

Combining near infrared spectra of feces and geostatistics to generate forage nutritional quality maps across landscapes

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Abstract. An important asset for the management of wild ungulates is recognizing the spatial distribution of forage quality across heterogeneous landscapes. To do so typically requires knowledge of which plant species are eaten, in what abundance they are eaten, and what their nutritional quality might be. Acquiring such data, however, may be difficult and time consuming. Here, we are proposing a rapid and cost-effective forage quality monitoring tool that combines near infrared (NIR) spectra of fecal samples and easily obtained data on plant community composition. Our approach rests on the premise that NIR spectra of fecal samples collected within low population density enclosures reflect the optimal forage quality of a given landscape. Forage quality can thus be based on the Mahalanobis distance of fecal spectral scans across the landscape relative to fecal spectral scans inside enclosures (referred to as DISTEX). The G_i^* spatial autocorrelation statistic can then be applied among neighboring DISTEX values to detect and map “hot spots” and “cold spots” of nutritional quality over the landscape. We tested our approach in a heterogeneous boreal landscape on Anticosti Island (Québec, Canada), where white-tailed deer (*Odocoileus virginianus*) populations over the landscape have ranged from 20 to 50 individuals/km² for at least 80 years, resulting in a loss of most palatable and nutritious plant species. Our results suggest that hot spots of forage quality occur when old-growth balsam fir stands comprise >39.8% of 300 ha neighborhoods, whereas cold spots occur in lags (i.e., transition zones from forest to peatland). In terms of ground-level indicator plant species, the presence of Canada bunchberry (*Cornus canadensis*) was highly correlated with hot spots, whereas tamarack (*Larix laricina*) was highly correlated with cold spots. Mean DISTEX values were positively and significantly correlated with the neutral detergent fiber and acid detergent lignin contents of feces. While our approach would need more independent field trials before it is fully validated, its low cost and ease of execution should make it a valuable tool for advancing both the basic and applied ecology of large herbivores.

Key words: forage nutritional quality; free-ranging ungulates; landscape ecology; mapping tool; near infrared spectroscopy; wildlife management.

INTRODUCTION

Successful wildlife management is contingent upon the ability to predict spatial patterns of habitat quality based on biotic and abiotic landscape features. To this end, habitat suitability indices (Brooks 1997, Roloff and Kernohan 1999) and resource selection functions (Manly et al. 2002, Hebblewhite and Merrill 2008) have been used to identify areas of conservation interest where large herbivore populations feed, aggregate or reproduce. These tools use relevant habitat data to explain changes in population densities (e.g., McLoughlin et al. 2010) or the fitness of individuals across the landscape (e.g., Fortin et al. 2008). Some of these studies suggested that the abundance of quality forage is an

important factor guiding habitat selection (Maklakov et al. 2008, Godvik et al. 2009, Samelius et al. 2013). Forage quality may vary over time, however, due to browsing, disturbance, or natural succession (Coley 1987, Hawkes and Sullivan 2001, Myrsetrud et al. 2001, Persson et al. 2007). There is, therefore, a need to develop rapid and cost-effective monitoring tools to describe changing patterns in forage nutritional quality across landscapes (Searle et al. 2007, DeGabriel et al. 2014).

The nutritional quality of forage is intrinsically linked to its chemical attributes in relation to nutritional needs of herbivores and the physiology of their digestive systems. For example, past studies on captive animals suggested a negative effect of plant secondary metabolites such as tannins and other phenolic compounds, and a positive effect of essential macronutrients such as nitrogen (N) and digestible energy on diet selection, digestibility, and reproduction (e.g., Dearing et al. 2005, McArt et al. 2009, Estell 2010). In the case of wild

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PLATE 1. High deer density on Anticosti Island is even more noticeable in open habitats, as in this seaside meadow near the Baie-Sainte-Claire area. Photo credit: Louis-Philippe Lavoie.

herbivores that feed across heterogeneous landscapes, the types and concentrations of nutrients and secondary metabolites may vary within and between multiple plant species (Moore et al. 2010, DeGabriel et al. 2014). Hence, spatial patterns of forage quality for wild herbivores may be hard to deduce from a few chemical traits measured on a few conspicuous forage types.

One approach, which has long been used to study forage quality and diet choice by wild herbivores, has been to collect and analyze fecal samples (e.g., Johnson 1994, Wam and Hjeljord 2010). Collecting fecal samples does not bias herbivore behavior as field observations of feeding animals may do. Furthermore, fecal abundances can provide information about population densities, while fecal chemical properties may reveal information about diet selection and diet quality. Codron et al. (2007) have shown a significant negative relationship between fecal lignin and the amount of highly digestible grasses in diets of many species of wild ungulates. Likewise, Jean et al. (2014) showed a positive correlation between fecal lignin and the amount of lignaceous forage in the diet of white-tailed deer. Similarly, several studies have shown total fecal fiber content to be negatively related to forage energy yields for wild herbivores (Brown et al. 1995, Hodgman et al. 1996). On the other hand, some fecal chemical properties are more difficult to interpret because of the confounding factors driving forage quality and digestive metabolism. For example, fecal N may be a good indicator of dietary N (Leslie and Starkey 1985), but not when a diet is rich in tannins that precipitate protein in the gut (i.e., leading to an overestimation of dietary N; Hobbs 1987). An

alternative option to fecal chemical analyses has been to identify consumed plant species using microhistological analyses (Dearden et al. 1975), plant wax alkane markers (Bugalho et al. 2004) or plant DNA bar-coding (Valentini et al. 2009a). These methods, however, are imprecise at estimating the proportion of each plant species in the original diet (Bugalho et al. 2002, Valentini et al. 2009b) and the information they provide is difficult to translate into indices of nutritional quality (DeGabriel et al. 2014).

In summary, patterns in forage nutritional quality across landscapes are difficult to describe based on current methodological approaches. Even remote-sensing methods developed to estimate spatial patterns of foliar protein and polyphenols (e.g., Skidmore et al. 2010) are relatively impractical in landscapes where forage is mainly found underneath tree canopies. For this reason, we are proposing a new approach that combines near infrared (NIR) spectra of fecal samples, geostatistical tools and easily obtained data on plant community composition to generate forage nutritional quality maps across heterogeneous landscapes. Ours is a holistic approach that explores the entire chemical signature of fecal samples using near infrared spectroscopy (NIRS), rather than focusing on specific compounds or plant fragments.

MATERIALS AND METHODS

Geography and history of the study area

Anticosti Island (7943 km²) is located in the Gulf of St. Lawrence, Canada (49°28' N, 63°00' W). It is part of

the eastern balsam-fir–white-birch bioclimatic zone (Grondin et al. 2007). The sub-boreal maritime climate results in cool summers (mean July temperature of 16°C) and cold winters (mean January temperature of –11°C), while the average annual precipitation is 917 mm (Environment Canada 2006) of which about one-third falls as snow.

About 200 white-tailed deer were introduced on the island in 1896 and the population increased rapidly in the absence of natural predators. Accordingly, the average white-tailed deer density over different sectors of the island has ranged from 20 to >50 individuals/km² for the past 80 years (see Plate 1; Gingras et al. 1993, Potvin 2000). Such elevated densities have stimulated economic activity on the island via tourism and game hunting (Potvin 2000). However, elevated white-tailed deer densities have also resulted in the over-browsing and loss of palatable summer plant species such as mountain maple (*Acer spicatum* Lam.), beaked hazel (*Corylus cornuta* Marsh.) and Canadian yew (*Taxus canadensis* Marsh.) (Potvin et al. 2003), and in the spread of browse-tolerant grasses such as Canada bluejoint (*Calamagrostis canadensis* (Michx.) (Dufresne et al. 2009). Balsam fir (*Abies balsamea* (L.) Mill.) currently is the preferred winter forage (Lefort et al. 2007), but the recruitment of balsam fir seedlings in the understory is substantially diminishing due to over-browsing. On the other hand, the recruitment of less palatable and less nutritious white spruce (*Picea glauca* (Moench) Voss) seedlings has been increasing (Hidding et al. 2013). Given these ongoing changes in habitat quality, the sustainability of elevated white-tailed deer populations on Anticosti Island may be compromised in coming years (Potvin et al. 2004).

Collection and spectral analysis of fecal samples

We established an 84-km² sampling grid in an area of Anticosti Island with a diverse landscape dominated by old-growth balsam fir stands in the south, peatlands in the center, and white and black spruce (*Picea mariana* (Mill.) BSP) stands in the north (Fig. 1a). This sector was also in proximity of two deer exclosures (680 and 560 ha) that had been erected in 2001 and 2003. In each exclosure, 70% of the area had been clearcut and 30% kept as old-growth forest the year prior to erecting a 12-foot-high (3.6 m) fence and culling the deer population inside the exclosures. At the time of sampling, white-tailed deer populations within the exclosures were estimated at 2–8 individuals/km² (Laprise 2014). The herbaceous vegetation and deciduous shrubs and saplings were strikingly more abundant within than outside the exclosures (Bachand et al. 2014; Fig. 2) and comprised an abundance of plant species with high nutritional quality such as fireweed (*Chamerion angustifolium* (L.) Holub.) (Dostaler et al. 2011). Consequently, the deer within these exclosures were in better physical condition than those living outside the exclosures (Giroux et al. 2014). Sampling locations ($N = 77$)

within the sampling grid were spaced 800 m apart, which corresponds to approximately the average diameter of the summer home range of females (~42 ha) on Anticosti Island (Massé and Côté 2009). Since females generally have smaller home ranges than males (Nelson and Mech 1984), we considered an 800-m spacing as the largest allowable sampling step to minimize our sampling effort without compromising the reliability of the data (Fortin and Dale 2005).

In the first two weeks of August 2011, we collected two to four fresh fecal samples within a 100 m diameter on each of the sampling locations ($N = 236$ outside exclosures; $N = 49$ within exclosures). We then identified the dominant ground layer vegetation within a 5 m radius around each fecal sample. In all, 10 ground-layer plant species or genera were identified outside the exclosures. These included thistle (*Cirsium* spp.), fireweed, sedges (*Carex* spp.), tufted vetch (*Vicia cracca* L.), Canada bunchberry (*Cornus canadensis* L.), clovers (*Trifolium* spp.), blue flag (*Iris versicolor* L.), graminoids, ferns, and mosses. We also identified seedlings of tamarack (*Larix laricina* (Du Roi) K. Koch), black spruce, white spruce, and ericaceous shrubs. Fecal samples were immediately frozen at –20°C, transported to the Soil Ecology Laboratory (Université de Sherbrooke) where they were freeze-dried, ground with a mortar and pestle, and passed through a 2-mm mesh sieve. Each fecal sample was scanned with an Antaris II Fourier Transform-NIR spectroscope (Thermo-Fisher Scientific, Waltham, Massachusetts, USA), which measures the absorbance of 1557 wavelengths at 0.4–2.5 nm intervals in the near infrared spectral region (1000–2500 nm). The spectroscope was supported by Omnic acquisition and processing software (Thermo-Fisher Scientific). Each sample was scanned 32 times from different angles, using the Antaris II Sample Cup Spinner, and the 32 spectra were subsequently averaged to cope with potential sample heterogeneity.

Sorting fecal samples by discriminant analysis

We first performed a principal-component-based discriminant analysis, using the TQ analyst software (Thermo-Fisher Scientific), to discriminate between the NIR spectra of feces from white-tailed deer foraging inside vs. outside the exclosures. The raw spectral data were transformed into first order derivative functions to remove baseline and spectral noise (Rinnan et al. 2009). The software algorithm subsequently converged on two regions of the spectra (1453–1726 nm and 1913–2288 nm) that were used in our discriminant analysis. The first 15 principal components, which explained 98% of the total spectral variation, were then used to calculate the Mahalanobis distance of each fecal sample to the centroid of fecal samples collected within vs. outside the exclosures. Mahalanobis distances controlled for multiple correlations within the spectral data sets and reduced dispersion-related classification errors that are frequently encountered with multivariate classification tech-

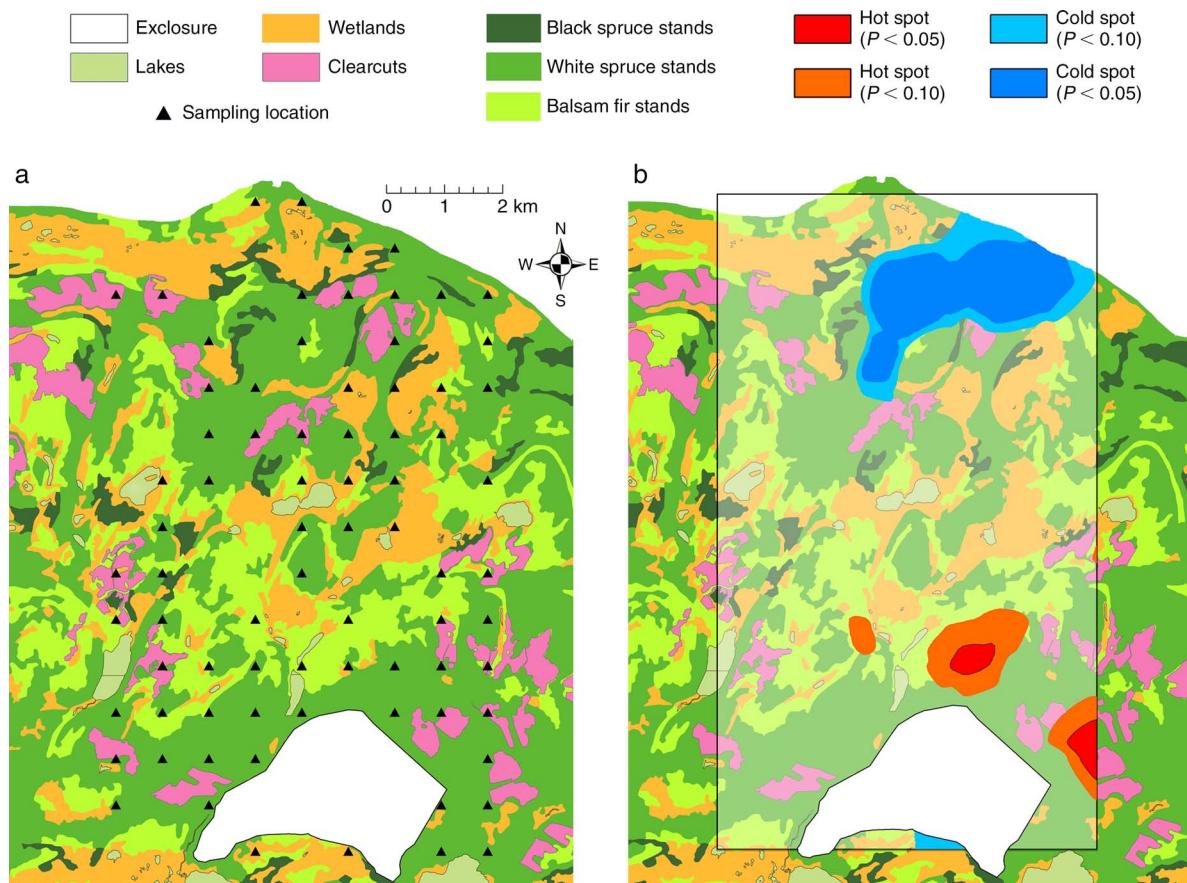


FIG. 1. (a) Map of the study area showing the various land cover classes obtained from the mapping geodatabase of the Quebec Ministry of Natural Resources and Wildlife (MRNFQ 2010) as well as each sampling location. (b) Map of our study area showing the occurrence of cold spots (low nutritional quality, in blue) and hot spots (high nutritional quality, in red) of forage nutritional quality, as determined by G_i^* analysis.



FIG. 2. Photo showing differences in vegetation within (right) and outside (left) an enclosure. The photo was taken 10 years after erecting the 12-foot fence. Photo credit: S. de Bellefeuille.

niques (De Maesschalck et al. 2000). Our discriminant model thus classified each fecal sample according to its shortest Mahalanobis distance to one or the other centroid. To verify the robustness of our discriminant model, we used 143 samples as a calibration data set and the other 142 samples as a validation data set. All validation samples were successfully classified into the correct class (i.e., inside vs. outside enclosures).

Mapping habitat nutritional quality

Our approach to describe the nutritional quality of the landscape rests on the premise that NIR spectra of fecal samples collected within enclosures reflect the optimal forage quality on Anticosti Island. Thus, nutritional quality of fecal samples collected outside the enclosures was based on the Mahalanobis distance of their NIR spectral scans to the centroid of spectral scans of samples collected within enclosures (i.e., computed using the output of the discriminant model previously described). For the sake of brevity, this distance is hereafter referred to as DISTEX.

We tested for local spatial autocorrelation among neighboring DISTEX values using the G_i^* statistic (Getis and Ord 1992) as implemented in ArcGIS software version 10.1 (ESRI 2013). The G_i^* statistic, expressed as a Z score, can detect “hot spots” (i.e., high nutritional quality) and “cold spots” (i.e., low nutritional quality) over the landscape by measuring the degree of clustering of neighboring samples based on their similarity to the mean of the global sample set (Nelson and Boots 2008). Thus, G_i^* values were calculated using a ~ 300 -ha “buffer” (i.e., neighborhood with a circular radius of 977 m) around each sampling point. This radius was selected because we considered it unlikely that a deer would process a food passage cycle in an area larger than 300 ha, based on reported home range sizes (Nelson and Mech 1984, Massé and Côté 2009) and gut passage rates (Mautz and Petrides 1971) for white-tailed deer. G_i^* values deviating from 0 by ± 1.65 and ± 1.96 respectively, corresponded to 90% and 95% confidence levels. To visualize the data, the calculated G_i^* values were mapped using a kriging procedure implemented in ArcGIS software version 10.1 (ESRI 2013).

Fecal chemical properties

We randomly selected 92 of the 285 fecal samples to characterize chemical properties related to diet quality. We estimated the neutral detergent fiber (NDF) and acid detergent lignin (ADL) concentrations by sequential extractions (Goering and Van Soest 1970) using an Ankom FiberAnalyzer 200 (Ankom Technology, Macedon, New York, USA). Total N was measured by high-temperature combustion followed by thermo-conductometric detection, using a Vario-Macro CN Analyzer (Elementar Analysensysteme, Hanau, Germany). From these data, we used the TQAnalyst software (Thermo-Fisher Scientific) to perform partial least-squares regres-

sions for estimating NDF, ADL, and total N from the NIR spectra of these 92 fecal samples. The robustness of these models was evaluated by using 68 samples for calibration and 24 samples for validation. Calibrations were robust for NDF ($R^2 = 0.94$, root mean square error of prediction [RMSEP] = 3.2), for ADL ($R^2 = 0.91$, RMSEP = 1.7) and for total N ($R^2 = 0.91$, RMSEP = 0.18). According to Williams (2001), this goodness-of-fit was suitable for predicting chemical properties of the remaining 193 fecal samples.

Inferring habitat attributes responsible for nutritional quality

To infer habitat attributes responsible for nutritional quality, we correlated G_i^* to the percent cover of clearcuts, peatlands, balsam fir stands, white spruce stands, and black spruce stands within the 300-ha buffer around each sampling location. These land cover classes were obtained using the mapping geodatabase of the Quebec Ministry of Natural Resources and Wildlife (MRNFQ 2010). We used univariate regression tree analysis (R party package, ctree function; Hothorn et al. 2006) to develop a conditional inference tree model with land cover classes as explanatory variables and G_i^* as the response variable. The most parsimonious conditional inference tree was set to identify habitat attributes responsible for hot spots ($G_i^* < -1.65$) and cold spots ($G_i^* > 1.65$).

As an extension of the mapping exercise, we attempted to identify indicator plant species and indicator fecal chemical properties of hot and cold spots. To do this, we used two-tailed Student t tests to compare the distribution of the G_i^* statistic and the distribution of each fecal chemical property in the presence or absence of individual plant species within the 300-ha buffers. We also applied type II regression models to test the relationships between DISTEX and fecal chemical properties, as the latter were random explanatory variables (Legendre and Legendre 2012). The slope of the relationship was estimated using the ranged major axis (RMA) method. The regression coefficients for these models were determined by permutation.

RESULTS

Significant hot spots of nutritional quality were found in the southeast sector of the study area, whereas cold spots were found in the northern sector (Fig. 1b). Conditional inference tree analysis showed that hot spots occurred where old-growth balsam fir stands comprised more than 39.8% of the land cover (Fig. 3). On the other hand, cold spots occurred in areas with more than 5.4% black spruce stands and less than 11.8% old-growth balsam fir stands. It should be noted, however, that black spruce cover was no more than 11% in any of the 300 ha neighborhoods (see *Discussion*). Other types of land cover classes did not significantly explain the occurrence of hot or cold spots.

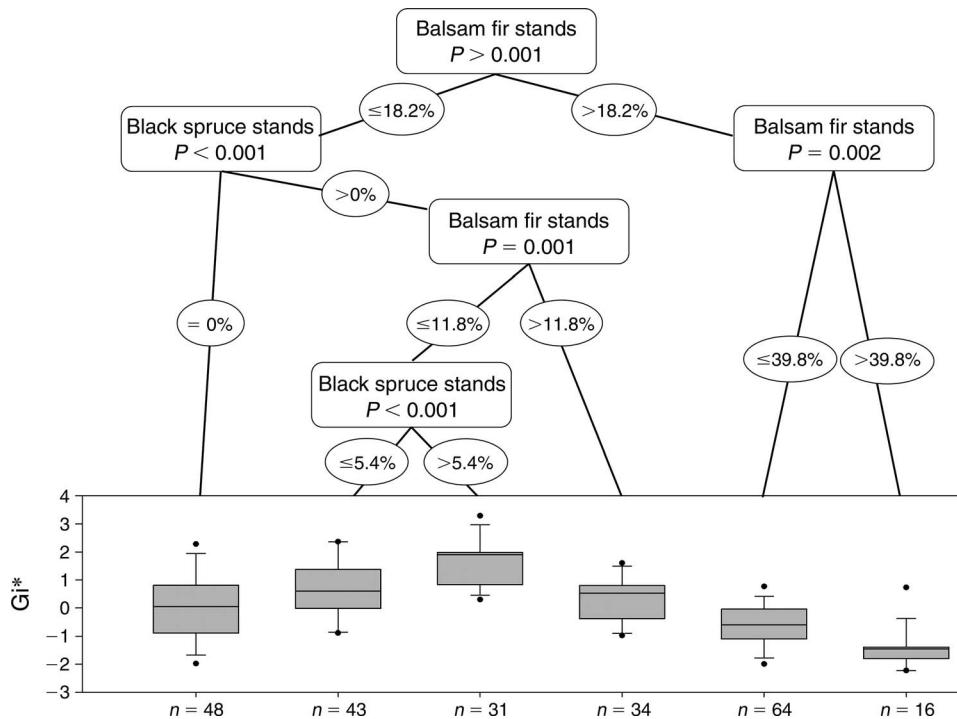


FIG. 3. Results of regression tree analysis using the G_i^* statistic as the response variable, with percent cover (in ovals) of different habitat types in 300 ha surrounding each fecal sample collected as the explanatory variable. The middle line represents the median value, the upper and lower bounds of the box represent the first and third quartiles, respectively. The lower bound of the whiskers extends to the first quartile (1.5IQR [interquartile range]) and the higher bound extends to the third quartile. Any value larger or smaller than the limits of the whiskers is considered an outlier (dots). The number of fecal samples is enumerated by n .

Forage quality was significantly higher (i.e., significantly lower G_i^* values, $t = -12.5$, $df = 234$, $P < 0.01$) in the presence of Canada bunchberry (Fig. 4a). In contrast, forage quality was significantly lower (i.e., significantly higher G_i^* values; $t = 8.8$, $df = 234$, $P < 0.01$) in the presence of tamarack (Fig. 4b). Fecal ADL was significantly lower ($t = -12.5$, $df = 234$, $P < 0.01$) in the presence of Canada bunchberry (Fig. 4c), and significantly higher ($t = 8.8$, $df = 234$, $P < 0.01$) in the presence of tamarack (Fig. 4d).

The mean DISTEX value of all 300-ha neighborhoods correlated significantly and positively with fecal ADL ($R^2 = 0.25$, $y = 0.028x + 0.94$, $P = 0.01$; Fig. 5) and with fecal NDF ($R^2 = 0.15$, $y = 0.017x + 0.69$, $P = 0.01$; not shown), but not with fecal N ($R^2 = 0.01$, $P > 0.05$).

DISCUSSION

In a recent review of the methods and concepts required for studying the nutritional ecology of wild herbivores, DeGabriel et al. (2014) pointed out the importance of knowing which plant species are eaten, in what abundance they are eaten, and what their nutritional quality might be. The same authors go on to explain why these objectives are difficult to achieve using conventional methods. The approach that we are proposing departs from convention in that NIR spectra of fecal samples allow us to circumvent the collection of

data on feeding habits and plant chemistry to describe the nutritional quality of landscapes. The robustness of NIR spectral analysis lies in its ability to detect similar multidimensional signals in fecal samples derived from different forages. In other words, small DISTEX values (i.e., statistically significant hot spots) are not necessarily indicative of diets comprising the same plant species as those consumed by white-tailed deer living within enclosures. Rather, the passage of food through the gut acts as a filter defining the complex chemical attributes of non-assimilated material, endogenous losses, and microbial tissues found in feces, from which NIR spectral analysis is able to detect levels of similarity between samples. One may argue that our designated cold spots simply reflect large differences in forage chemistry from the enclosures, regardless of nutritional quality. There is, therefore, a need to validate our underlying assumption that DISTEX is indeed correlated with forage quality. To do so would require that we relate DISTEX to the physical condition of each individual that produced each fecal sample, which is clearly not realistic. However, the fact that DISTEX was related positively to NDF, and even more so to ADL, is strong evidence of its ability to locate hot and cold spots of nutritional quality across the sampled landscape.

As revealed by the conditional inference tree, statistically significant hot spots of nutritional quality over

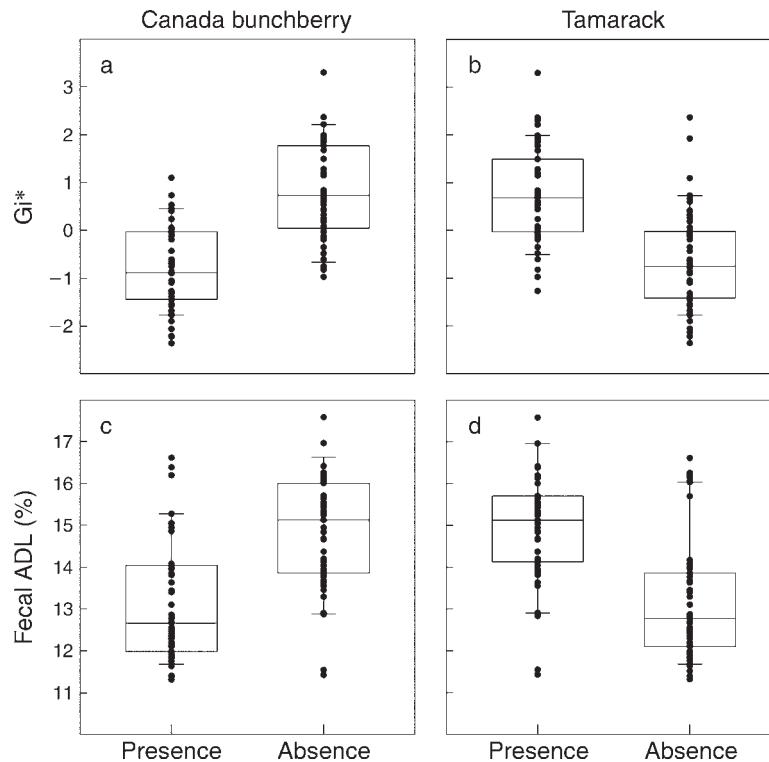


FIG. 4. Boxplots showing the distribution of (a, b) Gi^* or (c, d) fecal acid detergent lignin (ADL) when Canada bunchberry or tamarack were available within a 300-ha neighborhood surrounding each fecal sample. Gi^* values deviating from 0 by ± 1.65 correspond to cold spots and hot spots, respectively. Boxplot components are as in Fig. 3, black dots are data points.

the sampled landscape were associated with balsam fir stands located in the southern sector of the study area. One may argue that the vegetation found in these hot spots was not spatially independent from the vegetation found in the nearby enclosure. To demonstrate that this was not the case, we performed a similar analysis using feces from only one enclosure at a time as the reference sample set from which to compute DISTEX (see the Appendix). In both cases, we found a similar spatial pattern of hot and cold spots, in spite of the fact that the second enclosure lies 10 km west of the study area and differs in terms of its plant community composition compared to the first enclosure (MRNFQ 2010). Furthermore, the vegetation within any enclosure on Anticosti Island is unequivocally different from the vegetation outside enclosures, even at close proximity (Fig. 2). Thus, our results call for an ecological explanation as to why areas with a preponderance of mature balsam fir stands represent a higher nutritional value over the sampled landscape. For one, these stands are at least 90 years of age (MRNFQ 2010), corresponding to an old-growth senescent stage in balsam fir stand development (Burns and Honkala 1990). Balsam fir stands of this age class are particularly prone to windthrow (Ruel 2000), which creates patches of ground-level vegetation not seen in the younger (~ 40 years) stands of our study area. The particularly strong correlation of hotspots with Canada bunchberry, one of

the few herbaceous plants still available to deer on Anticosti Island, corroborates this point. This perennial forb can tolerate a wide range of light regimes, and its rhizomatous propagation is particularly responsive to canopy openings (Hall and Sibley 1976). Previous studies have also shown that the nutritional quality of Canada bunchberry increases with the age of the forest.

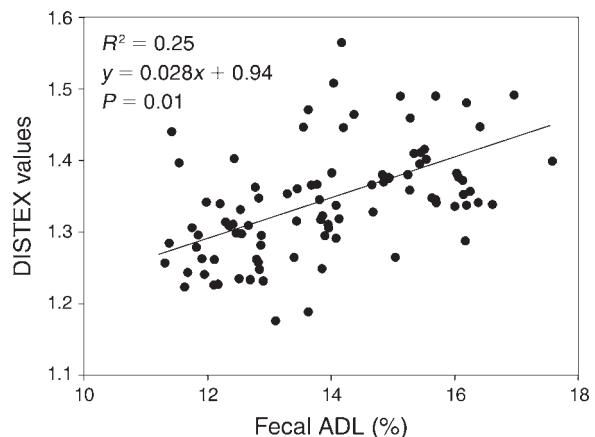


FIG. 5. Relationship between fecal acid detergent lignin (ADL) and the mean DISTEX values (the Mahalanobis distance of fecal spectral scans across the landscape relative to fecal spectral scans inside enclosures) of 300-ha buffers surrounding each collected fecal sample.

For example, Van Horne et al. (1988) assessed leaf chemistry of this species as a function of the seral stage of hemlock–spruce forests in Alaska. They found significantly higher concentrations of N and K, significantly lower concentrations of polyphenolics, and significantly lower astringency of Canada bunchberry leaves collected in 80–450-year-old stands than in regenerating stands of 5–11 years of age. They attributed this observation to lower light availability, which could decrease plant investments in herbivore defense (Bryant et al. 1983).

Our conditional inference tree also revealed statistically significant cold spots of nutritional quality in areas associated with black spruce stands located in the northern sector of the study area. The designation of “black spruce stand” is in fact an aberration arising from the legend presented in the MRNFQ’s forest cover map, as these areas had less than 11% black spruce cover. These areas would better be classified as lags, that is transition zones from forest to peatland. Lags on Anticosti Island consist of open woodlands dominated by graminoids, sedges, ericaceous shrubs, and stunted coniferous trees such as black spruce and tamarack. The significant correlation between cold spots and tamarack corroborates this point, as this species is almost exclusively found in lags on Anticosti Island (Grondin et al. 2007). Plant species occurring in these lags are richer in lignin and fibers compared to forbs such as Canada bunchberry (Oldemeyer et al. 1977), or richer in tannins and other phenolic compounds (Joanisse et al. 2009). Massé and Côté (2009) reported that lags on Anticosti Island provide more forage biomass and are more frequently browsed by white-tailed deer during the snow-free season compared to other habitats. Our results thus suggest that high population densities drive wild ungulates to feed where forage is abundant (Coulombe et al. 2011) rather than where forage is of the highest quality.

The approach that we are proposing for mapping the nutritional quality of landscapes may significantly improve landscape and wildlife management, if certain challenges can be met. The first challenge, and the most important one, is to provide further validation of hot spots and cold spots as comprising areas of contrasting forage quality. The best direct evidence would be body size and fitness of wild ungulates feeding exclusively in different habitat types. Obviously, this is difficult to achieve with free-ranging, furtive animals that are in constant movement over the landscape. On the other hand, our approach is original and alleviates the need to perform extensive vegetation surveys and chemical analyses. It is a rapid and cost-effective approach that is relevant and useful to wildlife management where the landscape is rapidly changing and needs to be continuously monitored. Coupled with other data, our approach could provide valuable information on the ecology of large herbivores. For example, combining nutritional quality maps with spatial patterns of fecal

abundance would allow us to determine the relationship between habitat nutritional quality and feeding patterns. Alternatively, fecal samples could be analyzed for steroids to determine gender (Barja et al. 2008), which would then allow us to explore how males and females react to changes in available forage. Correlating a wider hormonal profile of feces with DISTEX values would also allow us to explore relationships between forage nutritional quality and physiological stress. In fact, NIRS predictive models could themselves be calibrated to assess gender (Tolleson et al. 2005) or hormonal content (Santos et al. 2014) without the need for lengthy laboratory analyses. In summary, the approach that we are proposing is innovative and relevant to both the basic and applied ecology of large herbivores.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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