

Arctic-alpine vegetation biomass is driven by fine scale abiotic heterogeneity

Susanne Suvanto^{1,2,3}, Peter C. le Roux^{1,4}, Miska Luoto¹

¹ Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland

² Department of Geoinformatics and Cartography, Finnish Geodetic Institute, Kirkkonummi, Finland

³ Vantaa Research Unit, Finnish Forest Research Institute, P.O. Box 18, 01301 Vantaa, Finland

⁴ Department of Plant Science, University of Pretoria, 0028, Pretoria, South Africa

Suvanto, S., le Roux, P.C., Luoto, M., 20xx. Arctic-alpine vegetation biomass is driven by fine scale abiotic heterogeneity. *Geografiska Annaler, Series A: Physical Geography*, 96, 549–560. doi:10.1111/geoa.12050

ABSTRACT. During recent decades large changes in vegetation biomass have been observed in arctic and alpine areas. While these temporal trends have been clearly linked to changing climatic conditions, the drivers of local spatial variation in biomass are still relatively poorly understood. Thus, we examine the effects of abiotic conditions (as measured by ten variables representing topography, soil properties and geomorphological processes) on variation in aboveground vascular plant biomass to understand the determinants of contemporary fine scale heterogeneity in this variable. We also compare the results from one destructive biomass estimation method (clip-harvesting) to three non-destructive biomass estimates: vegetation cover, height and volume. To investigate the local drivers of biomass we analysed an extensive data set of 960 1 m² cells in arctic–alpine tundra using spatially-explicit generalized estimation equations to conduct variation partitioning. The abiotic environment had a clear impact on the fine scale distribution of biomass (variance explained 32.89 % with full model for sampled biomass). Soil properties (temperature, moisture, pH and calcium content) were most strongly related to aboveground biomass (independent effect in variation partitioning 7.03 % and combined effect including joined effects with topography and geomorphology 19.6 %). Topography had only a small influence after soil and geomorphology were taken into account (independent effect only 2.23 % and combined effect 18.73 %), implying that topography has only indirect effects on vegetation biomass. Of the three non-destructive biomass estimates, the results for vegetation volume were most similar to those for clip-harvested biomass samples. Thus, we recommend utilizing vegetation volume as a cost-efficient and robust non-destructive biomass estimate in arctic-alpine areas. Our results indicate that the fine

scale environmental variation has to be taken into account more carefully when modelling vegetation biomass and carbon budget, especially under changing climatic conditions.

Keywords: arctic-alpine, biomass, clip-harvesting, topography, vegetation volume

Introduction

A strong increase in vegetation biomass in arctic and alpine environments has been documented during the last decades (Sturm *et al.* 2001, Pouliot *et al.* 2009, Bhatt *et al.* 2010, Kullman 2010, Elmendorf *et al.* 2012), with the largest increases in the southernmost arctic tundra (Epstein *et al.* 2012). This is largely driven by vascular species, and is clearly associated with rising air temperatures (Elmendorf *et al.* 2012). Given the importance of increasing plant biomass at high latitudes for the global carbon budget (Callaghan *et al.* 2004, Sitch *et al.* 2007), understanding the determinants of contemporary biomass patterns is vital for improving predictions of climate change impacts on the high latitude carbon balance under warming conditions. Because local heterogeneity in abiotic conditions is pronounced in many arctic habitats (Shaver *et al.* 1996, Gould *et al.* 2003, Shaver *et al.* 2007, Fletcher *et al.* 2010), fine scale studies may be most appropriate for characterizing the importance and impacts of abiotic conditions on vegetation biomass.

While biome-scale studies have yielded important insights into vegetation and biomass patterns (e.g. Walker *et al.* 2003, Epstein *et al.* 2012, Elmendorf *et al.* 2012), detailed examination of the fine scale abiotic determinants of vegetation biomass is required due to the pronounced local heterogeneity in abiotic conditions in most arctic habitats (Fletcher *et al.* 2010). Previous studies in arctic-alpine environments have shown that local topography (Billings 1973, Fisk *et al.* 1998, Walker *et al.* 2001), soil properties (Walker *et al.* 1993, Walker *et al.* 1994, Fisk *et al.* 1998, Berdanier and Klein 2011) and earth surface processes (Jonasson 1982, Hjort and Luoto 2009, le Roux and Luoto 2014) have a strong effect on vegetation properties. Local biomass varies along a topographic gradient (Walker *et al.* 1994, Fisk *et al.* 1998) and the relationship between topography and biomass is most likely hump-shaped (Litaor *et al.* 2008), since the growing season length restricts plant growth in depressions (due to late snow melt) and harsh abiotic conditions restrict productivity on exposed ridge tops (Billings 1973, Campioli *et al.* 2009). Soil properties, especially soil moisture, have been shown to be key factors limiting plant productivity (Walker *et al.* 1994). In arctic-alpine environments the importance of soil moisture for vegetation appears to be mainly due to its effect on nutrient availability, via its impact on soil microbial activity (Fisk *et al.* 1998,

Berdanier and Klein 2011). Geomorphological processes cause physical disturbance, but may also increase soil moisture and nutrient availability, and therefore may have mixed impacts on plant biomass in arctic-alpine environments (Jonasson 1982, Virtanen *et al.* 2010).

Plant biomass is usually measured as the dry weight of a harvested biomass sample. However, this process is time consuming and destructive (Bobek and Bergström 1978, Axmanova *et al.* 2012, Redjadj *et al.* 2012), and in environments with a heterogeneous distribution of biomass, a large number of samples are required for an accurate estimation (Tsutsumi *et al.* 2007; see also Walker *et al.* 1994). A time-efficient and non-destructive alternative would therefore be useful (Chen *et al.* 2009, Axmanova *et al.* 2012, Redjadj *et al.* 2012), especially in remote high-latitude and -altitude regions. The simplest alternative measure of biomass is percentage cover of vegetation (e.g. Röttgermann *et al.* 2000, Krebs *et al.* 2003, Muukkonen *et al.* 2006), while a more accurate estimate can be achieved by using vegetation volume that takes into account both vegetation cover and height (Chen *et al.* 2009, Axmanova *et al.* 2012).

The aims of this study are (1) to investigate the effects of small scale variation in topography, soil properties and geomorphology on vascular biomass and (2) to test whether the results from three non-destructive biomass estimation techniques (vegetation cover, vegetation height and vegetation volume) differ from those of clip harvesting. Here we do this by analysing an extensive fine scale dataset from arctic-alpine tundra in north-western Finland.

Methods

Field and laboratory methods

Data were collected during summer 2011 on the northern slope of the Saana massif, north-western Finland (Fig 1). The study site was approximately 100 – 200 meters above the birch (*Betula pubescens* ssp. *czerepanovii*) treeline at c. 700 m a.s.l, and is characterized by shrubs (including *Juniperus communis* and *Betula nana*), dwarf-shrubs (*Vaccinium* spp., *Empetrum hermaphroditum*) and graminoids (*Deschampsia flexuosa*, *Carex bigelowii*). The study design consisted of six 8 x 20 m grids, comprising a total of 960 1 m² cells. The six grids were located inside the area of less than 2 ha to minimize variation in altitude, bedrock and macroclimate. For a more complete description of the study site see le Roux *et al.* (2013a).

(Insert Figure 1 here)

The biomass samples were collected in July 2011 during peak growing season. All living aboveground vascular biomass was collected from a randomly located 20 x 20 cm subplot within

each 1 m² cell. The biomass samples were dried at 65 °C for 48 hours and then weighed (Sartorius PT3100, accuracy 0.1 g). Vascular plant cover was visually estimated in each cell and median vegetation height measured (excluding graminoids due to their disproportionate height : biomass ratio). Vegetation volume was calculated as the product of plant cover and vegetation median height.

Soil moisture was determined on three occasions during mid-summer with a FieldScout TDR 300 moisture meter (FieldScout TDR 300, Spectrum Technologies, Plainfield, USA; using 7.5 cm sensor rods), recording the mean of three measurements in each cell. The correlation between the different sampling events was high ($r > 0.88$) and so the mean of all measurements was used in the analysis. Soil temperature was measured at 10 cm depth on two occasions (mid and late summer), using a digital thermometer (TFX 392 SKW-T thermometer, Ebro Electronic, Ingolstadt, Germany). From each grid 18 measurements were taken at 4 m intervals, with the resulting values interpolated for all cells with the *interp.surface* command in the *fields* package (Furrer *et al.* 2011), using R statistical software (R Development Core Team 2011).

In late summer soil samples were collected from the same locations where soil temperature was measured. These samples were air dried and subsequently analysed to determine soil pH and calcium content in the Laboratory of Geosciences and Geography (University of Helsinki) following the standardized ISO 10390 and ISO 17294-2 procedures (Nham 2010). As for soil temperature, results were interpolated to all other cells.

Local topography (i.e. mesotopography) was classified on a 10-point scale, following the methods of Bruun *et al.* (2006; see also Billings 1973, Walker *et al.* 2001, le Roux and Luoto 2014) where the lowest value (1) represents the bottom of a depression and the highest value (10) a ridge top. The end-points of this gradient both represent extreme environmental conditions. Exposed ridge positions have lower winter temperatures, higher mechanical stress (due to wind-blown ice crystals), and more variable water availability, while sheltered depressions have short snow-free periods (i.e. limited growing season length; Bruun *et al.* 2006). Slope and aspect were measured for each cell and maximum potential annual solar radiation (i.e. assuming clear sky conditions, MJ cm⁻² a⁻¹) was calculated following McCune & Keon (2002).

Geomorphological processes were recorded as the percent cover of six different geomorphologic processes – solifluction, cryoturbation, deflation, nivation, fluvial accumulation and erosion – in each cell by visually measuring the area affected by each process (following the method of Hjort and Luoto 2009). All investigations were performed by the same geomorphologist, who focused

only on ESP (earth surface process) variables, to ensure independence of the botanical and geomorphological data. The activity of cryoturbation (soil frost processes), deflation (wind-driven erosion) and solifluction (gravity-driven down-slope soil creep) were defined based on observations of topsoil material (focusing on sorting of the substrate, the absence of fine sediment, and the presence of soil lobes perpendicular to the slope, respectively). Fluvial processes were similarly quantified, paying particular attention to soil textural properties, with their contributions combined into a single variable representing water-driven soil erosion and accumulation. Nivation (processes related to long-lasting snow patches) was measured from the depth of snow cover remaining in early/mid summer, and confirmed by observations of the temporal patterns of snowmelt (le Roux and Luoto, 2014). The geomorphological processes were combined for the analysis into three groups: frost-related processes (solifluction and cryoturbation), wind-related processes (deflation and nivation), and fluvial processes (erosion and accumulation). The influence of herbivory was not considered in the present analyses for two reasons; 1) this would add considerable further complexity to this research, and 2) herbivores have previously been shown to have relatively small impacts on vegetation properties in this study design (le Roux *et al.* 2013a).

Statistical analyses

To model the relationship between biomass and topographic, soil and geomorphological variables, generalized estimating equations models (GEEs, see Carl and Kühn 2007) were used to conduct variation partitioning (Borcard *et al.* 1992). GEEs are an extension of generalized linear models that allow the spatial non-independence of observations to be incorporated into analyses, and perform better than many other techniques for spatially-referenced data (Carl and Kühn 2007, Dormann *et al.* 2007). The data were analysed assuming a Gaussian distribution of errors for biomass, vegetation height and vegetation volume, and a binomial distribution of errors for vegetation cover. Prior to analysis biomass and vegetation volume were log-transformed and vegetation height was square root-transformed. To account for the spatial structure in the data, a fixed correlation structure was used to model spatial dependency in GEEs (following Carl and Kühn 2007; method also described in Hardin and Hilbe 2003, Dormann *et al.* 2007). The fixed correlation structure used in the GEE models was parameterized from the spatial autocorrelation observed in the residuals of the corresponding GLM, by fitting a negative exponential curve to residual autocorrelation over distance lags shorter than the distance class of the first non-significant autocorrelation value (see le Roux *et al.* 2013b for details). Because preliminary analyses showed that spatial autocorrelation was negligible between the six grids, points from separate grids were considered as independent. Thus a fixed correlation structure was modelled for each grid, allowing for the decay in spatial

dependence to vary between grids. The analysis was conducted using the `gee` function from the `geepack` library (Højsgaard *et al.* 2005) in the statistical package R (R Development Core Team 2011), and was implemented using a modification of Carl and Kühn's (2007) GEE function.

Following a best subsets regression approach, all combinations of predictor variables were modelled. Both linear and second-order polynomial terms were included for each predictor variable to model potentially non-linear relationships. Initial analyses showed that multicollinearity between predictor variables within each variable group was minimal (maximum variation inflation factor = 1.9; Fox & Monette 1992), and therefore all predictors were retained for subsequent modelling. Models were ranked by the quasi-likelihood-under-the-independence-model information criterion (QIC, the GEE-equivalent of the Akaike's Information Criterion; Pan 2001), calculated using a modification of the code outlined by Kraan *et al.* (2010) (see also Burnham and Anderson 1998), with the best fit model identified as having the lowest QIC value. Models containing second-order polynomial terms were only retained if each polynomial term's linear equivalent was also present in the model.

Variation partitioning was used to quantify the unique and shared contributions of the predictor variable groups and the total explanatory power of the models (Borcard *et al.* 1992). First, the best model within each group of explanatory variables (topography, soil and geomorphology) was determined (using GEEs, as detailed above). Second, all combinations of the three best models were analysed (i.e. modelling biomass as a function of the variables selected by, e.g., the best topography model and the best soil model). Finally, the variance explained by the full model (the variables selected by the best topography model, the best soil model and the best geomorphology model) was partitioned between the three predictor variable groups; creating eight fractions: (a) unique effect of soil, (b) unique effect of topography, (c) unique effect of geomorphology; and variation due to the shared effects of (d) soil and topography, (e) soil and geomorphology, (f) topography and geomorphology and (g) all the three variable groups; and (h) the unexplained variation. The procedure for variation partitioning with three explanatory matrices has been described in detail by Anderson & Gribble (1998) and Heikkinen *et al.* (2004).

Results

The sampled grids included areas with differing conditions regarding to soil properties, topography and geomorphological activity, as well as variation in the amount of aboveground biomass (Table 1, Fig 2). Of the non-destructive biomass estimates, vegetation volume was most strongly correlated with the observed biomass (Spearman's rank correlation = 0.662, $p < 0.001$), and vegetation height

the most weakly correlated. Overall the correlations between all the biomass variables were relatively high, with the weakest correlation between vegetation cover and height (Table 2, Fig 3).

(Insert Fig 2 and 3 and Tables 1 and 2 here)

The best GEE models of biomass included all the variables except the second order terms of temperature and pH, the best vegetation volume model excluded only the second-order term for fluvial processes, while the best vegetation height model excluded slope and the second order term of solar radiation. (Table 3; selected univariate relationships shown in Fig. 4). By contrast, the best model for vascular cover included all the variables and their second-order polynomial terms (Table 3).

(Insert Table 3 and Figure 4 here)

Variation partitioning revealed that soil variables have the largest unique contribution to explain variation in biomass, while topography had the smallest independent effect (Fig. 5). This pattern was consistent for biomass, vegetation volume and cover, but differed for vegetation height (where geomorphology had the strongest independent effect and soil properties the weakest). The amount of unexplained variation was close to 50 % for vegetation volume and vegetation height, slightly lower for biomass sample and remarkably lower for vascular cover. A negative shared contribution of two variable groups (as seen in Fig. 5) indicates that strong collinearity between predictors in the different variable groups. As a result, less variation is explained when the two groups of variables are included together than is expected based on their effects in isolation (Chevan and Sutherland 1991).

(Insert Figure 5 here)

Discussion

Considerable spatial variation was observed in plant biomass, as has previously been reported for arctic and alpine areas (Fisk *et al.* 1998, Fletcher *et al.* 2010), with this fine scale heterogeneity strongly correlating with components of the abiotic environment. All three groups of abiotic predictors (soil properties, geomorphological processes, topography) contributed to explaining variation in biomass, reflecting the multivariate nature of the environmental constraints on plant productivity (in agreement with, e.g., Gould *et al.* 2003, Berdanier and Klein 2011). This pattern is likely to hold true in other areas of low biomass and similar climates in arctic and alpine environments in northern Europe (Kjelvik and Kärenlampi 1975, Jonasson 1982, Kyllönen 1988, Campioli *et al.* 2009) and North America (e.g. Walker *et al.* 1994, Fisk *et al.* 1998).

Our results indicate that fine scale variation of vegetation biomass is mainly driven by soil properties, in agreement with previous studies that have shown the influence of these abiotic characteristics (Walker *et al.* 1994, Fisk *et al.* 1998, Berdanier and Klein 2011). Soil moisture was most strongly related to biomass, with the highest biomass values at the areas of intermediate moisture (Tables 3 and S1, Fig. 4), which supports the findings in earlier studies (Litaor *et al.* 2008, Berdanier and Klein 2011). Calcium content showed similar effects on biomass as soil moisture, although the correlation was much weaker (Table S1). Soil pH and temperature were also weakly related to biomass, but showed inconsistent relationships with biomass and the three biomass surrogates. The results suggest that soil resources (e.g. moisture, energy and nutrients) are more important drivers of biomass than disturbance processes (i.e. geomorphology) or landform position and orientation (i.e. topography), highlighting their importance under changing environmental conditions (e.g. rising temperatures increasing nutrient availability; Chapin *et al.* 2005).

Geomorphological processes generally did not explain as much variation in biomass as soil properties, but were particularly important for vegetation height. Our study provides empirical evidence that geomorphological processes affect vegetation structure and biomass, with geomorphologic activity decreasing arctic-alpine plant biomass, probably through mechanical disturbance (Jonasson 1986, le Roux and Luoto 2014). The effect of geomorphology was the strongest for vegetation height which may be explained by the fact that generally taller woody plants are more sensitive to disturbance and soil instability (Jonasson 1986, Haugland and Beatty 2004, Manninen *et al.* 2011). For vegetation height the shared effects of geomorphology and topography are also strong (Fig. 4), which may be due to snow cover being linked to topography and to woody plants responding positively to increased snow cover (Wahren *et al.* 2005, Wipf and Rixen 2010). Thus, in agreement with previous studies, investigating the effects of geomorphological processes on arctic-alpine vegetation have offered evidence that plant communities are affected by different earth surface processes (Malanson *et al.* 2012, le Roux and Luoto 2014).

While many abiotic and biotic characteristics are strongly related with local topography, our results suggest that the importance of mesotopography to vascular biomass is largely due to its indirect effect through soil properties and physical disturbances caused by geomorphological processes (see Hjort and Luoto 2009, le Roux and Luoto 2014). Topography affects the soil properties mainly by controlling fluvial processes and snow distribution which, in turn, affect soil moisture, temperature and growing season length (Taylor and Seastedt 1994, Walker *et al.* 1993, Fisk *et al.* 1998, Walker *et al.* 2001). Consequently, local topography, by controlling snow accumulation and drainage,

affects arctic-alpine plant patterns, including for example species regrowth after disturbance (Evju *et al.* 2012). However, fine scale soil characteristics appear to be stronger predictors of biomass than more distally related topography variables. Nonetheless, as topography can be easily measured (including by remote sensing techniques) and does contribute to explaining some additional heterogeneity in biomass, this group of variables may represent a simple way to refine biomass models based on soil properties and earth surface processes.

From an applied perspective, the results highlight that vegetation volume is a useful surrogate of biomass as there is strong and significant correlation between the two variables. This supports the use of non-destructive methods in estimating biomass since both variables have similar responses to abiotic drivers. For vegetation cover, the amount of explained deviation is very low compared with the results for biomass samples and therefore its use as an approximation of biomass can be less appropriate than the use of vegetation volume. Consequently, these results suggest that vegetation volume could be used successfully as an estimate for biomass in arctic-alpine areas. This is particularly important finding in areas with low vegetation growth or highly sensitive species, where destructive sampling could conflict with vegetation monitoring programmes or strict conservation regulations.

The observed positive correlation between air temperature and productivity at high latitudes (Walker *et al.* 2003, Elmendorf *et al.* 2012), indicates a clear impact of climate warming on plant productivity. However, since local abiotic conditions strongly affect biomass and may also be affected by changing climatic conditions, the landscape cannot be considered as a homogenous background against which climate change will act. Indeed, through the cascading effects of local soil properties and earth surface processes, the impact of rising air temperatures could be strongly mediated by local abiotic heterogeneity. For example, increasing temperatures can lead to greater nutrient availability and changes in frost-related disturbance, with all of these environmental conditions affecting plant productivity in some manner (Chapin *et al.* 2005, Macias-Fauria and Johnson 2013). Thus, predictions of changes in biomass at local to regional levels cannot be based solely on broad scale climate scenarios.

Conclusions

In arctic-alpine tundra the variation in vegetation biomass is largely driven by the fine scale heterogeneity of the abiotic environment. The most important drivers of aboveground biomass are soil properties and especially soil moisture. Plant biomass is also affected by geomorphological processes that typically decrease the amount of biomass, mostly through mechanical disturbance.

The effect of local topography on vegetation biomass is largely indirect and it has little independent influence on biomass after soil properties and geomorphology have been taken into account. All in all, our results indicate that fine scale environmental variation has to be taken into account more carefully when modelling vegetation biomass in arctic-alpine conditions. Even though climatic conditions are fundamental drivers of biomass, their effects are filtered through local abiotic conditions which may strongly mediate plant responses to changing temperature and precipitation regimes. Therefore, where data relating to local environmental conditions are available, these should be included in analyses of vegetation biomass patterns to improve estimates of the current biomass patterns and predictions of their future changes.

Acknowledgements

We acknowledge funding from the Academy of Finland (Project Number 1140873), and thank A. Kulonen, H. Mod and A. Niskanen for helping collect the data and J. Virkanen for soil analyses.

Susanne Suvanto

Vantaa Research Unit, Finnish Forest Research Institute, P.O. Box 18, 01301 Vantaa, Finland

E-mail: susanne.suvanto@metla.fi

Peter C. le Roux

Department of Plant Science, University of Pretoria, 0028, Pretoria, South Africa

E-mail: peter.leroux@up.ac.za

Miska Luoto

Department of Geosciences and Geography, University of Helsinki

P.O. Box 64, FI-00014 University of Helsinki, Finland

E-mail: miska.luoto@helsinki.fi

References

- Anderson, M.J. and N.A. Gribble, 1998. Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. *Australian Journal of Ecology* 23, 158–167.
- Axmanová, I., Tichý L., Fajmonová, Z., Hájková, P., Hettenbergerová, E., Li, C.-F., Merunková, K., Nejezchlebová, M., Otýpková, Z., Vymazalová, M. and Zelený, D., 2012. Estimation of herbaceous biomass from species composition and cover. *Applied Vegetation Science* 15, 580–589.

- Berdanier, A.B. and Klein, J.A., 2011. Growing season length and soil moisture interactively constrain high elevation aboveground net primary production. *Ecosystems* 14, 963–974.
- Bhatt, U.S., Walker, D.A., Raynolds, M.K., Comiso, J.C., Epstein, H.E., Jia, G.S., Gens, R., Pinzon, J.E., Tucker, C.J., Tweedie, C.E. and Weber, P.J., 2010. Circumpolar Arctic undra vegetation change is linked to sea ice decline. *Earth Interactions* 14, 1–20.
- Billings, W.D., 1973. Arctic and alpine vegetations: Similarities, differences, and susceptibility to disturbance. *Bioscience* 23, 697–704.
- Bobek, B. and Bergström, R., 1978. A rapid method of browse biomass estimation in a forest abitat. *Journal of Range Management* 31, 456–458.
- Borcard, D., Legendre, P. and Drapeau, P., 1992. Partialling out the spatial component of ecological ariation. *Ecology* 73, 1045–1055.
- Bruun, H.H., Moen, J., Virtanen, R., Grytes, J.-A., Oksanen, L. and Angerbjörn, A., 2006. Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *Journal of Vegetation Science* 17, 37–46.
- Burnham, K.P., Anderson, D.R., 1998. *Model Selection and Inference: a Practical Information Theoretic Approach*. Springer, New York.
- Callaghan, T.V., Björn, L.O., Chernoc, Y., Chapin, T., Christensen, T.R., Hunstley, B., Ims, R.A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikoc, N., Oechel, W., Shaver, G., Schaphoff, S., Sitch, S. and Zöckler, C., 2004. Synthesis of effects in four arctic subregions. *AMBIO* 33, 469–473. doi:/10.1579/0044-7447-33.7.469
- Campioli, M., Michelsen, A., Demey, A., Vermeulen, A., Samson, R. and Lemeur, R., 2009. Net primary production and carbon stocks for subarctic mesic-dry tundras with contrasting microtopography, altitude and dominant species. *Ecosystems* 12, 760–776.
- Carl, G. and Kühn, I., 2007. Analyzing spatial autocorrelations in species distributions using Gaussian and logit models. *Ecological Modelling* 207, 159–170.
- Chapin, F., Sturm M., Serreze, M., McFadden, J., Key, J., Lloyd, A., McGuire, A., Rupp, T., Lynch, A., Schimel, J., Beringer, J., Chapman, W., Epstein, H., Euskirchen, E., Hinzman, L., Jia, G., Ping, C., Tape, K., Thompson, C., Walker, D., Welker, J., 2005: Role of the land-surface changes in arctic summer warming. *Science* 310: 657–660.
- Chen, W., Li, J., Zhang, Y., Zhou, F., Koehler, K., Leblac, S., Fraser, R., Olthof, I., Zhang, Y. and Wang, J., 2009. Relating biomass and leaf area index to non-destructive measurements in order to monitor changes in arctic vegetation. *Arctic* 62: 3, 281–294.

- Chevan, A. and Sutherland, M., 1991. Hierarchical partitioning. *The American Statistician* 45, 90 – 96.
- Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. and Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609–628.
- Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Boulanger-Lapointe, N., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Dorrepaal, E., Elumeeva, T.G., Gill, M., Gould, W.A., Harte, J., Hik, D.S., Hofgaard, A., Johnson, D.R., Johnstone, J.F., Jónsdóttir, I.S., Jorgenson, J.C., Klanderud, K., Klein, J.A., Kohl, S., Kudo, G., Lara, M., Lévesque, E., Magnússon, B., May, J.L., Mercado-Díaz, J.A., Michelsen, A., Molau, U., Myers-Smith, I., Oberbauer, S.F., Onipchenko, V.G., Rixen, C., Schmidt, N.M., Shaver, G.R., Spasojevic, M.J., Pórhallsdóttir, P.E., Tolvanen, A., Troxler, T., Tweedie, C.E., Villareal, S., Wahren, C.-H., Walker, X., Webber, P.J., Welker, J.M. and Wipf, S., 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2: 453–457.
- Evju, M., Hagen, D. and Hofgaard, A., 2012. Effects of disturbance along snow pack gradients in alpine habitats. *Plant Ecology* 213, 1345–1355.
- Epstein, H.E., Reynolds, M.K., Walker, D.A., Bhatt, U.S., Tucker, C.J. and Pinzon, J.E., 2012. Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. *Environmental Research Letters* 7, 015506. doi:10.1088/1748-9326/7/1/015506
- Fisk, M.C., Schmidt, S.K. and Seastedt, T.R., 1998. Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. *Ecology* 79, 2253–2266.
- Fletcher, B.J., Press, M. C., Baxter, R. and Phoenix, G.K., 2010. Transition zones between vegetation patches in a heterogeneous Arctic landscape: how plant growth and photosynthesis change with abundance at small scales. *Oecologia* 163, 47–56.
- Fox, J. and Monette, G., 1992. Generalized collinearity diagnostics. *Journal of the American Statistical Association* 87, 178–183.
- Furrer, R., Nychka, D. and Sain, S., 2011. *fields: Tools for spatial data* (R package).

- ould, W.A., Reynolds, M. and Walker, D.A., 2003. Vegetation, plant biomass, and net primary productivity patterns in the Canadian Arctic. *Journal of Geophysical Research* 108, D2, 8167. doi:10.1029/2001JD000948.
- Hardin, J.W. and Hilbe, J.M., 2003. *Generalized estimating equations*. Chapman and Hall/CRC, Boca Raton, Florida, USA.
- Haugland, J.E. and Beatty, S.W., 2005. Vegetation establishment, succession and microsite frost disturbance on glacier forelands within patterned ground chronosequences. *Journal of Biogeography* 32, 145–153.
- eikkinen, R.K., Luoto, M., Virkkala, R. and Rainio, K., 2004. Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. *Journal of Applied Ecology* 41, 824–835.
- Hjort, J. and Luoto, M., 2009. Interaction of geomorphic and ecologic features across altitudinal zones in a subarctic landscape. *Geomorphology* 112, 324–333.
- Højsgaard, S., Halekoh, U. and Yan, J., 2006. The R Package geepack for Generalized Estimating Equations. *Journal of Statistical Software* 15: 2, 1–11.
- ISO 10390. Soil quality-Determination of pH. International Organization for Standardization. 6 p.
- SO 17294-2. Water quality-Application of inductively coupled plasma mass spectrometry (ICP-MS). Part 2:Determination of 62 elements. International Organization for Standardization. 22 p.
- Jonasson, S., 1982. Organic matter and phytomass on three north Swedish tundra sites, and some connections to adjacent tundra areas. *Holarctic Ecology* 5, 367–375.
- Jonasson, S., 1986. Influence of frost heaving on soil chemistry and on the distribution of plant growth forms. *Geografiska Annaler, Series A. Physical Geography* 68, 185–195.
- Kjelvik, S. and Kärenlampi, L., 1975. Plant biomass and primary production of Fennoscandian subarctic and subalpine forests and of alpine willow and heath ecosystems. *Ecological Studies* 16, 111–120.
- raan, C., Aarts, A., van der Meer, J. and Piersma, T., 2010. The role of environmental variables in structuring landscape-scale species distributions in seafloor habitats. *Ecology* 91, 1583–1590.
- Krebs, C.J., Danell, K., Angerbjörn, A., Agrell, J., Berteaux, D., Bråthen, K.A., Danell, Ö., Erlinge, S., Fedorov, V., Fredga, K., Hältén, J., Högestedt, G., Jónsdóttir, I.S., Kenney, A.K., Kjellén, N., Nordin, T., Roininen, H., Svensson, M., Tannerfeldt, M. and Wiklund, C., 2003. Terrestrial trophic dynamics in the Canadian Arctic. *Canadian Journal of Zoology* 62, 281–294.

- Kullman, L., 2010. A richer, greener and smaller alpine world: Review and projection of warming-induced plant cover change in the Swedish Scandes. *AMBIO* 39, 159–169.
- Kyllönen, H. (1988) Alpine and subalpine vegetation at Kilpisjärvi. Finnish Lapland. Distribution of biomass and net production and annual variations in biomass. *Acta Universitatis Ouluensis A* 202. 78 p.
- le Roux, P.C. and Luoto, M., 2014. Earth surface processes drive the richness, composition and occurrence of plant species in an arctic-alpine environment. *Journal of Vegetation Science* 25, 45-54..
- le Roux, P.C., Lenoir, J., Pellisier, L., Wisz, M. and Luoto, M., 2013a. Horizontal, but not vertical, biotic interactions affect fine-scale plant distribution patterns in a low energy system. *Ecology* 94: 671–682..
- le Roux, P.C., Ramaswiela, T., Kalwij, J.M., Shaw, J.D., Ryan, P.G., Treasure, A.M., McClelland, G.T.W., McGeoch, M.A. and Chown, S.L., 2013b. Human activities, propagule pressure and alien plants in the sub-Antarctic: Tests of generalities and evidence in support of management. *Biological Conservation* 161: 18-27.
- Litaor, M.I., Williams, M. and Seastedt, T.R., 2008. Topography controls on snow distribution, soil moisture, and species diversity of herbaceous alpine vegetation, Niwot Ridge, Colorado. *Journal of Geophysical Research* 113: G2, 1–10.
- Macias-Fauria, M. and Johnson, E.A., 2013. Warming-induced upslope advance of subalpine forest is severely limited by geomorphic processes. *Proceedings of the National Academy of Sciences USA* (in press, preprint online). doi: 10.1073/pnas.1221278110.
- Malanson, G.P., Bengtson, L.E. and Fagre, D.B., 2012. Geomorphic determinants of species composition of alpine tundra, Glacier National Park, U.S.A. *Arctic, Antarctic and Alpine Research* 44, 197–209.
- Manninen, O.H, Stark, S. Kytöviita, M.-M. and Tolvanen, A., 2011. Individual and combined effects of disturbance and N addition on understorey vegetation in a subarctic mountain birch forest. *Journal of Vegetation Science* 22, 262–272.
- McCune, B. and Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* 13, 603–606.
- Muukkonen, P., Mäkipää, R., Laiho, R., Minkkinen, K., Vasander, H. and Finér, L., 2006. Relationship between biomass and percentage cover in understorey vegetation of boreal coniferous forests. *Silva Fennica* 40, 231–245.
- Nham, T.T. (2010). Analysis of soil extracts using the Varian 725-ES. *ICP OES Application note* 34.

- Pan, W., 2001. Akaike's information criterion in generalized estimating equations. *Biometrics* 57, 120–125.
- Pouliot, D., Latifovic, R. and Olthof, I., 2009. Trends in vegetation NDVI from 1 km AVHRR data over Canada for the period 1985–2006. *International Journal of Remote Sensing* 30, 149–168.
- R Development Core Team, 2011. *R: A language and environment for statistical computing*. R Project for Statistical Computing. Vienna, Austria <<http://www.r-project.org>>
- Redjadj, C., Duparc, A., Lavorel, S., Grigulis, K., Bonenfant, C., Maillard, D., Saïd, S. and Loison, A., 2012. Estimating herbaceous plant biomass in mountain grasslands: a comparative study using three different methods. *Alpine Botany* 122, 57–63.
- Röttgermann, M., Steinlein, T., Beyschlag, W. and Dietz, H., 2000. Linear relationships between aboveground biomass and plant cover in low open herbaceous vegetation. *Journal of Vegetation Science* 11, 145–148.
- Shaver, G.R., Laundre, J.A., Giblin, A.E. and Nadelhoffer, K.J., 1996. Changes in Live Plant Biomass, Primary Production, and Species Composition along a Riverside Toposequence in Arctic Alaska, U.S.A. *Arctic and Alpine Research* 28, 363–379.
- Shaver, G.R., Street, L.E., Rastetter, E.B., van Wijk, M.T. and Williams, M., 2007. Functional convergence in regulation of net CO₂ flux in heterogeneous tundra landscapes in Alaska and Sweden. *Journal of Ecology* 95, 802–817.
- Sitch, S., McGuire, A.D., Kimball, J., Gedney, N., Gamon, J., Engstrom, R., Wolf, A., Zhuang, Q., Clein, J. and McDonald, K.C., 2007. Assessing the carbon balance of circumpolar arctic tundra using remote sensing and process modeling. *Ecological Applications* 17, 213–234.
- Sturm, M., Racine, C. and Tape, K., 2001. Increasing shrub abundance in the Arctic. *Nature* 411, 546–547.
- Taylor, R.V. and Seastedt, T.R., 1994. Short- and long-term patterns of soil moisture in alpine tundra. *Arctic and Alpine Research* 26, 14–20.
- Tsutsumi, M., Itano, S. and Shiyomi, M., 2007. Number of samples required for estimating herbaceous biomass. *Rangeland Ecology & Management* 60, 447–452.
- Virtanen, R., Luoto, M., Rämä, T., Mikkola, K., Hjort, J., Grytnes, J.-A. and Birks, H.J.B., 2010. Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity. *Global Ecology and Biogeography* 19, 810–821.

- Wahren, C.-H.A., Walker, M.D. and Bret-Harte, M.S., 2005. Vegetation responses in Alaskan arctic tundra after 8 years of summer warming and winter snow manipulation experiment. *Global Change Biology* 11, 53–552. doi: 10.1111/j.1365-2486.2005.00927.x.
- Walker, D.A., Epstein, H.E., Jia, G.J., Balsler, A., Copass, C., Edwards, E.J., Gould, W.A., Hollingsworth, J., Knudson, J., Maier, H.A., Moody, A. and Reynolds, M.K., 2003. Phytomass patterns across a temperature gradient of the North American arctic tundra. *Journal of Geophysical Research* 113: G03S02. doi:10.1029/2007JG000555.
- Walker, D.A., Halfpenny, C., Walker, M.D. and Wessman, C.A., 1993. Long-term studies of snow-vegetation interactions. *BioScience* 43, 287–301.
- Walker, D.A., Molenaar, J.G. and Billings, W.D., 2001. Snow-vegetation interactions in tundra environments. In Jones, H.G., Pomeroy, J., Walker, D.A. and Wharton, R. (eds): *Snow Ecology*. Cambridge University Press, Cambridge. 264–322.
- Walker, M.D., Webber, P.J., Arnold, E.H. and Ebert-May, D., 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. *Ecology* 75: 2, 393–408.
- Wipf, S. and Rixen, C., 2010. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Research* 29, 95–109. doi:10.1111/j.1751-8369.2010.00153.x.

Manuscript Received 22 May, 2013 , revised and accepted 3 May, 2014

Table 1. Summary of site characteristics across the six sampled grids (n = 960), showing the maximum, minimum and mean (median for pH) values and standard deviations for response and predictor variables.

	max.	min.	mean	standard deviation
Biomass				
sample (g/sample)	101.4	0.0	9.9	10.5
sample (g/m ²)	2535.0	0.0	246.5	262.3
cover (%)	100.0	0.0	51.6	26.8
height (cm)	15.0	0.0	4.2	2.0
volume (100 cm ³)	1252.5	0.0	132.2	150.5
Topography				
mesotopography	10.0	1.0	5.0	2.1
slope (radians)	1.3	0.0	0.4	0.2
radiation (MJ cm ⁻² a ⁻¹)	0.7	0.1	0.3	0.1
Soil				
moisture (%)	67.3	8.4	27.4	10.3
temperature (°C)	10.0	7.9	8.9	0.5
pH	5.5	3.8	4.6	0.3
Ca (ppm)	3566.8	13.5	665.3	743.9
Geomorphology				
frost processes (%)	0.0	70.0	4.6	10.6
wind processes (%)	0.0	100.0	6.6	19.5
fluvial processes (%)	0.0	100.0	3.9	13.1

Table 2. Spearman rank correlation coefficients for the relationship between the biomass variables: sampled biomass, cover of vascular vegetation, median height of vegetation and vegetation volume (calculated as the product of vegetation cover and height). All correlations are significant at $p < 0.001$.

	sampled biomass	cover	height
cover	0.577		
height	0.540	0.405	
volume	0.662	0.851	0.799

Table 3. Best-fit GEE models for each predictor variable group (i.e. best fit models using only topography, soil or geomorphology variables).

	Sampled biomass	Vegetation volume	Vegetation cover	Vegetation height
	coefficient	coefficient	coefficient	coefficient
intercept	-0.319	10.252	99.207	-4.412
<i>Topography</i>				
mesotopo	0.107	0.047	-0.017	0.081
mesotopo ²	-0.011	-0.006	-0.003	-0.012
slope	0.233	0.720	1.918	--
slope ²	-0.047	-0.600	-1.558	--
radiation	4.155	2.050	7.714	0.610
radiation ²	-3.994	-2.074	-8.274	--
<i>Soil</i>				
moisture	0.089	0.032	0.128	0.008
moisture ²	-0.001	-0.001	-0.002	0.000
temperature	-0.193	-2.759	-20.350	0.228
temperature ²	--	0.152	1.115	-0.014
pH	0.091	1.167	-6.112	2.064
pH ²	--	-0.089	0.857	-0.196
Ca	9.60×10^{-7}	1.74×10^{-4}	0.001	1.12×10^{-4}
Ca ²	-4.85×10^{-9}	-3.96×10^{-8}	-1.49×10^{-7}	-1.81×10^{-9}
<i>Geomorphology</i>				
frost processes	-0.025	-0.020	-0.082	-0.020
frost processes ²	2.80×10^{-4}	2.05×10^{-4}	0.001	1.70×10^{-4}
wind processes	-0.017	-0.012	-0.022	-0.012
wind processes ²	1.60×10^{-4}	1.21×10^{-4}	4.00×10^{-4}	7.47×10^{-5}
fluvial processes	-0.021	-0.006	-0.016	-0.020
fluvial processes ²	2.25×10^{-4}	--	2.00×10^{-2}	1.48×10^{-4}

-- not included in the best model

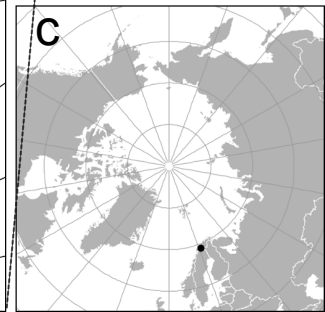
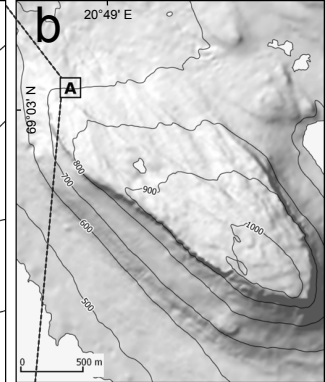
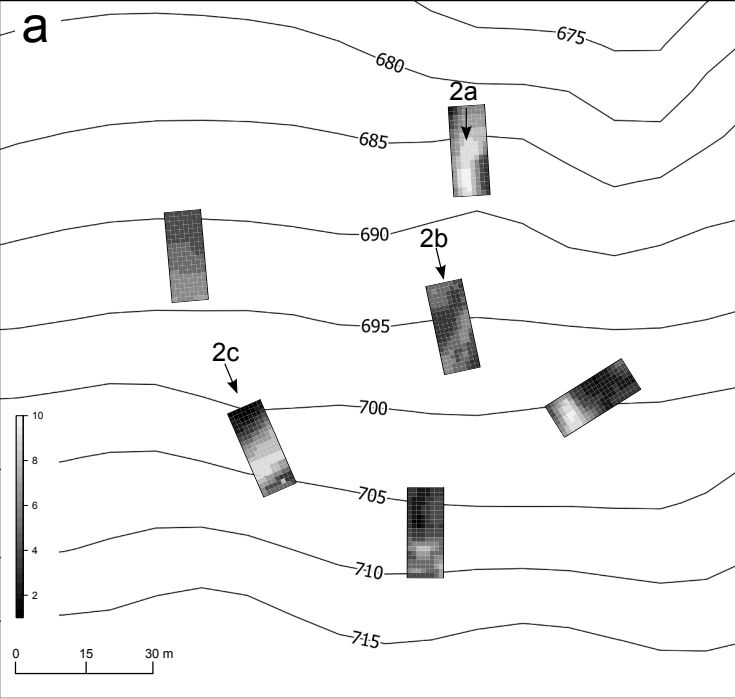
Figure 1. a) Sampled grids and the variation of mesotopography in the cells: color white represents value 10 (ridge top) and black value 1 (bottom of depression). Places and directions of photographs in Fig 2 are marked with black arrows. b) The location of the field site on mount Saana, indicated by the black rectangle and letter A. c) The location of the study area in north-western Finland, indicated by the black circle.

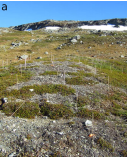
Figure 2. Photographs showing different conditions on the study area: a) an exposed and dry area with convex topography, b) high biomass area with *Empetrum hermophroditum* and *Betula nana* as dominant species c) local depression with low biomass. All photos were taken on 9 July 2012. Locations of the photographs can be seen in Fig 1.

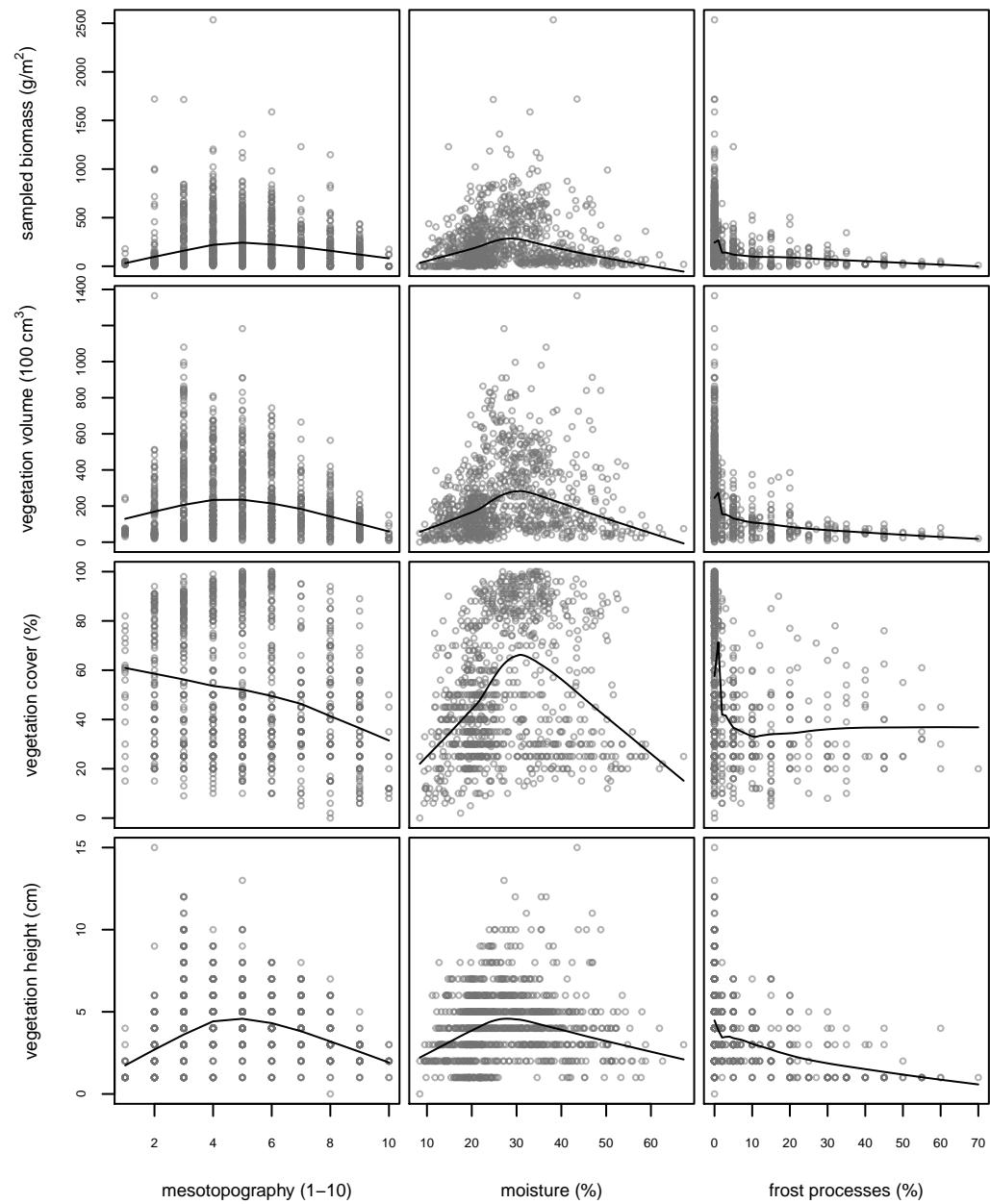
Figure 3. The relationships between sampled biomass and the three non-destructive biomass estimates as scattergrams and loess lines.

Figure 4. The relationships between the four biomass variables and selected predictor variables from each variable group, as indicated by loess lines. Mesotopography presents the local topography on a 10-point scale, value 1 representing a bottom of a depression and value 10 a ridge top.

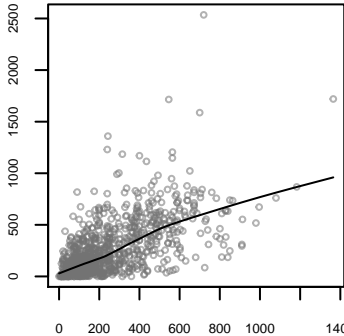
Figure 5. Variation partitioning for the four biomass variables. Variation in the response variables is partitioned between three groups of environmental variables: soil properties, topography and geomorphology. Sections a, b and c represent the unique effects of the predictor variable groups, while d, e, f and g indicating shared effects.



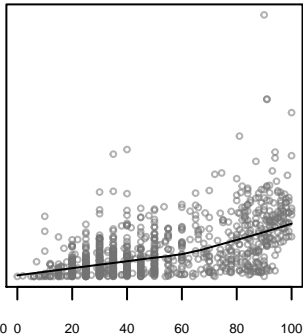




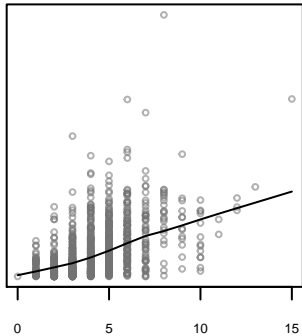
sampled biomass (g/m²)



vegetation volume (100 cm³)



vegetation cover (%)

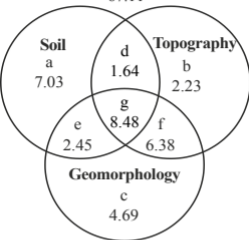


vegetation height (cm)

SAMPLED BIOMASS

Unexplained

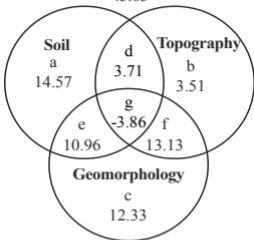
67.11



VEGETATION VOLUME

Unexplained

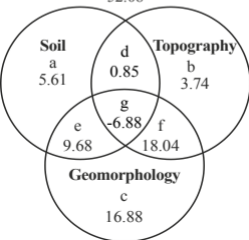
45.63



VEGETATION HEIGHT

Unexplained

52.08



VEGETATION COVER

Unexplained

88.84

