*) populations in Ungava Bay, Quebec. Areas of summer range grazed heavily by caribou have reduced lichen cover and consequently retain less water during spring melt and summer rains, causing a drop in ground water levels. During dry spells in late summer, stream flows may be insufficient to allow char to migrate upstream to spawn. Thus during periods of high caribou numbers, char populations may be depressed or even lost from the most severely affected streams.

Caribou presently inhabit ecosystems along both the northern limits of land and the higher elevation sites of mountains. Thus in one direction, caribou have no place to go should the boundaries of their ecosystem move north or to higher elevations with global warming. Whitehead *et al.* (1982) proposed that a rapid 75% decline in the area of boreal forest between 11,000 and 8,000 yr BP, likely caused by a 7 °C increase in global temperature at the end of the Pleistocene (Hoffmann & Taber, 1967), significantly reduced mastodon (*Mammuthus*) populations, making them vulnerable to stochastic events and leading to their eventual extinction.

Caribou exploit spatial aspects of their arctic and alpine tundra ecosystems in predator avoidance (Bergerud & Page, 1987). To pay off, this strategy requires an adequate distance between calving grounds and areas of wolf activity (Heard & Williams, 1992). Extensive loss of tundra habitat, expected in some models of global warming (i.e., Solomon, 1992), could make this strategy less viable.

Boreal forest is also expected to retreat northward with global warming (Kullman, 1983; Solomon, 1992), displacing tundra in the process (Payette,

1983). Such change in itself does not necessarily mean a decline in the areal extent of the forest, although one estimate sees it declining by 25% (Solomon, 1992). At present, however, boreal forest is being affected by forestry practices, which at best return the forest to an earlier successional stage and at worst lead to fragmentation and degradation through export of biomass (Freedman, 1989) with an increased risk of local extinction for species with small populations (Diamond, 1984).

Space is also employed in predator avoidance by woodland caribou, which disperse to reduce predation on calves (Bergerud & Page, 1987; Ferguson *et al.*, 1988). The success of spacing out appears to be dependent on predator density, which is likely affected by distance from habitat used by other ungulates (i.e., moose and white-tailed deer (*Odocoileus virginianus*)) (Thomas, 1995). Thus changes in ecosystem spatial distributions can influence the viability of spacing out, and caribou population dynamics as a result.

Temporal scale

The characteristics of an ecosystem at any given time are determined by three sets of successional (temporal) processes: allogenic, autogenic and biogenic (Kimmings & Wein, 1986). Allogenic processes are external to the biota but have significant impacts on it, such as seasonal or global climate change, wildfires or other perturbations. Some may follow specific time courses (i.e., annual temperature and solar cycles), but many are unpredictable. Wildfires in black spruce taiga, for example, may occur today at 60–120 yr intervals, *on average*, but variation is great (Dyrness *et al.*, 1986; Payette, 1992). In the past, wildfires have occurred at both significantly longer and shorter intervals (Johnson, 1983).

Wildfires release nutrients and destroy a portion of the above ground biomass, allowing earlier successional flora to recolonize (Dyrness *et al.*, 1986; Kimmings & Wein, 1986). Soil temperature, a primary determinant of productivity in northern areas (Van Cleve & Yarie, 1986; Bonan, 1992b), rises for a number of years following a fire, accelerating both the growth of a palatable post-fire vegetation (Bryant & Chapin, 1986) and the decomposition of its litter (Van Cleve & Yarie, 1986). As Dyrness *et al.* (1986:84) comment, "it is essential that we view fire as an ecosystem process in taiga communities rather than as a catastrophic event", as "fire can be

interpreted as an essential agent of renewal." Thus climatic and anthropogenic factors that influence fire rate can have far-reaching affects on an ecosystem in both the short term and the long term.

Autogenic processes are those generated by the biota that change the physical environment of the ecosystem (Kimmings & Wein, 1986). Over several decades following a fire or other major disturbance in the boreal forest, slower growing plants characteristic of later successional stages overtake the pioneer species, and an important autogenic process comes into play. Late successional plants invest more heavily in defense than those in the post-fire flora (Guthrie, 1984; Bryant & Chapin, 1986). The combination of increased canopy cover and thicker layer of toxic litter leads to soil cooling, movement of permafrost toward the surface, a shorter growing season, and decreased decomposition of litter, thus lowering productivity and reducing the availability of nutrients for future growth (Guthrie, 1984). Whatever growth is produced, being unpalatable, is largely unavailable to consumers. Thus the late successional community modifies the environment to favour its long-term survival, at least until the next wildfire or other disturbance.

As Larsen (1980) noted, calling the late successional flora a 'climax' community may be misleading, as few communities remain free from disturbance for any long period. Also, some subclimax communities remain relatively stable for long periods in arctic and boreal habitats. Where the environment is very harsh, competition among plants may be unimportant, so any plant that gains a foothold can survive, and succession to a climax community characteristic of more benign environments does not occur. The ecosystem that we see before us is thus a product of both general successional rules and specific historical circumstances.

Biogenic processes involve the web of direct interrelationships among species within the ecosystem (Kimmings & Wein, 1986). Ecological processes such as population growth, competition, predation and parasitism, and species adaptations to these processes (as well as failures to adapt) (Ricklefs, 1979), give a dynamic form to the biotic community of the ecosystem.

Diamond (1984) has shown that ecological (biotic) stasis on relatively short time scales (i.e., years to decades) resides more in the human mind than in nature. Studies of birds and invertebrates have shown that species composition typically varies from year to year as some species disappear while

others reappear. The probability that a species will disappear from a local habitat, or an ecosystem, is dependent on its population size and area occupied and is greater for carnivores than herbivores, larger than smaller species, and specialists rather than generalists (Diamond, 1984). Thus remnant populations of caribou in fragmented boreal forest are vulnerable to extinction. On the other hand, the smaller populations of their predators are even more vulnerable, as the Isle Royale moose-wolf system demonstrates (Peterson, 1995). During the late-Pleistocene, caribou comprised about 5% of the large ungulate fauna in numbers of individuals, but only a fraction in terms of biomass (Guthrie, 1968). Could persistent low density have allowed caribou then, and today (Bergerud, 1992), to wait out their predators, and see them disappear first?

On a longer time scale, ecosystems change as their biota respond to stochastic and selective pressures. The alpine and arctic tundra biomes are likely the youngest of terrestrial ecosystems, originating at the end of the Tertiary (Hoffmann & Taber, 1967; Bliss, 1981). Caribou appeared during the mid-Pleistocene, about 2.0 m-yr ago, likely originating in central Asia (Anderson, 1984) in taiga-tundra environments (Bergerud, 1974). Until the late Pleistocene, caribou shared tundra, boreal forest and grassland ecosystems with a variety of other often more numerous and larger herbivores, including horses (*Equus caballus*), moose (*Alces alces*) and musk oxen (*Ovibos moschatus*), as well as the now extinct woolly mammoth (*Mammuthus primigenius*), giant bison (*Bison priscus*), woolly rhino (*Coelodonta*) and ground sloth (*Megalonyx*) (Guthrie, 1968; Caughley & Sinclair, 1994). In one now-vanished ecosystem, the mammoth steppe, they typically ranked a distant third or fourth in abundance behind bison, horses and mammoths (Guthrie, 1968; 1984; 1990). Where did caribou fit within this broad array of herbivores? How did caribou fare against a predatory guild of wolves (*Canis lupus*), lions (*Felis*), brown bears (*Ursus arctos*) and the occasional sabre-toothed cat (*Smilodon*)? What affect did the late-Pleistocene extinctions have on caribou?

The cause or causes of the late Pleistocene megafaunal extinctions are still debated, with climate change one strong contender pitted against the "overkill" hypothesis (Martin & Klein, 1984). Climate-centred hypotheses are ultimately grounded in ecosystem change, arguing either massive changes in plant abundance or composition (i.e., Whitehead *et al.*, 1982) or changes in the relative

investment made to growth and defense as plants responded evolutionarily to changes in climate (Guthrie, 1990). Even Martin's (1984) "over-kill" hypothesis is rooted in an ecosystem change: the arrival of a new predator to which a number of species had inadequate defenses. Whatever the case, caribou have distinguished themselves for another 10,000 years by surviving in the face of this new predator, even though highly sought after throughout their range (Anderson, 1984).

We, along with caribou, stand poised to witness what many believe may become a major extinction event (Wilson, 1988). Habitat change caused directly (i.e., deforestation) and indirectly (i.e., global warming) by human activity is likely to have far-ranging effects on ecosystems well into the future. How will caribou fare as these changes unfold?

Caribou and their knowledge of ecosystems

Like any species, caribou have evolved an array of adaptations which have thus far enabled them to meet the various selective challenges provided by the ecosystems they have inhabited. In addition to morphological and physiological traits, their behavioral repertoire has been shaped by natural selection to enable them to respond adaptively to the spatial and temporal heterogeneity of boreal and tundra environments. This environmental variation includes both the unpredictable and patchy distribution of food and predators and the stochastic vagaries of climate. An attempt to understand caribou ecosystems from a caribou perspective, that is, to understand how caribou make decisions about foraging sites, calving areas, and movements both localized and migrational, will better enable us to understand both the evolution of their behaviour and the consequences of ecosystem change on their future behaviour and survival.

Caribou and ecosystem management

A recent development in wildlife conservation is ecosystem management (i.e., Seip, this issue). Rather than developing a variety of specific management programs focused on individual species,

this approach seeks to preserve biodiversity by mimicking the natural disturbances that historically were responsible for the development of the ecosystem and the evolution of the species in its biota. Thus we might hypothesize: if an ecosystem (forest, tundra, etc.) continues to function, spatially and temporally, as it did in the past, species of that ecosystem, such as caribou, will continue to exist. This approach has great promise, but two aspects of ecosystem history need to be kept in mind when applying it.

First, stochastic processes have long been at play in ecosystems. If, for example, timber harvesting is to substitute for wildfire in perpetuating forest ecosystem structure, we must realize that beyond characteristics of the forest (i.e., species composition, age, site) and recent climate (i.e., rainfall, winds, thunderstorms), chance played a major role in determining where fires would start and how long and wide they would burn once started. Thus we must be careful to ensure our management plans retain that natural element of chance, despite the cost in terms of economic gain from timber harvest or other human endeavour. We must be wary about placing an unnatural human-derived pattern on the ecosystem, lest we lose important random features, including local extinctions, which may have allowed rare species like caribou to survive through the past.

Second, we need to remember that the ecosystems we study and seek to preserve are unique in the history of life. Their present form is the result of a long series of evolutionary and stochastic events stretching far back in time and poised to continue far into the future. But just as change has been a dominant characteristic of ecosystem form and function in the past, it will continue to be so in the future. One factor often lacking from our considerations of ecosystems is change and its inevitability, and a failure in this regard is our exclusion of humans, both local and global, as driving forces in this change. Thus it is not sufficient to manage ecosystems based on the unique historical processes that gave them their current form. We must place humans into the ecosystem and manage adaptively, based both on past processes and a sensitivity to how humans are changing those processes.

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