A rapid method for landscape assessment of carbon storage and ecosystem function in moss and lichen ground layers

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Abstract. Mat-forming "ground layers" of mosses and lichens often have functional impacts disproportionate to their biomass, and are responsible for sequestering one-third of the world's terrestrial carbon as they regulate water tables, cool soils and inhibit microbial decomposition. Without reliable assessment tools, the potential effects of climate and land use changes on these functions remain unclear; therefore, we implemented a novel "Ground Layer Indicator" method as part of the U.S.D.A. Forest Inventory and Analysis (FIA) program. Non-destructive depth and cover measurements were used to estimate biomass, carbon and nitrogen content for nine moss and lichen functional groups among eight contrasted habitat types in Pacific Northwest and subarctic U.S.A. ($N = 81$ sites). Ground layer cover, volume, standing biomass, carbon content and functional group richness were greater in boreal forest and tundra habitats of Alaska compared to Oregon forest and steppe. Biomass of up to 22769 $\pm$ 2707 kg ha^{-1} (mean $\pm$ SE) in upland *Picea mariana* forests was nearly double other reports, likely because our method included viable, non-photosynthetic tissues. Functional group richness, which did not directly correspond with biomass, was greatest in lowland *Picea mariana* forests (7.1 $\pm$ 0.4 functional groups per site). Bootstrap resampling revealed that thirty-two microplots per site were adequate for meeting data quality objectives. Here we present a non-destructive, repeatable and efficient method (sampling time: ca. 60 min per site) for gauging ground layer functions and evaluating responses to ecosystem changes. High biomass and functional distinctiveness in Alaskan ground layers highlight the need for increased attention to currently under-sampled boreal and arctic regions, which are projected to be among the most active responders to climate change.

Keywords. Biomass, boreal forests, bryophyte and lichen ecology, carbon sequestration and cycling, climate change, ecosystem functions, Forest Inventory and Analysis program, land-use change, soil nutrient cycles.

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Terrestrial mosses and lichens are influential drivers of global biogeochemistry (Cornelissen et al. 2007; Elbert et al. 2012; Turetsky 2003) and are ubiquitous, integral components of landscapes across North America, from dry deserts and temperate forests to arctic tundra (DeLucia et al. 2003; Ponzetti & McCune 2001; Turetsky et al. 2010). Virtually all ecosystems have a "ground layer" component, defined here as the living and dead organic layer on the surface of the earth that is composed primarily of lichens and bryophytes, but excluding vascular plants. Despite their proportionally small stature, terrestrial mosses and lichens in ground layers often contribute substantial biomass to landscapes—exceeding, for example, 1075 kg ha^{-1} in old-growth *Pseudotsuga menziesii* forests of the U.S. Pacific Northwest (Binkley & Graham 1981) and 2240 kg ha^{-1} in *Picea mariana* (black spruce) woodlands of interior Alaska (Ruess et al. 2003). As mosses and lichens grow and die, they accumulate

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organic material in soils, often developing thick, decomposition-resistant peat horizons in cold, oligotrophic locations. Although moss-dominated peatlands cover only 3% of the world's land area, they store nearly 33% of all global terrestrial carbon (~540 billion t C), an amount that is nearly twice the amount of all atmospheric carbon (Turetsky 2003; Yu 2012; Yu et al. 2011). In high-latitude areas, the potential loss of peat-forming, permafrost-insulating mosses (in particular, the genus *Sphagnum*) would mobilize large amounts of C into the atmosphere in a positive-feedback cycle of climate change (McGuire et al. 2009; Schuur et al. 2009; Koven et al. 2011).

Among the many ecological roles and human uses of ground layer organisms (**Table 1**) are their influences on global nutrient cycles. In arctic and subarctic areas, they promote C sequestration by lowering soil temperatures, insulating permafrost (Gornall et al. 2007), slowing decomposition, reducing water drainage and acidifying upper organic layers (van Breeman 1995). Moisture retained by *Sphagnum* peat-mosses decreases wildfire severity, which curbs soil organic C losses during burning (Shetler et al. 2008). Nitrogen (N) budgets in many ecosystems are also enhanced by ground-dwelling lichen genera (e.g., *Peltigera*) and moss genera (e.g., *Pleurozium*, *Hylocomium*) that harbor N-fixing cyanobacterial symbionts (DeLuca et al. 2002). Lichens and mosses (including epiphytes) represent ~30% of the world's eukaryotic biological N-fixation, depending on region (Elbert et al. 2012), and are a nearly exclusive source of biological N-fixation in nutrient-limited systems (Lange et al. 2001). Ground layers also influence cycling of soil phosphorus and other important macronutrients (Chapin et al. 1987; Lang et al. 2009). Especially in low-fertility, oligotrophic soils, ground layers substantially change nutrient availability and ecosystem productivity.

Uncertainty regarding future climate makes it difficult to project trends in productivity and species distributions among North American landscapes. Changing climates can either decrease or increase ground layer productivity (Chapin et al. 2010; Walker et al. 2006), shift species ranges (van Herk et al. 2002), and cause the gain or loss of major functional groups. Climate-induced ecotype conversions can also occur as warmer, drier climates promote shrub expansion into boreal tundra that excludes wildlife forage lichens (Cornelissen et al. 2001; Heggberget et al. 2002), while in wetlands, lowered water tables coupled with severe wildfires can eliminate *Sphagnum* peat-mosses and peat deposits (Turetsky et al. 2011). Because high-latitude ground layers retard permafrost melt by their soil-insulating and waterlogging properties (Turetsky et al. 2012), large-scale losses of these layers would not only eliminate a large global C sink, but would also create a potential source of labile C as thawed soil organic matter decomposes and releases atmospheric C (Neff & Hooper 2002). Broad uncertainty among possible outcomes highlights the need to monitor ground layers for the sake of understanding ecosystem functioning and global C budgets.

Forest inventory programs in the United States have long sought reliable procedures for quantifying terrestrial C and nutrient cycling at landscape scales (Woodall et al. 2012). The USDA Forest Service's Forest Inventory and Analysis (FIA) program employs standardized sampling methods across a nationwide grid system to provide a systematic inventory of forest attributes and to detect trends in forest health and processes through time (Bechtold & Patterson 2005). Yet, existing FIA sampling protocols (i.e., Soils and Vegetation protocols) do not adequately capture ground layers even where they are primary understory components. Although moss and lichen mats cover more than half of all forestlands in coastal Alaska (~3.2 million ha; USDA 2014), much of interior Alaska remains sparsely sampled. This is of particular concern because arctic and subarctic regions are projected to be among the most active responders to ongoing global climate change (Chapin et al. 2010).

Our purpose was to establish a rapid, non-destructive method for estimating the biomass, C and N content of terrestrial moss and lichen ground layers, which would simultaneously allow us to estimate the landscape-level effects of important functional groups in ground layers. Nine functional groups (**Table 2**) included those that fix N (i.e., N-fixers), are used by wildlife (i.e., forage lichens), or have significant influence on soil hydrology and nutrient cycles (i.e., *Sphagnum* peat-moss). Our method was based on the premise that simple, non-destructive measurements of the depth and area covered by different functional groups (Rosso et al. 2014) can be scaled into landscape-level estimates of biomass and elemental content based on prior calibrations. We sought a method that was simple and practical for field crews, took $\leq$ 1.5 h field time

Table 1. Ecosystem roles and economic uses of terrestrial mosses and lichens in selected habitat types, from the literature. "Terrestrial" substrates include soil, woody debris, rocks, other mosses and other lichens, but exclude trees, branches, or un-decomposed woody material with bark.

	Boreal peatlands	Boreal forest	Temperate rainforest	Semi-arid steppe and woodland	Alpine tundra
Ecosystem processes and services					
Carbon storage	Turetsky 2003, Yu et al. 2011, Elbert et al. 2012	Elbert et al. 2012, Benscoter & Vitt 2007	Elbert et al. 2012, Binkley & Graham 1981, DeLucia et al. 2003	Elbert et al. 2012, Evans & Lange 2001	Elbert et al. 2012
Nutrient capital and processing	Vitt 2000	Chapin et al. 1987, Oechel & Cleve 1986, Weber & Cleve 1984	Binkley & Graham 1981	—	Shaver & Chapin 1991
Nitrogen fixation	Turetsky 2003, Elbert et al. 2012	Turetsky 2003, Elbert et al. 2012	Turetsky 2003, Binkley & Graham 1981, DeLuca et al. 2002	Elbert et al. 2012, Evans & Lange 2001, Belnap 2001	Elbert et al. 2012
Hydrobuffering	Holden 2005	—	Pypker 2005, Pypker 2006	Belnap 2006	—
Freshwater storage	Holden 2005, Holden et al. 2006	—	—	—	Prowse et el. 2006
Soil stabilization	—	—	—	Belnap 2001, Hardman & McCune 2010	—
Wildlife forage (lichens)	Dunford et al. 2006	Dunford et al. 2006	Varner & Dearing 2013	—	Heggberget et al. 2002, Holleman et al. 1979
Other vertebrate uses (nesting)	—	—	Naslund et al. 1995, Hamer & Nelson 1995	—	—
Invertebrate use (habitat, food)	—	—	Gerson 1973	—	—
Bioindication					
Indicator of air quality	Vile et al. 1999	Poikolainen et al. 2004, Harmens et al. 2008, Wilkie & Farge 2011	—	—	Wilkie & Farge 2011
Indicator of coarse woody debris	—	Söderström 1989, Andersson & Hytteborn 1991	Rambo & Muir 1998	—	—
Indicator of soil surface disturbance	—	Rai et al. 2012	—	Hardman & McCune 2010, Belnap & Eldridge 2001	—
Indicator of climate change	Gignac 2001	Gignac 2001	—	—	—
Economic uses					
Moss and peat harvesting	Bain et al. 2011	—	Muir et al. 2006	—	—
Cranberry production	Johnston et al. 2008	—	—	—	—

for one worker to complete, required no sample collection or processing, had short training times (0.5 to 1 day) for workers with no previous experience, and generated accurate estimates of biomass, C and N. Additionally, the method must be adaptable to all forest and range habitats of North America, including (but not limited to) boreal forests, continental montane forests, alpine tundra, interior shrub-steppe and grasslands. Here we report results of a project that implemented the method across a spectrum of habitat types to provide preliminary baseline estimates for biomass, C and N content, and functional group diversity in the U.S. Pacific Northwest and subarctic Alaska.

Methods

Field methods: calibration set. All field sampling occurred in July and August of 2012 and 2013 at 81

Table 2. Nine functional groups used with the Ground Layer Indicator method for landscape assessment of ecosystem functioning. Each of the mutually exclusive groups integrates growth forms, potential indicator status and functional effects on ecosystems. Abbreviations apply to **Figs. 3 & 4**.

Abbreviation	Functional group	Definition	Ecosystem functions	Example taxa
SphMoss	*Sphagnum* peat mosses	Ecosystem-engineering mosses of genus *Sphagnum*	Carbon storage (peat), water regulation, soil cooling	*Sphagnum* spp.
NfixMoss	N-fixing feather mosses	Feather mosses that fix biological N	N-fixation, soil cooling	*Pleurozium* and *Hylocomium*
FthrMoss	Feather mosses	Other feather mosses, not known to fix N	Rainfall interception, soil cooling	*Kindbergia, Drepanocladus, Thuidium*
TurfMoss	Turf mosses	Mosses with upright or cushion-like growth	Soil accrual, bare site colonization	*Bryum, Mnium, Polytrichum*
Livwrt	Liverworts, hornworts	Non-moss bryophytes	Soil/detritus binding, water infiltration	*Anthelia, Cephaloziella, Marchantia, Anthoceros*
ForagLich	Forage lichens	Fruticose macrolichens important for wildlife	Wildlife forage	Branched-*Cladonia, Bryocaulon, Bryoria, Cetraria, Masonhalea*
NfixLich	N-fixing lichens	Macrolichens with N-fixing symbionts	N-fixation	*Peltigera, Nephroma, Solorina, Lobaria, Sticta, Stereocaulon*
OtherLich	Other lichens	Lichens that are not crusts, forage, or N-fixing	Invertebrate habitat, bare site colonization	Unbranched-*Cladonia, Hypogymnia, Parmelia, Physcia*
CrustLich	Biotic soil crust	Crustose/squamulose lichens, cyanobacteria	Soil trapping, water influx, disturbance indicator	*Placidium, Psora, Collema, Nostoc*

sites throughout Alaska and Oregon among 8 habitat types representing forests, treeless steppe and treeless tundra of differing vegetation compositions and climates (**Fig. 1**). All data are available in **Supplementary Table S1**. We targeted ground layer mosses and lichens that represented each of 9 functional groups (**Table 2**), and harvested 150 samples for biomass, C and N measurements. For this calibration set, we selected only monotypic, single-species clumps of moss or lichen that filled at least 75% of a 20 × 20-cm square aluminum frame, used a soil knife to cut and remove a monolithic sample from surrounding vegetation, and recorded the area covered and depth of each sample to the nearest 1 cm before transport to the lab in breathable paper bags. Depth was recorded to the bottom of the layer at which lichen or bryophyte parts were no longer visually distinguishable, and so sometimes included both "green" and "brown" materials. We avoided sharp distinctions between "live" and "dead" tissues because brown tissues originating from >30 cm deep may remain metabolically viable and able to produce new growth (Clymo & Duckett 1986). Any adherent soil particles, vascular vegetation and all roots > 1 mm diameter were manually removed in the field, and samples were thoroughly inspected again after transport to the lab. In the lab we oven-dried each sample at 55°C for a minimum of 24 h (or until no additional mass loss was observed), measured the mass of each sample to the nearest 0.01 g (Fisher model 610 mass balance), and ground each sample to a fine powder before determining organic C and total N content (Leco TruSpec analyzer, St. Joseph, MI, USA). Preliminary analyses (not reported) showed no significant difference in mass, bulk density or elemental content between separated "green" and "brown" components, so we considered them jointly in all subsequent analyses. The final calibration set was used in regressions for landscape-scale estimation using an implementation set.

Field methods: implementation set. We sampled bryophyte and lichen ground layers at the same sites described above ($N = 81$; **Fig. 1**). We restricted sampling to moss/lichen functional groups (**Table 2**) growing over terrestrial substrates only including other mosses, rock, soil or downed wood, but excluding rocks >20 cm in any one dimension, and also excluding persistent epiphytes on downed branches or any wood that possessed bark. At each site, we established one circular, 0.38-ha plot based on the FIA Lichen Communities Indicator protocol (Will-Wolf 2010). At each plot center, we recorded site attributes (longitude, latitude, elevation, slope and aspect) with a GPS device and a clinometer. From each plot center, we established three, 40-m transects with a tape measure along compass bearings (azimuths) of 0°, 120° and 240°. Each tape measure was allowed to deviate no more than ± 1 m from the true azimuth if there were trees or other major obstructions; tape measures were also permitted to undulate

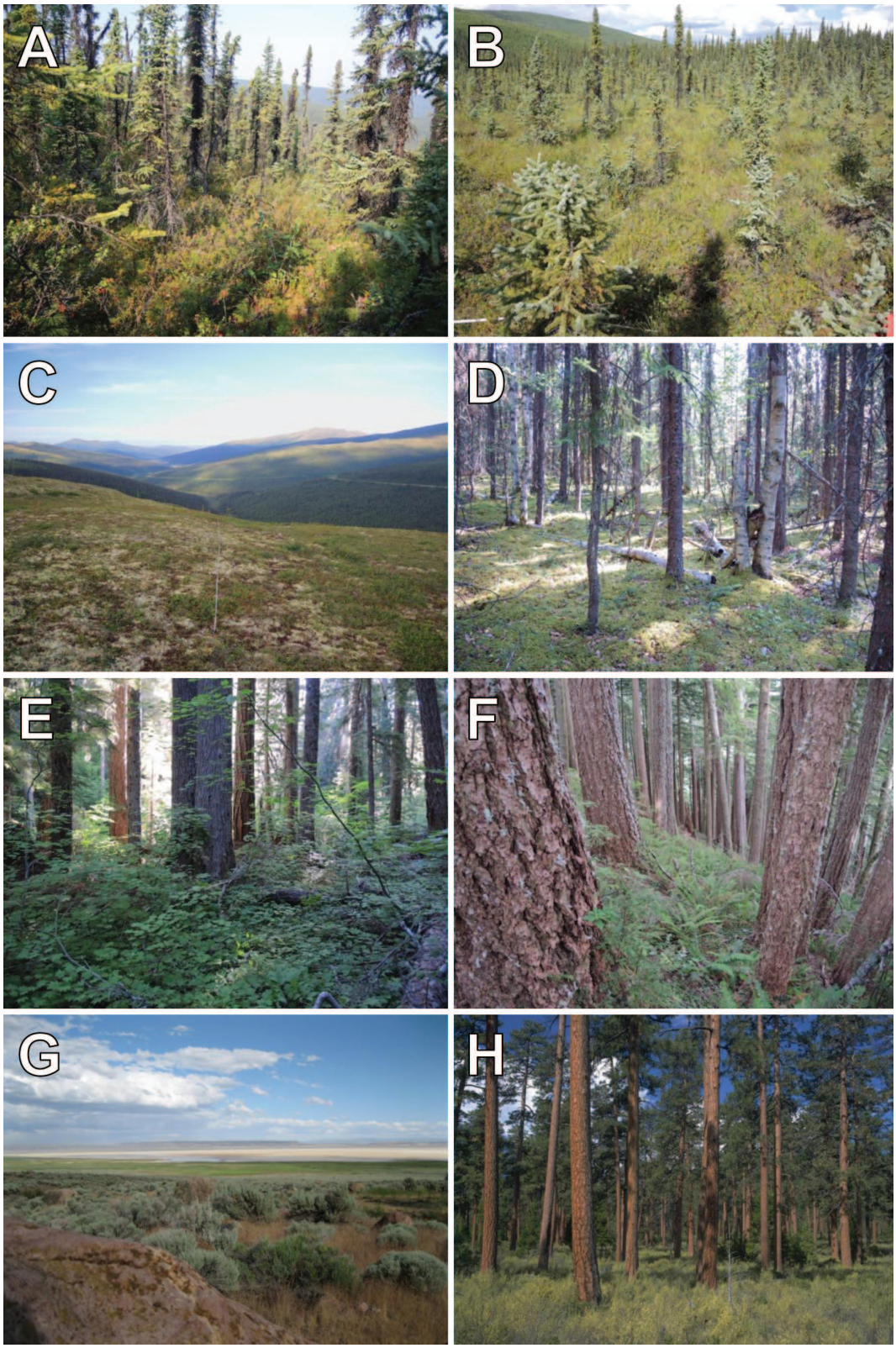

Figure 1. Eight habitat types in which ground layers were sampled. The Alaska habitats: **A.** Upland black spruce forest. **B.** Lowland black spruce woodland. **C.** Alpine tundra. **D.** Mixed hardwood-conifer forest. The Oregon habitats: **E.** Montane conifer forest. **F.** Coastal conifer forest. **G.** Shrub-steppe. **H.** Dry ponderosa pine forest.

vertically across hills or other gross topographic features, but we avoided sharp dips into tussock-hollows, animal burrows or other minor features.

We placed 33 microplots at 4-m intervals along each 40-m transect beginning at the plot center (11 microplots for each of the three transects); microplots were 20 × 50-cm quadrats with the long side parallel to transects on the left side of the tape measure (facing away from plot center). If placement was obstructed by a tree, cliffs, or excessively thick brush stems, we re-positioned each frame at the nearest available point within 1 m. Frames were placed flat on the ground surface, but could encompass internal complications due to, for example, bunchgrass tufts or hummock-hollow formations.

We visually estimated cover and depth (thickness) for each functional group encountered in the microplots. For cover estimates, we visually estimated the vertically projected areal cover of each functional group in the microplot using the cover classes of Peet et al. (1998): 0 = 0%, 1 = 0–0.1% (trace), 2 = 0.1–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95% and 10 ≥ 95%. Groups could overlap vertically, so total cover in microplots could exceed 100%. For depth estimates, we recorded the depth (to the nearest 1 cm) of each functional group within the microplot by inserting a graduated steel measuring rod (7 mm diameter, 23 cm length, marked at 1-cm intervals, with a narrowly pointed tip) through the ground layer until meeting firm resistance of underlying soil layers, or until the bottom of the layer at which lichen or bryophyte parts were no longer visually distinguishable, (including both "green" and "brown" materials). We included in one measurement all living and dead material for which identifiable parts/organs were visually distinguishable, and included any litter or fine roots (< 1 mm) that happened to be trapped within the ground layer, but we excluded any overlying litter, any humified (unrecognizable) plant matter, peat, organic soil, mineral soil, litter or other decomposed matter that may have formed beneath ground layers. In microplots with high variability in mat depth for a functional group, we obtained a representative depth by recording the most frequent (mode) value from five test probes in a microplot. For mats deeper than the graduated rod, we used a soil knife for pushing aside upper material to visually inspect deeper layers. In no case was the ground layer >50 cm, though permafrost occasionally truncated our measurements. Although implementation of the method never requires sample collection after the calibration stage, we collected at least one voucher for every species (Oregon State University herbarium, OSC). Functional groups were assigned to each species according to **Supplementary Table S1**.

Analysis: calibration set. Calibration curves of bulk density (mass per unit volume) were the basis for constructing landscape-level estimates of biomass and elemental content. We established calibration curves for bulk density of the 150 calibration samples through a two-stage process: first, we used nonparametric multiplicative regression (NPMR; McCune 2006) as an exploratory model-selection tool for determining significant predictors of bulk density; and second, we parameterized a separate nonlinear regression based on the best NPMR model. Bulk density was calculated as the oven-dry mass of each sample divided by the product of the depth and cover. Rosso et al. (2014) previously demonstrated that accurate mass estimates must include both depth and cover, rather than either measure alone.

For the NPMR stage, we regressed bulk density on an optimized subset of predictor variables, including areal cover (cm^2), depth (cm), habitat type, functional group (**Table 2**), and organism type (moss vs. lichen). NPMR uses smoothing functions to describe variation in the bulk density response as a function of all possible interactions among the predictors. Model fit was measured with a leave-one-out cross-validated R^2 (xR^2), which is the same as the traditional R^2 statistic, except that it is penalized by cross-validation, such that the regression error better approximates the true prediction error. In our implementation, we used a local linear model with the default parsimony criteria settings (overfitting control setting = "medium", minimum average neighborhood size = 7.5, improvement criterion = 5%, and minimum data:predictor ratio = 10) in the NPMR software HyperNiche (version 2.25; McCune & Mefford 2011a).

After deciding on a negative exponential model form, we then fit a parametric nonlinear model with maximum-likelihood parameter estimation (*nls* function in R version 3.0.1; http://www.R-project.org). This was the calibration curve. Annotated scripts for this and subsequent analyses are available in **Supplementary Table S2**.

Analysis: implementation set. We used the parametric calibration curve to estimate bulk density based on the depth of ground layers in each of 33 microplots at each of the 81 implementation sites. We then multiplied each bulk density estimate by its corresponding field-measured volume (cover × depth) to obtain estimates of standing biomass, which were averaged within sites and expressed in kg ha^{-1}. Similarly, we multiplied each within-microplot biomass estimate by organic C and total N percentages to yield estimates of mean elemental content on a per-site basis. One-way ANOVA showed that N content and C:N ratios differed significantly among functional groups, so we applied separate mean values by functional group.

For functional group analyses, we determined the number of unique functional groups present within each site (functional group ''richness,'' analogous to species richness), then calculated Shannon's index (Hill 1973) based on cover of each functional group per site. Among different habitats, we compared differences in site-level functional group richness using one-way analysis-of-variance (ANOVA), and compared differences in functional group composition using permutational multivariate analysis-of-variance (PERMANOVA). PERMANOVA has no distributional assumptions and can handle non-Euclidean distance measures, which are often appropriate for species composition data (Anderson 2001; Anderson et al. 2006). We used 9999 permutations and Bray-Curtis distances (Bray & Curtis 1957) based on transformed functional group cover.

Finally, we visualized functional group compositional differences among habitat types with nonmetric multidimensional scaling ordination (NMS; Kruskal 1964) implemented in PC-ORD version 6.15 (McCune & Mefford 2011b). For this, we employed Bray-Curtis distances (based on generalized-log-transformed cover of functional groups), a random starting configuration, instability criterion = 0.000001, step length = 0.20, a maximum of 500 iterations, 100 runs using real data, and a randomization test with 300 runs of randomized data to evaluate the likelihood of the strength of the result (final stress) by chance.

Analysis: minimum sampling requirements. When vegetation is highly variable or patchy, it can be difficult to accurately estimate biomass from a fixed number of sample units. Therefore, we assessed the minimum number of microplots required to accurately represent biomass by using bootstrap resampling (simulating a large number of samples and determining summary statistics for each set of replicates). For each of the 81 implementation sites, and for a range of sample sizes from 1–33 microplots, we performed 999 bootstrap replicates (resampling the field-measured data with replacement). For each of the 1–33 ''sample sizes'' for each site, we then calculated the mean of the 999 sample means, standard deviations (SD), standard errors (SE) and relative standard errors (RSE = (SE / mean) × 100)). The RSE permits equal-footing comparisons among sites whose means may differ by orders of magnitude. Our criterion for acceptable accuracy (measurement quality objective) was the minimum number of microplots required to obtain a mean $RSE \leq 25\%$ within each habitat type.

Results

Calibration set. The best NPMR model for explaining bryophyte and lichen bulk density used ''depth'' and ''cover'' as explanatory variables ($xR^2 = 0.2118$); when the model was pruned to use ''depth'' as the sole predictor, $xR^2 = 0.1737$. For ease of interpretation, we used only ''depth'' as the predictor in the parametric nonlinear model (**Fig. 2**), which followed a negative exponential model of the form:

$$y = m + a \cdot e^{(-b \cdot x)} \quad (1)$$

where y is bulk density (g cm^{-3}), x is depth (cm), m is the asymptote, $m + a$ is the y-intercept, e is the base of the natural logarithm, and b is the decay constant describing the concavity of the curve. Maximum-likelihood estimates of the parameters were: $m = 0.0205$, $a = 0.0512$ and $b = -0.3448$. This model represents our bulk density calibration curve to be applied when estimating mass from cover and depth.

We found no significant difference among functional groups for organic C content (ANOVA $F = 1.64$, $p = 0.128$), but total N and C:N ratios differed significantly (ANOVA $F = 64.4$, $p < 0.0001$ and $F = 52.9$, $p < 0.0001$ respectively). N-fixing foliose lichens and soil crust lichens had the greatest N content (**Fig. 3**), while forage lichens and most moss groups had lower N content.

Implementation set. Based on ground layer cover, depth, and bulk density (**Fig. 2**), we estimated site-level standing biomass, C and N content according to habitat type (**Table 3**). Each of these three measures was greatest in the Alaskan habitats,

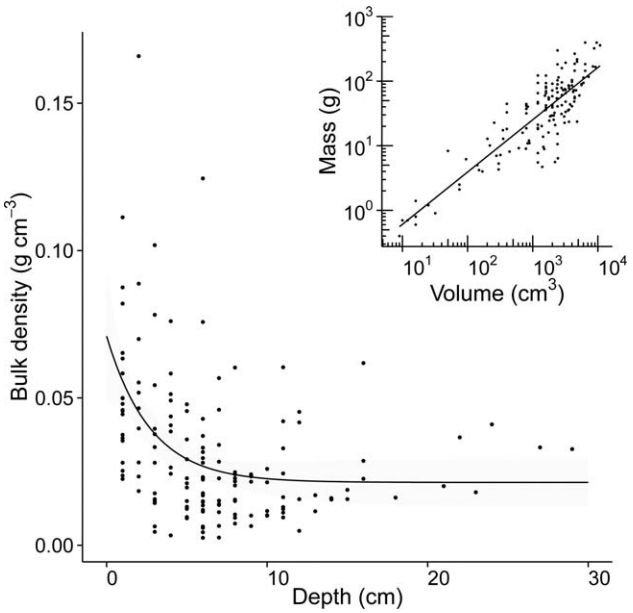

Figure 2. Mass-volume relationship (inset) and the bulk density calibration curve (main) fitted to biomass harvest data (points). Solid black line in main figure is the fitted calibration curve, bounded by 95% prediction intervals (shaded area). The calibration curve improves bulk density estimates by considering the dependence of bulk density on mat depth; bulk density estimates are later used to estimate mass from volume (the product of cover × depth).

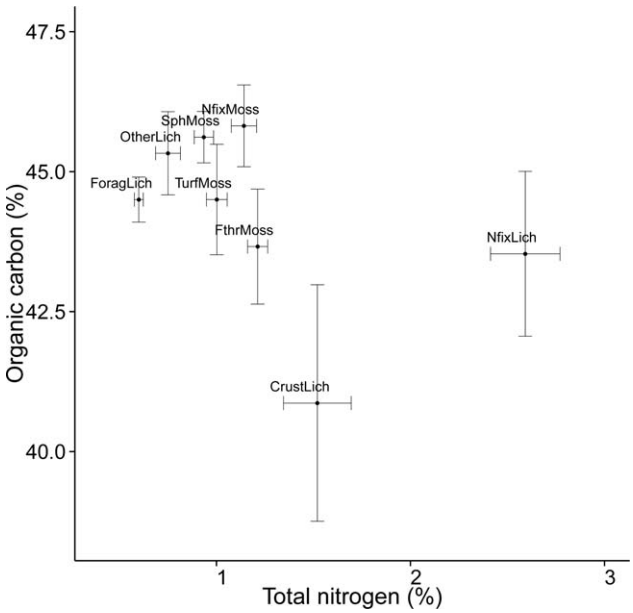

Figure 3. Means (± 1 SE) for carbon and nitrogen tissue content among functional groups. Abbreviations follow **Table 2**. Liverworts and hornworts generally occur in trace amounts and were not included in elemental content analysis.

particularly in moist sites such as upland black spruce habitats, which had a mean ± SE biomass of 22769 ± 2707 kg ha^{-1}, mostly due to mosses (22513 ± 2726 kg ha^{-1}). Upland sites, which frequently had very high coverage of N-fixing feather mosses, also had correspondingly high C content (7969 ± 1152 kg C ha^{-1}) and N content (194 ± 28 kg N ha^{-1}). Biomass in upland habitats represented nearly 200% of that for lowland black spruce habitats, 400% of mixed conifer-hardwood forests, 600% of alpine tundra, and nearly 2000% of Oregon coastal forest habitats (**Table 3**). Coastal forest habitats in Oregon had an estimated 835 ± 308 kg ha^{-1} biomass, which is roughly 160% that of montane conifer forests, 260% of dry ponderosa pine forests, and 140% of shrub-steppe habitats (**Table 3**). In general, mosses contributed more to ground layer biomass than lichens, though lichens often had substantial contributions. For example, lichens contributed ~25% of all ground layer biomass in Alaskan alpine tundra (lichens: 1139 ± 369 kg ha^{-1}), and were ~10% of all ground layer biomass in Oregon shrub-steppe habitats (lichens: 66 ± 30 kg ha^{-1}; **Table 3**).

Functional group richness in Alaska was nearly double that of Oregon habitats, mainly because key groups (like forage lichens and *Sphagnum* mosses) common in Alaska were scarce or absent in Oregon. In Alaska, the greatest functional group richness was found in lowland black spruce sites (7.1 ± 0.4 functional groups per site, mean ± SE) and alpine tundra (6.9 ± 0.3 functional groups). In Oregon, functional group richness was greatest in montane habitats (4.2 ± 0.4 functional groups), followed by shrub-steppe and dry pine forests (3.7 ± 0.2 functional groups for each). Shannon's index exhibited similar patterns (**Table 3**).

The selected NMS solution, depicting functional group compositions for each site, was a 2-dimensional configuration reached in 48 iterations, with a final stress value = 13.2 (**Fig. 4**). From the NMS randomization test, the proportion of randomized runs with stress less than or equal to the stress observed in the final configuration (i.e., the *p*-value) was 0.02. Functional group compositions differed significantly among the eight habitats (PERMANOVA pseudo-F = 11.9, p = 0.0001). Certain functional groups were characteristic of specific habitat types; for example, forested habitats in Alaska were characterized by N-fixing feather mosses, N-fixing lichens, and *Sphagnum* peatmosses. In Alaskan tundra, forage and other lichens were major components. Feather mosses were dominant in Oregon's coastal and montane forests.

Table 3. Summary statistics of ground layers among habitats in Alaska and Oregon (mean ± 1 *SE*). The Ground Layer Indicator provided information on biomass, carbon and nitrogen content, and functional group diversity.

Habitat	State	*N*	Biomass: moss+lichen (kg ha^{-1})	Biomass: moss only (kg ha^{-1})	Biomass: lichen only (kg ha^{-1})	Carbon content (kg ha^{-1})	Nitrogen content (kg ha^{-1})	Sampling time (min site^{-1})	Cover (cm^2 1000cm^{-2})	Depth (cm)	Functional group richness (site^{-1})	Functional group Shannon's index
Upland	AK	9	22769 ± 2707	22513 ± 2726	256 ± 77	7969 ± 1152	194 ± 28	47 ± 3	353 ± 14	15.9 ± 0.4	5.8 ± 0.3	1.75
Lowland	AK	10	10093 ± 2383	9798 ± 2359	295 ± 94	3258 ± 889	79 ± 22	59 ± 5	141 ± 7	10.5 ± 0.4	7.1 ± 0.4	1.94
Mixed	AK	11	6334 ± 1487	6260 ± 1474	74 ± 31	2252 ± 519	58 ± 14	46 ± 4	195 ± 12	6.3 ± 0.3	5.4 ± 0.6	1.60
Alpine	AK	9	4126 ± 819	2986 ± 864	1139 ± 369	1019 ± 217	22 ± 6	76 ± 13	113 ± 6	5.0 ± 0.2	6.9 ± 0.3	1.93
Coastal	OR	7	835 ± 308	826 ± 309	9 ± 5	340 ± 135	9 ± 4	96 ± 8	107 ± 11	1.0 ± 0.1	3.1 ± 0.4	1.04
Montane	OR	7	525 ± 238	512 ± 232	14 ± 6	182 ± 85	5 ± 2	95 ± 9	61 ± 8	1.0 ± 0.1	4.2 ± 0.4	1.42
Dry forest	OR	10	318 ± 116	278 ± 115	39 ± 6	44 ± 14	1 ± 0.3	36 ± 2	21 ± 3	0.9 ± 0.1	3.7 ± 0.2	1.28
Steppe	OR	6	603 ± 305	537 ± 275	66 ± 30	63 ± 24	2 ± 1	46 ± 3	21 ± 3	1.0 ± 0.1	3.7 ± 0.2	1.29
All	–	81	–	–	–	–	–	60 ± 3	144 ± 4	6.6 ± 0.1	5.8 ± 0.3	1.75

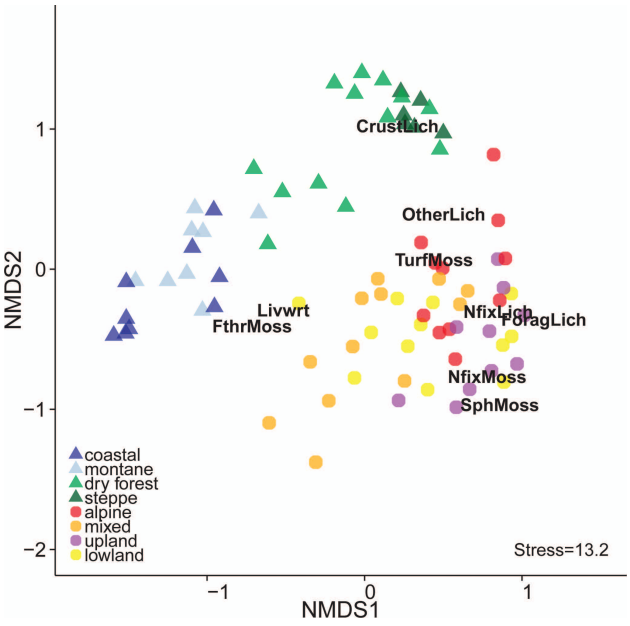

Figure 4. Nonmetric multidimensional scaling (NMS) ordination of sites (circles = Alaska, triangles = Oregon) arrayed in functional group space, based on cover abundance (generalized-log-transformed). Label position indicates weighted average position of each functional group (abbreviations in **Table 2**). Note that *Hylocomium* and *Pleurozium* have been separated from the feather moss "FthrMoss" group. Two-dimensional NMS solution, stress = 13.2. Functional group compositions differed significantly among habitat types (PERMANOVA F = 11.9, p = 0.0001).

Other groups such as turf mosses occurred more generally across the habitats we assessed (**Fig. 4**).

Minimum sampling requirements. Based on a criterion of 25% or lower relative standard error (RSE) in biomass, fewer microplots per site were required in habitats having high biomass and continuous cover (e.g., fewer than about 20 were adequate in upland black spruce habitats and most other Alaskan sites; **Fig. 5**). However, more microplots were required to achieve measurement quality objectives in habitats with very patchy or sparse cover of ground layers, such as dry forest habitats where RSE did not meet the 25% criterion even with the full complement of 32 microplots (**Fig. 5**). Sampling time across all habitats averaged 60 ± 3 min (SE). Sampling was fastest in habitats with lower cover of ground layers (**Table 3**) and slowest at sites where steep topography and dense undergrowth complicated laying out the plot.

Discussion

We developed and implemented a novel method for rapidly and non-destructively estimating bio-

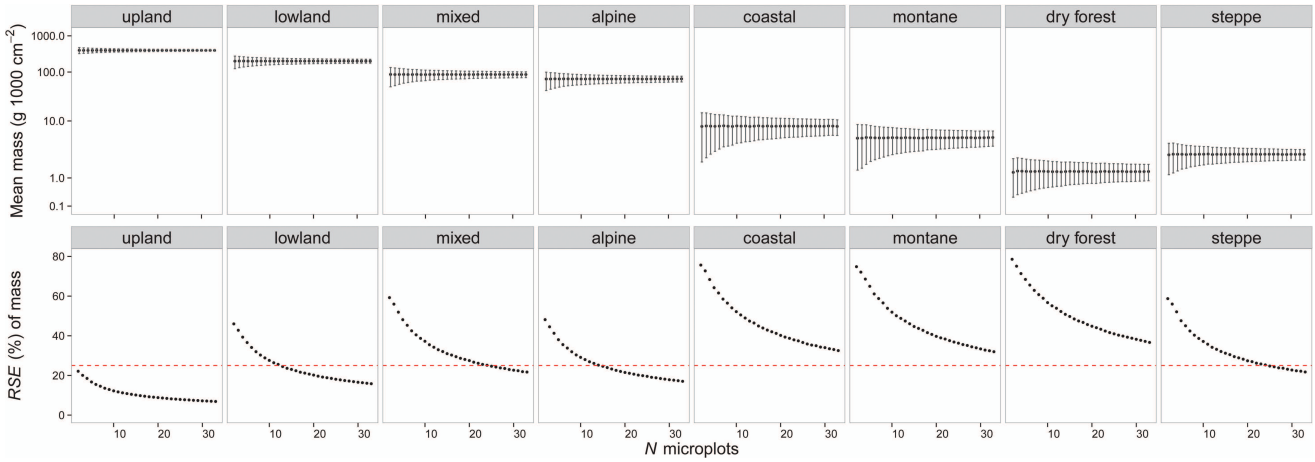

Figure 5. Results of minimum sampling requirements analysis for ground layer biomass. For each of the 81 implementation sites, and for a range of sample sizes from 1 to 33 microplots, there were 999 bootstrap replicates (resampling the field-measured data with replacement) from which summary statistics were calculated. Mean biomass per microplot (± 1 SE) varies among habitat types (upper series), as does relative standard error (RSE, lower series), where dotted line at 25% RSE indicates the measurement quality objective. Simulating larger sample sizes (adding microplots) yielded a decrease in sample SE and RSE.

mass, C and N content, and functional importance of ground layers across North American landscapes. We present this method as the "Ground Layer Indicator," an Ecological Indicator protocol for the FIA program of the USDA Forest Service, which complements existing protocols (Will-Wolf 2010) for epiphytic lichens. The Ground Layer Indicator arose from pressing needs in interior Alaska where ground layers are substantially developed and functionally diverse, but where national inventories have historically neglected them. Despite its utility for boreal and arctic applications, the Ground Layer Indicator is not constrained to any geographical region and has the flexibility to be implemented in any kind of terrestrial ecosystem. Its biggest appeals are that it is non-destructive, fast, and easy to implement, while requiring only minimal expert training.

Efficiency and accuracy. How fast and how accurate is the Ground Layer Indicator? In most situations it took an hour or less to implement, though sometimes longer when there was steep topography or very dense understory vegetation or debris. To our surprise, sampling times were not obviously associated with average biomass or functional group richness, but were rather a joint function of topography, understory vegetation complexity and crew experience as gained during a field season.

Resource practitioners will find the Ground Layer Indicator most useful when the objective is to manage ecosystems and habitats rather than individual rare species. In cases when management goals include species inventory or rare species detection, practitioners may be better off employing taxonomic experts with larger plots or guided-intuitive methods that promote species capture (McCune & Lesica 1992). We found that a sampling intensity of 32 microplots per site yielded variation in biomass within acceptable tolerances for most habitats While we do not recommend the Ground Layer Indicator for species inventories, we suggest that it is superior for situations when an understanding of ecosystem functioning is preferred. The Ground Layer Indicator is also unconstrained by the need for trained taxonomic experts (which are often in short supply), and provides an index of potential C storage, N fixation, forage availability, soil stability and site disturbance.

Ecosystem functions. Three moss genera (*Sphagnum*, *Hylocomium* and *Pleurozium*) comprise the vast majority of ground cover and ground layer biomass in boreal conifer forests (Ruess et al. 2003), which we confirmed using a functional rather than taxonomic approach. Monitoring ground layers in boreal forests will allow resource managers to understand how shifts in vegetation, disturbance and land-use (e.g., wildfire prescription, timber harvest, and groundwater withdrawal) can modify landscapes which were historically dominated by ground layers (Turetsky et al. 2012). Functional group richness was greater in boreal forest and

tundra habitats of Alaska compared to Oregon forest and steppe, probably due to a combination of climate effects, moist, oligotrophic soil conditions, and reduced productivity of otherwise competitive vascular plants.

In contrast to forested areas, we observed that ground layers in non-forested habitats (e.g., alpine tundra) were dominated by wildlife forage lichens, soil crust lichens and N-fixing lichen groups that were scarce elsewhere, reinforcing the functional distinctiveness of those sites. One interesting finding was relatively low C content among soil crust lichens (**Fig. 3**), which could be due to adherent inorganic material retained by appressed crustose growth forms that would overstate biomass and underestimate the proportion of organic C. Compositional differences between forested and non-forested areas imply that a full accounting of ground layer ecosystem functioning should not be restricted to forested landcover types, but should also include other habitats where mosses and lichens are the principal determinants of soil fertility, soil stability and other ecosystem functions (Elbert et al. 2012).

Biomass and carbon. Initial estimates of biomass, C and N using the Ground Layer Indicator were considerably greater than those reported in the literature for similar sites. For example, our total biomass estimates were 148% of those previously estimated for alpine tundra (Shaver & Chapin 1991), 369% for coastal conifer forest (Yarie 1980), 606% for lowland black spruce sites (Ruess et al. 2003), and 236% for upland coniferous sites (Auclair & Rencz 1982). We offer two possible explanations for these discrepancies. The first is that we preferentially avoided sites that exhibited signs of recent disturbance. Our estimates would be revised downward if we were to include sites where biomass had been recently removed. Nationwide FIA implementation of the Ground Layer Indicator would not be hindered by this bias because the systematic FIA sampling grid integrates all disturbance situations (Bechtold & Patterson 2005).

The second and perhaps more important reason for discrepancies with literature values is the result of different biomass harvest methods among studies. Most other workers clipped only photosynthetically active ''green'' tissues, while our method included any ''green'' or ''brown'' materials that possessed visually distinguishable moss and lichen parts. More specifically within the framework of peatland classification (*sensu* Rydin & Jeglum 2013), our Ground Layer Indicator includes ''fibric'' and ''mesic'' organic materials, while avoiding decomposed ''humic'' material. Ground layer organisms (peat-mosses in particular) exhibit indeterminate growth and accumulate organic matter continuously, which means that vertical layers are a graduated continuum of living and dead tissues that does not always possess distinct stratigraphic boundaries. ''Brown'' tissues that have been buried in peatlands for decades at depths $>$ 30 cm can retain the ability to generate new vegetative growth (Clymo & Duckett 1986), and constitute enormous C pools, therefore we caution against neglecting these tissues in models of biomass and ecosystem C.

Needs and development. In addition to fibric and mesic organic matter, future versions of the Ground Layer Indicator should somehow account for humic (decomposed) layers, especially in *Sphagnum*-dominated wetlands, if terrestrial organic C is to be accurately estimated. Ignoring or undersampling organic layers has led previous workers to underestimate soil organic C by as much as 68% (Ping et al. 2010). Although humic layer depth is not easy to measure in areas that may be waterlogged or frozen in permafrost, we suggest that the Ground Layer Indicator could be readily adapted to include humic layers when paired with soil coring techniques. Because manual probing (with a tile rod) is prone to error where organic layers are intermixed with debris or frozen strata (permafrost), using a lightweight, powered drill rig (e.g., Nørnberg et al. 2004) might be feasible. Current national FIA protocols for soil sampling allow drilling but never exceed 20 cm deep, regardless of soil condition. Because peatlands by definition possess at least 30 cm of organic matter (Rydin & Jeglum 2013), FIA at present does not account for these important C components, though optional ''enhanced'' FIA protocols would permit sampling to 30 cm in some localities. Especially in northern latitudes where peatlands comprise the bulk of North America's C storage (Yu et al. 2011), small adaptations to the current Ground Layer Indicator will make it a key tool for nationwide carbon accounting when integrated into the platform of FIA inventory and monitoring.

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Supplementary documents online:

Supplementary Table S1. Comprehensive dataset, including calibration and implementation sets, site descriptors, and species list with functional group assignments.

Supplementary Table S2. Annotated computer scripts (R format).