To: Professor William Lahey, Nova Scotia Forest Practices Review

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Re: Response to Workshop on DNR's Framework for Ecosystem-Based Forest Management (including DNR's Work on Natural Disturbance Regimes)

Date: March 18, 2018

Thank you for the opportunity to participate in the Workshop at the Lord Nelson on February 21, 2108, and to submit my summary comments.

I offer my observations and potential recommendations to address identified weaknesses of DNR's current approach to NDR and how it influences harvest decisions. My comments are based on my understanding of Nova Scotia's system of ecological land classification, natural disturbance and potential climax forest interpretations, and forest ecosystem classification at the site level. While I applaud the effort, there are a few omissions and inconsistencies in the interpretation of natural disturbance regime, associated indicator targets, and other factors. These may lead to forest composition planning guidelines with potentially negative implications for forest health, ecological integrity and biodiversity at the strategic, landscape and larger, provincial levels.

I acknowledge that implementing an ecosystem-based approach grounded in DRN's NDR interpretations would likely lead to better outcomes for the forest than those that occur with current management practices. Nonetheless, as presented the framework does not accurately characterize 'natural' disturbance regimes in frequency, extent or magnitude; harvest indicator targets derived from it are intended only to apply on the public (Crown) portion of the working land base; and thus, its provisions are unlikely to support ecologically-sustainable forest management practices, or lead to maintenance or restoration of important forest ecological structures and functions over local or regional spatial scales, or short or long time frames. Though better than existing practices, and representing a positive step forward, it remains insufficient.

Sustainability and ecosystem-based management of forests

I posit my remarks by being explicit in my presumption that the Review of Forest Practices and Ecosystem-Based Forest Management are indeed concerned with the 'forest', rather than more narrowly with 'forestry'. If the 'forest' is not the focus, this represents the first fundamental flaw in the approach. Forests contain values more irreplaceable than biomass and board feet, and relevant users and stakeholders extend well beyond timber harvesters, and indeed beyond humans. Planning for its sustainability should consider the broader provincial and regional context, and multiple species, structures and processes. The Mi'kmaq should be invited to co-manage, government to government. All of NS is un-ceded Mi'kmaw territory, and we are all Treaty people. Reconciliation requires de-colonizing of people and of our relation to the land.

Indications that forest practices need to be sustained or sustainable beg the question of 'Sustainable for what?'. What exactly is it that we are trying to 'sustain'? If terms such as 'sustainable' are to be used, they must be defined. Practices that aim to sustain a steady or growing volume of biomass or income would results in significantly different practices than those that aim to sustain sufficient forest habitat to support viable populations of native species, including allowing for spatially contiguous forest land cover to allow for adaptation, movement and dispersal in response to climate and other environmental changes over short and long terms. Such ecological sustainability would require ~ 60-65 percent of NS land base to be managed for biological diversity (biodiversity) conservation objectives (see Beazley et al. 2005; Reining et al. 2006). This 60-65% figure is consistent with analyses conducted in other regions to identify how much area is enough to maintain native biodiversity over time. Area-based recommendations range from 25-75%, varying with the heterogeneity of the region (Noss and Cooperrider 1994; Soulé and Sanjayan 1998; Noss et al. 1999; Cowling et al. 2003; Solomon et al. 2003; Noss et al. 2012). Relatively heterogeneous regions will be represented by higher percentages than would be needed to represent less diverse regions. Temperate forests, such as in Nova Scotia, are relatively heterogeneous, and thus higher percentages of land are required to maintain and recover biodiversity.

Nearly continuous forests dominated by older-age classes is/was the predominant natural land cover in Nova Scotia as indeed in other regions of the Acadian Forest. Accordingly, forest management should consider the spatial context of the entire land base, and account for cumulative losses of forest cover, especially of older age classes, to date. Given the current state of the forest in NS, arguably the most ecologically responsible and highest objective for all public forests would be to manage them for older-age class recovery. Further, as forest is/was the predominant ecosystem, forest management should be synonymous with biodiversity conservation, not solely with timber or biomass harvesting. Native biodiversity in NS exists predominantly in forests. The Province needs strong biodiversity legislation and other structures for biodiversity conservation planning and implementation. Forest planning and management should take place within its parameters. Until such time as these measures are in place, forest management should take the maintenance and recovery of biodiversity into account.

Wildlife species selection

DNR's SMPs omit considerations of many important species of wildlife, and for those that are considered, the provisions are inadequate. The species considered are too few, currently limited to provincially-listed endangered species and deer, and too narrowly distributed. By definition, rare and endangered species are currently very limited in their distribution and occurrence patterns, representing a very small footprint that is subject to special management practices. Deer, on the other hand, are widespread, and thrive in many human modified landscapes; however, SMPs apply only to a few wintering areas. Deer were not historically native to NS and moved in only after humans altered the landscape and extirpated wolf, caribou, cougar and nearly moose and lynx. Deer pose a threat to the endangered moose (as hosts to the brainworm, *P. tenuis*, which deer can live with but kills moose; and competition) (Beazley et al. 2006). Deer thus require very little if anything, by way of special management practices, and arguably should be dramatically reduced in numbers to more closely reflect historical conditions and assist with moose recovery.

Ecosystem-Based Forest Management should instead take into account the habitat requirements of a wide range of carefully selected species that collectively serve as surrogates for many other species (Lambeck 1989; Beazley and Cardinal 2004). Appropriate surrogate species for forest planning and management include those that are sensitive to human changes to the landscapes. Key species to include are those that are functionally important, forest habitat specialist, sensitive and/or vulnerable, and/or wide-ranging or have large area requirements. Surrogate species should be selected for each habitat type (e.g., forested wetlands; coniferous, mixed, and deciduous forests; highlands; etc) and to represent multiple taxon (e.g., mammals, birds, reptiles and amphibians, fish, etc). Appropriate surrogate species for NS include moose, lynx, martin, river otter, little brown bat, southern flying squirrel, Gaspe shrew, Blandings turtle, wood turtle, northern ribbon snake, brook trout, Atlantic salmon, northern goshawk, several forest interior birds, etc (Beazley and Cardinal 2004; Kanno and Beazley 2004).

SMPs

SMP guidelines prescribe safeguards that are too spatially limited and do not take adequate account of fragmentation and other deleterious impacts of forest roads. Moose require extensive areas of contiguous habitat with low road densities (<0.6 km/km2) (Forman and Alexander 1998; Snaith et al. 2004; Beazley et al. 2004). Clearcutting results in loss of security and thermal cover, the latter of which is critical year round in NS due to being within the southern limits of its range (Snaith et al. 2004; Broders et al. 2012; Timmerman and Rodgers 2017). Negative road influences on moose extend more than 1 km from forest road edges (Forman and Alexander 1998; Boer 1990). Indirect effects include increased access for competitors such as deer and predators, including illegal hunting/poaching by humans, among others (see Beazley et al. 2004 for a review; Boer 1990).

Lynx suffer similar impacts from forest roads and forest harvesting (Beazley et al. 2004 for a review). Snow clearing or compaction on roads and trails facilitate the movement of coyotes and bobcat into lynx habitat, decreasing the competitive advantage lynx obtain from their showshoe-like paws. Given lynx dependence on snowshoe hare as its primary/sole prey, such decreased competitive advantage, especially during points in the low-hare part of their ten-year cycle, represent the difference between make or break for lynx. Roads facilitate trapping for bobcat, to which lynx is vulnerable as bycatch. Thus, forest SMPs, including partial harvests that might be conducted in ways that retain habitat suitability values for lynx, are ineffective because of the forestry roads and tracks that are introduced, providing access for competitors and predators, including humans.

Accordingly, while moose and lynx are good choices as part of a multi-species suite of surrogate species, the SMPs for these species are inadequate and do not take into account the wide range of requirements of their persistence, let alone their recovery. SMPs for these species apply only in the very limited refuges of very small remnant local groups, rather than to the larger area required to recovery the species. Based on genetic and demographic factors alone, lynx require 154 males with average home-ranges of 100 km2, and thus 15,400 km2 of habitat to support a short-term (decades) viable population (Manerikar, unpublished; Manerikar and Beazley, in prep). (Males are considered because they will tolerate females but not other males within their home range.) Long-term viability entails about an order of magnitude higher, which would require maintaining/restoring connectivity with habitat extending into NB. Remaining effective habitat patches for lynx (habitat suitability and road density < 0.6 km/km2) total only 1669 km2 (figure 1); these patches, if connected, would support only 7 males over decades, far short of a viable population. Remaining habitat for lynx in NS is thus functioning as a ‘sink’ (more deaths than births). Many species have recovered from severe bottlenecks in their populations; however, sufficient ‘source’ (more births than deaths) habitat is required. If lynx are to be recovered, forest management practices need to allow for sufficient areas of unroaded forest habitat suitable for lynx. This would entail decreasing the density of forest roads in lynx habitat to <0.6 km/km2, and attention to much larger areas than currently considered, ultimately providing at least 15,400 km2 to support a short-term viable population of lynx. In contrast, DNR lynx habitat buffers are currently 24,492 ha (<25 km2), and thus of insufficient size to for 1 male to persist over time.

Similar conditions pertain to American martin and moose. American martin is a forest-interior species, requiring habitat well away from edges, including edges caused by forest roads and harvesting. Moose are sensitive to road influences and have large area requirements, with an average home range of 25 km2 (Leptich and Gilbert 1989; Remple et al. 1997; Snaith and Beazley 2004a). DNR moose habitat buffers are 28,991 ha (<29 km2), and thus sufficient to support 1.2 moose. To support a viable short-term population of moose in NS requires ~14,000 km2 of connected, suitable habitat in areas with road density <0.6 km/km2 (figure 2) (Snaith and Beazley 2004b; Beazley et al. 2005). This broad habitat area needs to contain a high proportion of forest cover to provide relief from heat stress during summer and winter Snaith et al. 2004). Arguably, forest management that considers moose would require attention in areas well beyond the DNR-identified moose concentration areas. It would also employ a range of measures beyond reducing harvest rates by 20% within concentration areas, including practices that limit and decommission forest roads and increase thermal cover.

Broader thinking: larger scales in space and time

In general, forest management planning in NS needs to address serious issues of fragmentation of the forest by roads and harvest practices (Beazley et al. 2006; Fudge et al. 2007). Planning should take into account the bigger picture, beyond the stand level and even beyond the landscape level, to the broader region, including connections to New Brunswick and the rest of continental North America (Beazley et al. 2005). Nova Scotia functions much like an island, tenuously joined to NB at the Chignecto Isthmus. This narrow connection (~532km in width) is further threatened by sea level rise. In climate change scenarios especially, this connection beyond NS is important for species movements and adaptions over both short and long-terms. Multiple conflicting demands on the ~5km width of higher-elevation lands across the isthmus will put further pressures on forest connectivity with implications for species migrations and other movements. Care should be taken to maintain and recover an intact contiguous forest system into New Brunswick from NS, including engagements with forest planners in NB for cross/transboundary considerations. This is consistent with the Province of NS's commitment as signatory to the New England Governors and Eastern Canadian Premiers resolution 40-3 on Ecological Connectivity, Adaptation to Climate Change, and Biodiversity Conservation, for which DNR has been assigned the lead for NS (http://www.scics.ca/en/product-produit/resolution-40-3-resolution-on-ecological-connectivity-adaptation-to-climate-change-and-biodiversity-conservation/).

Sampling biases and data deficiencies

Harvest decisions based on the mapped presence of rare and endangered/listed species of concern are at high risk of errors of omission. There have been no province-wide systematic inventories of such species. Occurrence data are largely based on reported opportunistic sightings and targeted small-scale inventories. These records understandably are concentrated around roads, universities, and parks, all of which are easily accessible and therefore where most of the sightings occur and inventories are conducted. The most systematic inventories and records are for species of interest for hunting, namely deer, which is not a species of conservation concern. These sampling biases create significant deficiencies in the occurrence data for most species, and if not very carefully accounted for in distribution modeling, the outputs risk being seriously flawed. Thorough inventories of lands should be undertaken by qualified third parties for accurate inclusions in data sets and in decision trees for harvesting options.

NDR classification framework

DNR has created a framework that characterizes disturbances as frequent, infrequent and gap. This represents a basic logistical flaw in the framework because these classes differ in kind. ‘Frequent’ and ‘infrequent’ are classes that indicate frequency. ‘Gap’, on the other hand represents extent: disturbance sizes are typically classed as ‘gap’ (e.g., an old or diseased tree falls down or blows down) or ‘stand’ replacing (e.g., fire, windthrow, disease or insect infestations affects a larger area). A more sophisticated framework would also consider magnitude or intensity (e.g., is the disturbance sufficiently intense as to cause mortality of all of the trees in the stand, or is the damage less severe). At a minimum, the NDR framework should be based on a two-by-two matrix that accounts for frequent and infrequent disturbances at both stand and gap levels. Ideally, magnitude or intensity should also be included to differentiate between disturbances that kill the trees and/or damage the soil (e.g., high intensity burns and prolonged infestations) and those that do not (low intensity). It is my understanding that this weakness with the NDR framework has been pointed out by Bob Seymour, of your expert committee, so I will leave it at that. Forest management interpretations and decisions based in guidance derived from the NDR framework current form could have potentially extensive negative repercussions for forest ecosystems.

Characterization of extent and frequency of NDRs in NS

When compared with findings reported in peer-reviewed scientific studies of natural disturbance regimes in Nova Scotia and other areas within the same Northern Appalachian/Acadian ecoregion (i.e. NS, NB, Maine, Vermont, New Hampshire, and parts of New York and St Lawrence lowlands of Quebec), DNR’s NDR overestimates the frequency and extent of disturbances. Although the NDR framework does not explicitly incorporate magnitude or intensity of natural disturbances, many of the harvest management guidelines derived from it seem to assume intensity severe enough to kill the trees or eliminate the above-ground portion, representing an overestimate of severity. Two potential reasons for DNR’s overestimation of the NDR could be (1) a reliance on studies conducted outside of the province or beyond the ecoregion, and/or (2) that they are not based on ‘natural’ disturbances, per se, but rather on disturbances, both natural and anthropogenic, in the present-day context, in which the landscape is so changed that disturbances are more frequent and widespread. For example, stands that are surrounded by clearcuts or converted lands are more susceptible to blow down; monoculture and even-ages stands are more susceptible to insects and disease; fire suppression has resulted in built up fuel wood, leading to more intense and widespread fires; and, forest roads provide access for disturbances such as human-caused fire and vectors for invasion of insects and diseases. To base harvesting guidelines on disturbance regimes that are already beyond natural levels, and thus no longer representative of them, could potentially have negative implications for forested ecosystems.

Art Lynds has provided a submission that details the natural disturbance regimes in NS. I will not repeat the many well substantiated points that he makes in his submission; however, I will vouch for the veracity of the information, as it is consistent with my understanding gained from the literature, and he refers to many scientific papers and studies that I have also examined. Instead, I will focus on a few additional points. The palaeological record, as indicated by the presence or charcoal or pollen in sediment cores, suggests that after about 4400 BP, fires in NS were small and infrequent (Green 1981; 1982). Use of fire on the land by the Mi'kmaq was uncommon (Miller 1986; Joudry, unpublished) and produced no noticeable effect on forest composition (Livingston 1968). Fires caused by Mi'kmaq in NS, like those in Maine, were infrequent and in close proximity to camps (Russell 1983). This pattern remained until after Euro-American settlers burned forests to clear land for agriculture (Livingston 1968). High levels of human-set fires occurred in the settlement period until the early 19th century. For the years from 1915 to 1975, Wein and Moore (1979) calculated a mean annual burn of approximately 2400 hectares, generalized for NS. Fire is considered the predominant 'natural' disturbance regime, with both gap and stand-level events (Loucks 1970; Pickett and Thompson 1978). Wind throw and insect infestations are predominantly gap level, though stand-level windthrows have occurred infrequently, such as during the Saxby gale in 1867 (Gimbarzevsky 1975) and Hurricane Juan in 2003. Most stand level insect infestations, such as hemlock looper outside of highland areas in Cape Breton, are largely confined to managed forests and are related to human-caused changes.

Accordingly, looking at relatively long-term averages and patterns, natural disturbance regimes in NS are infrequent and small, with the predominant stand-replacing natural disturbance being lightning caused fire. Combined with human-caused fire, averages over the past century are around 2400 ha/year generalized for all of NS (Wein and Moore 1979). Recent studies suggest that intermediate intensity disturbances, such as ice storms and microburst wind events, may be more prevalent than previously recognized (Ziegler 2002; Millward and Kraft 2004; Woods 2004; Hanson and Lorimer 2007). These events, however, tend to produce partial canopy mortality and leave abundant residual live and dead or damaged trees (North and Keeton 2008).

If DNR were to mimic this natural disturbance regime, the forest ecosystems of NS would be provided a very good opportunity for recovery. The majority of the province should be classified as 'gap' disturbance, and localized stand-replacing disturbances should be understood as occurring very infrequently. No area of the province should be classified as frequent stand replacing.

NDRs in spatial context

To adopt a management approach based on natural disturbance regimes sounds intuitively appealing. The reality remains, however, that mimicking natural disturbance regimes in forest harvesting practices runs the risk of at least 'doubling' the disturbance regime, since it is likely that the pre-existing natural disturbance regimes will cease to continue. Care should be taken to not use the idea that it is 'natural' to justify over harvesting or expansion of harvesting beyond levels that the forest ecosystem can absorb at any given time. Landscape ecologists have derived sophisticated concepts and means of taking disturbance regimes into account, including providing management guidelines or rules of thumb for ‘shifting mosaic steady states’ (Bormann and Likens 1979), ‘quasi-equilibrating landscapes’ (Shugart and West 1981) or ‘minimum dynamic area’ (Pickett and Thompson 1978). Similar concepts have been explored in percolation theory (Gardner et al. 1989, 1992; O’Neill et al. 1992) and watershed studies (Kanno and Beazley 2004). These guidelines, based on studies on the ground, indicate that, for example, for a forest patch to be quasi-equilibrating over time, the ratio between the size of the quasi-equilibrating patch and the largest disturbance regime (both natural and anthropogenic) should be 50:1 (Shugart and West 1981; Urban et al. 1987). Studies based in percolation theory have found that if a landscape falls below a threshold of 60% natural land cover, the likelihood that a species can find a path through the landscape is dramatically decreased (Gardner et al. 1989, 1992), and the likelihood that an invading species can colonize the area is dramatically increased (O’Neill et al. 1992). Similarly, other studies have shown that watersheds that lose 40% of their natural cover have dramatically reduced water quality, with impacts on characteristics of the fish communities (e.g., shifts from cold-tolerant to warm water species) (Kanno and Beazley 2004). These studies support the previously mentioned indication that ~ 60-65% of NS should be managed primarily for biodiversity objectives to maintain current levels.

Historically, fire has been the largest ‘natural’ disturbance regime, estimated at about 2400 ha/year in NS (Wein and Moore 1979), though less in the pre-Euro-American-settlement landscape. Considering this disturbance alone, a quasi-equilibrating landscape would be about 50 time this size, or 120,000 ha. However, other natural and anthropogenic disturbances have occurred and continue to occur on the NS landscape. These other disturbances also need to be factored into the equation. Together these should not exceed 20% of the entire forest land base of NS if a quasi-equilibrating landscape is to be maintained or recovered.

Indicator targets for NDR classes

While DNR’s proposed indicator targets for each disturbance-regime region probably represent a better scenario than is currently being applied, they over-represent younger classes (<40 years) and under-represent older classes than a more accurate natural disturbance regime assessment would recommend. The proposed targets work towards 60% of the working land base in <40 years old classes in ‘frequently’ disturbed regions; 40% at <40 years old in ‘infrequently’ disturbed regions; and, 30% at <40 years old in ‘gap’ regions. These large percentages of young forest cover are not consistent with the extent and frequency of the natural disturbance regime in NS. This is not surprising, because these targets are taken from guidelines apparently derived for disturbance regimes in forests in Ontario and Minnesota. If this is indeed the case, it represents a flaw with potentially serious implications for age-class distributions of NS’s future forests.

Studies in NS and in Maine show similarly small and infrequent natural disturbance regimes reflective of their location within the same ecoregion and the temperate forest (Loucks 1970; Lorimer 1977; Pickett and Thompson). If anything, natural disturbance regimes in NS may be smaller and less frequent due to the greater area of coast and oceanic influence on a wetter climate and the numerous lakes and rivers that serve as fire breaks. In Maine, small scales disturbances occur every 250-300 years, and large-scale disturbance occur at a site in the order of every 800 years for fire and every 1150 years for wind (Lorimer 1977). Similarly, Seymour et al. (2002) found that gap disturbances (means of 24-126 m2) occurred every 50-200 years; and, stand-replacing fires (means of 2-200 ha) occurred every 806-9000 years, and winds (means of 14-93 ha) every 855-14,300 years in northeastern forests, excluding boreal. In contrast, in boreal forests in Minnesota, fires occur every 5-50 years (Heinselman 1971), similar to boreal forests in Ontario. DNR's NDR characterizes 30.5% of NS forests as experiencing stand-replacing disturbances frequently, defined as 40-60 years (versus 250-300 years [Lorimer 1977]), and 28.3% infrequently, defined as 400 years (versus 800-1150 [Lorimer 1977] and 800-14300 years [Seymour et al 2002]). Only 30.5% is classified as 'gap', in contrast to widespread indications in the literature that the predominant natural disturbance regime is at the gap level.

Targets derived from regions like Minnesota and Ontario, where disturbances are more frequent and larger than those in NS, should not be applied in NS, where disturbances are small and infrequent. For example, Fraver et al. (2009) found a mean canopy loss of 9.6% per decade in old-forest classes in northern Maine. If this figure is adopted and extended, this would accumulate over four decades (40 years) to 38.4% canopy loss, or 38.4% in forest class <40 years old, if 'canopy loss' is considered equivalent to mortality. This figure, based on natural disturbance regimes in forests in Maine, might represent a good comparator for NS indicator targets derived from NDRs. By this figure, NS would have 61.6% (all but 38.4%) of its forests in age classes older than 40 years, whereas DNR's targets recommend a mix of 40% in 'frequent', 60% in 'infrequent', and 70% in 'gap' regions. If frequent, infrequent and gap classes were evenly distributed, this would represent an average of 57% in age classes over 40 years. This is close, but the difficulty comes in it being applied only on public (Crown) lands, which represents only 31% of the working land base. If higher harvest levels and other forest cover conversions occur on many other forested lands in NS, then losses of forest age classes > 40 years will be much more extensive, certainly beyond the natural disturbance regime. If targets are not to be applied in all working forest lands, then targets on public (Crown) lands should be adjusted to provide for more extensive older age classes, particularly old growth.

The proposed targets derived from regions with larger, more frequent disturbances under estimate the proportion of older and mature classes, which should predominate in the forests of NS. These targets exacerbate the problem accruing from inappropriately large proportions of NS being classified as 'frequent' NDR. If the indicator targets have been tempered to achieve political acceptability (a potentially realistic scenario, given that they are likely more stringent than current practices), then this should be stipulated. In such a case, however, best practice would advise that ecologically-based targets derived from ‘natural’ disturbance regimes be calculated for comparison, so that decision makers and the public are aware of the trade off.

Buffers and Wildlife Patches

Watercourse and bog buffers of 20 m are inadequate and not based in ecosystem science. Buffers of such narrow widths may in some cases serve to reduce erosion into streams, but that is only one function. Leaving trees in narrow strips in clearcut situations is likely to result in blow down. At a minimum, they should be wide enough to retain a buffer function after anticipated blow down and other edge effects accrue (e.g., 100 m). Beyond this minimal buffer function, buffers should also provide habitat and connectivity for riparian species. Ideally, they should be wide enough to encompass half the home-range size for the riparian species with the largest area requirement. Further, riparian corridors represent good opportunities to provide habitat connectivity for other, non-riparian, volant species in the area. To accommodate a range of species, the corridors should be wide enough to encompass higher elevation area as to function as habitat for non-riparian species. DNRs patch and buffer guidelines are far too limited to provide for functions other than seed trees and stream bank erosion/sedimentation control. Patch and buffer retentions are too few, small, dispersed, and isolated to provide habitat functions for most species of wildlife. Harvesting should be done in a spatial pattern that retains well-connected, large patches of suitable habitat for a wide suite of forest species, sufficient to maintain viable populations and movements pathways over time. Current wildlife guidelines around patches and buffers do not achieve this.

Figures

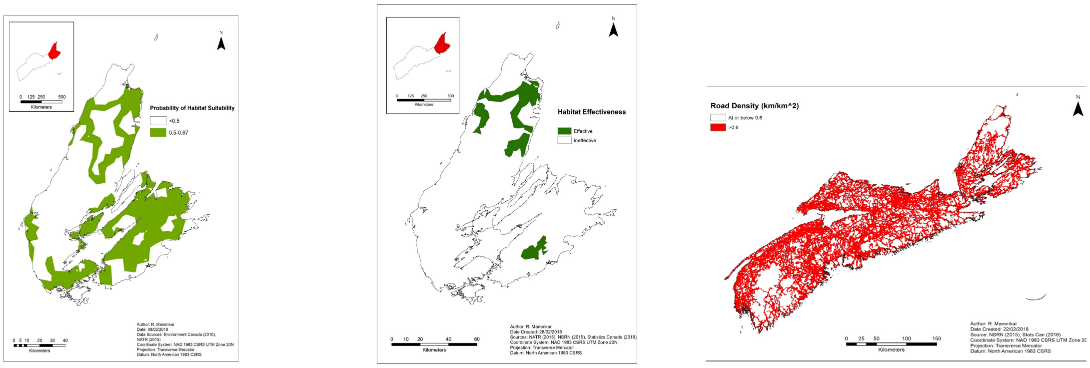

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Figure 1. Habitat suitability for lynx (a); habitat effectiveness for lynx (b); and road density (c) (Manerikar unpublished; Manerikar and Beazley, in prep.)

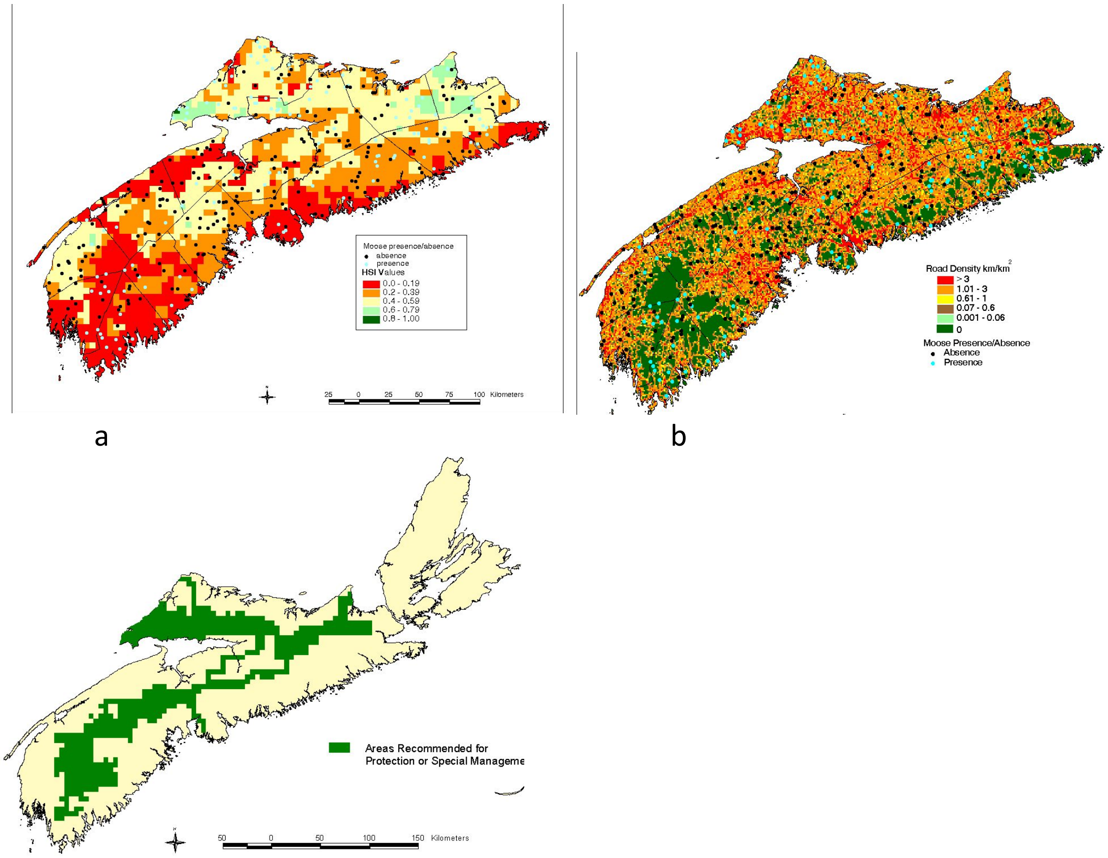

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Figure 2. Habitat suitability for moose (no significant correlation with moose pellet presence/absence) (a); road density classes (significant positive correlation with moose pellet and road density classes <0.6 km/km^2) (b); minimum critical area to recover short-term viable population of moose, delineated on the basis of highest habitat suitability and lowest road density (c) (Snaith et al 2004; Beazley et al. 2005).

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