Comparing the effect of landscape context on vascular plant and bryophyte communities in a human-dominated landscape

Running title: Bryophyte response to landscape context

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Abstract

Aims: It is important to understand the effect of landscape context on biological communities to predict how biodiversity will be affected on human-dominated landscapes. While many studies have tested the effects of landscape context on the species richness and composition of vascular plants, few have compared the responses of vascular plants and bryophytes on the same landscape. We sampled non-epiphytic bryophytes and vascular plants in 184 plots to test whether three landscape context factors measured four years or four decades previously could predict bryophyte or vascular plant species richness and composition after accounting for local factors.

Location: temperate forests and oak savannahs, Vancouver Island, British Columbia, Canada.

Methods: We used model selection and comparisons to test the effects of surrounding road density, total amount of forest, and distance to the nearest forest edge on species richness, species richness of non-disturbance-associated species, and community composition after controlling for important local predictors including substrate availability and topography.

Results: The species richness of non-disturbance-associated vascular plants was lower in plots with greater surrounding historical road density, and perennial stayer bryophyte richness declined with increasing historical road density and lower historical forest amount, suggesting a potential extinction debt. Landscape context significantly affected total species richness and community composition of vascular plants, but not bryophytes.

Conclusion: While bryophytes appear to be less sensitive overall to landscape context than vascular plants, disturbance-intolerant perennial stayer bryophytes may decline in the future in response to the increased road density and loss of forest cover that has occurred over the past four decades.

Keywords: bryophytes, forest, life-history, landscape, liverwort, moss, plant communities, roads, savannah, vascular plants

Introduction

As our population continues to grow, humans are modifying landscapes, creating patches of remnant natural vegetation that are smaller, isolated from other patches, and surrounded by urban and agricultural land use. Habitat loss leads to a decline in the number of species and their abundance, but the impact of habitat fragmentation *per se* and changing landscape context on species and communities is still debated (e.g. Fahrig 2003; Fahrig 2017; Haddad et al. 2017). In order to conserve species in human-dominated landscapes, we need to understand how much the landscape context – i.e. the size and shape of habitat patches and the type of land use that surrounds them - affects species richness, abundance, and community composition.

Within a patch of natural vegetation, local factors are important predictors of species richness and community composition. For example, the soil type, moisture availability, and microclimate all influence which species and how many species are present at a particular location (e.g. Rambo and Muir 1998; Wright et al. 2003; Baldwin and Bradfield 2010). In fragmented landscapes, a key question is how important landscape context is in determining species diversity and/or composition, relative to these local factors. Some studies have found that landscape context can be at least as important as local factors in predicting species presence or community composition of vascular plants (Rogers et al. 2009; McCune and Vellend 2015; McCune 2016).

Ecologists have not studied the role of landscape context on bryophyte diversity as often as for other taxonomic groups, especially vascular plants, mammals, and birds (Löbel et al. 2006;

Pharo and Zartman 2007). Studies on bryophytes in fragmented vegetation have shown mixed results. For example, Gignac and Dale (2005) found that bryophyte species richness in woodlots of Northern Alberta increased with distance from the forest edge, while Hylander and Hedderson (2007) found no correlation between bryophyte species richness and distance to forest edge in South African ravine forests. Although local habitat diversity and soil pH were the most important predictors, Löbel et al. (2006) found that bryophyte species density increased with the size of a grassland patch in dry Swedish grasslands. Baldwin and Bradfield (2007) found that patch size affected the species density of only some bryophyte species, depending on their life history characteristics. Vanderpoorten et al. (2004) found that species richness of obligate epiphytic bryophytes in Belgium correlated negatively with the extent of spruce plantations on the surrounding landscape. In contrast, Pharo et al. (2004) found that bryophyte species richness in Tasmanian vegetation fragments did not depend on whether a patch was surrounded by native forest or exotic pine plantations; rather, the local presence and quality of decaying logs was the most important determinant. The relative importance of landscape context for bryophyte species diversity and composition compared to other taxonomic groups is not clear, and may vary with different spatial scales, different vegetation types, or different sub-sets of the bryophyte community.

It is also important to recognize that there can be time lags between changes in landscape context (e.g. reduction in patch size and/or increase in patch isolation) and the response of the animal or plant community. Such time lags can lead to an 'extinction debt', whereby the species richness of a site is doomed to decline as the community gradually equilibrates to landscape changes (Kuussaari et al. 2009). In plants, these time lags can result from two factors, (1) the ability of long-lived adult individuals to survive for a long time at a site even though conditions

90 are no longer ideal and new individuals are not able to establish there, and (2) a delay in
91 colonization of newly suitable sites due to dispersal limitation (Lindborg and Eriksson 2004;
92 Helm et al. 2006; Kuussaari et al. 2009; Jackson and Sax 2010). Some studies have shown
93 evidence of such time lags in bryophyte and vascular plant community responses to landscape
94 change, while others have not (e.g. Paltto et al. 2006, Löbel et al. 2009).
95 Very few studies have directly compared local and landscape effects on bryophyte and
96 vascular plant richness and composition (but see Löbel et al. 2006; Paltto et al. 2006). It is
97 thought that bryophytes may be (1) more sensitive to local conditions, because they must absorb
98 moisture and nutrients from the atmosphere directly (Pharo and Zartman 2007); and (2) less
99 sensitive to landscape context, because their very small propagules and large distributions
100 suggest dispersal limitation may be less common for them (Löbel et al. 2006; Paltto et al. 2006).
101 In this study, we test the hypothesis that the bryophyte community is less sensitive than the
102 vascular plant community to differences in landscape context. To do this, we analyze the species
103 richness and community composition of non-epiphytic bryophytes and understory vascular plants
104 in 184 vegetation plots on the Saanich peninsula, British Columbia, Canada, a highly developed
105 area near the city of Victoria. By examining the influence of landscape context on bryophytes
106 and vascular plants in the same plots, in the same region, we are able to avoid differences in
107 region, plot size, or time period that impedes a direct comparison of bryophyte and vascular plant
108 responses. We test whether landscape context can explain variation in bryophyte or vascular
109 plant richness or composition after accounting for local factors. Given that there may be time
110 lags in vascular plant or bryophyte community response to changing landscape context, we use
111 both current and past measures of landscape variables. We already know that vascular plant
112 communities in this region respond to changes in landscape context (Lilley and Vellend 2009;

McCune and Vellend 2015). If the bryophytes are indeed less sensitive to landscape context, we predicted that we would not find an effect of landscape conditions – present or past – on bryophyte species richness or community composition.

Methods

Sampling Method

We sampled 184 20m x 20m relevé plots on the Saanich Peninsula, a region of approximately 330 km^2 (Appendix S1 Figure A1). The region is part of the coastal Douglas-fir biogeoclimatic zone (Meidinger and Pojar 1991), which has a "cool Mediterranean" climate, with mild winters and long, dry summers (Meidinger and Pojar 1991). The average total annual precipitation is approximately 87 cm, with only about 10 cm of precipitation falling in the summer months (June to September). This region has a warmer and drier climate compared to the rest of coastal British Columbia because it is in the rain shadow of the Olympic and Vancouver Island Mountains. Since European settlement, over 90% of the native forests and savannahs have been cleared to make way for settlements and agriculture (Flynn 1999; Lea 2006). Land elevation is an important predictor of climate in this area, with higher altitude areas receiving more precipitation and having a lower mean temperature (Lilley and Vellend 2009).

The vegetation of the Saanich peninsula consists mainly of *Pseudotsuga menziesii* (Douglas-fir) dominated forests, sometimes mixed with *Arbutus menziesii* (Arbutus) on warmer and drier sites, as well as *Quercus garryana* (Garry oak) dominated woodlands and savannahs, which tend to be found on the warmest, driest sites, often on shallow soils (Meidinger and Pojar 1991; Flynn 1999). The surveyed plots include a gradient of vegetation types, from the very shady Douglas-fir (115 plots), to what we refer to as "Arbutus" (Douglas-fir-dominated forests

136 with a significant component of Arbutus trees; 26 plots), to Garry Oak woodland or savannah (43
137 plots), which tend to have a more open canopy and thus a higher diversity of understory plant
138 species (Appendix S1 Figure A2). These broad vegetation types are based on the classification
139 by Roemer (1972), who divided each of these three broad types into specific associations (e.g.
140 Garry oak-dominated vegetation includes both woodland and savannah-type associations). The
141 Douglas-fir and Arbutus forest types are mostly second-growth (i.e. they have been logged or
142 selectively logged in the past), but they are not currently managed as plantations for future
143 cutting, and most now occur on protected conservation lands. The Garry oak vegetation is now
144 mostly limited to rocky sites that are unsuitable for agriculture or housing development.
145 We selected plot locations non-randomly based on a previous study done in 1968 and
146 1969 (Roemer 1972). From May to August 2009, we resurveyed 184 of the original 409 plots.
147 We resurveyed plots only if they were forested and if permission to access them was granted by
148 landowners. We relocated the original plots using a grid system on aerial photos used by the
149 original surveyor, along with physical descriptors (see McCune and Vellend 2013). In each plot,
150 we identified all vascular plants and estimated the percent cover of each. We also identified all
151 bryophyte species occurring on soil, rock, or decomposing wood, and estimated the percent
152 cover of each. If a species was estimated to cover less than 1% of the plot, we entered "0.5" in
153 the data, and if it covered much less than 1%, we entered "0.1". We did not survey epiphytic
154 bryophytes on living trees. Complete species capture of ground-dwelling bryophytes can be very
155 difficult without intensive searches (on hands and knees) given the inherent habitat heterogeneity
156 of the ground layer (McCune and Lesica 1992) and the capacity of some bryophytes – especially
157 leafy liverworts - to exist as isolated strands on fine coarse woody debris (Söderström 1993).
158 However, we made every effort to document all vascular plants and bryophytes, spending

159 approximately 4-6 person hours surveying each plot. Vascular plant nomenclature follows
160 Douglas et al. (1988), while bryophyte nomenclature follows the Flora of North America (Flora
161 of North America Editorial Committee 1993+). We collected specimens that we could not
162 identify in the field for examination under a microscope, and deposited these specimens in the
163 University of British Columbia herbarium, where experts on staff later confirmed or corrected
164 our identifications.
165 The original objective of the data collection was to measure the change in plant
166 community composition since the original survey, particularly with reference to landscape
167 change, rather than to explain vascular plant or bryophyte diversity based on local
168 characteristics, therefore we did not take detailed measurements of soil characteristics such as
169 nutrient levels or pH. However, we did measure the slope and aspect of each plot, and estimated
170 the percent cover of soil, exposed rock, and decomposing wood substrate. Unfortunately, we
171 could not compare the bryophyte data from our survey to the original survey due to differences
172 in survey methods and criteria for inclusion of species discovered after we collected the 2009
173 data.
174
175 *Dependent Variables*
176 For both vascular plants and bryophytes we calculated the total species richness and the richness
177 of non-disturbance-associated species only in each plot. Because this is a measure of species
178 richness in each equal-sized plot (not total species richness per variable-sized forest patch), it is
179 in effect "species density" (Cousins et al. 2007; Fahrig 2013). We examined the effects of
180 landscape context on non-disturbance-associated species because in some cases landscape
181 context is important only for species with certain life history traits (e.g. Baldwin and Bradfield

2007), or, alternatively, different types of species can have opposite responses to landscape context factors (e.g. Lilley and Vellend 2009). For bryophytes, we used Baldwin and Bradfield's (2007) classification of bryophyte species, which was based on the classification system proposed by During (1979, 1992). We counted the number of species classified as 'perennial stayers' in each plot as a representation of richness of species not associated with disturbance. Perennial stayers have large spores (>20 μm), tend to live in stable habitat types, have long life spans and high capacity for vegetative reproduction (Baldwin and Bradfield 2007). For vascular plants, we classified each species as "disturbance-associated" or "non-disturbance-associated" according to the "Habitat/Range" description in the Electronic Atlas of the Flora of British Columbia (Klinkenberg 2017). If we encountered any of the following phrases in the habitat description, we classified the species as disturbance-associated: *burns*, *continuously disturbed sites*, *disturbed areas/sites*, *disturbed communities*, *ditches*, *fencelines*, *fencerows*, *fields*, *fire-disturbed sites*, *lawns*, *pastures*, *railways*, *roadsides*, *waste places*, *early-seral/young-seral/early successional forests*, *garden*, or *garden escape*. We considered all other species to be non-disturbance-associated. Disturbance-associated vascular plants in this dataset tend to be shade intolerant species with small seeds, and are often exotic (McCune and Vellend 2013). We also measured overall bryophyte and vascular plant community composition by calculating a resemblance matrix for each group based on the Bray-Curtis similarity metric calculated on the square-root transformed percent cover estimates of each species.

Independent Variables

We measured two categories of predictor variables: local variables and landscape context variables. We first collected data on local variables that could affect vascular plant and

bryophyte species diversity and composition. These included elevation, slope and aspect as measures of microclimate, since microclimate influences both vascular plant and bryophyte diversity (e.g. Hylander 2005; Lilley and Vellend 2009). We did not include climate variables (e.g. temperature or precipitation) because these are very strongly correlated with elevation in this region (Lilley and Vellend 2009). We converted aspect to a categorical variable, with plots having aspect between 316° and 45° classified as "north", 46° – 135° classified as "east", 136° – 225° classified as "south", 226° - 315° classified as "west", and completely flat plots classified as "undefined". We also included percent cover of bare rock and decomposing wood because the presence and quality of substrate is a known determinant of cryptogam species richness (Rambo and Muir 1998). Note that by "bare rock", we mean rock not covered by soil, but that may be well-covered with bryophytes. We had categorized soil depth at each plot, but because this was very highly correlated with the percent cover of rock, we did not include it in our analysis. We also considered including vegetation type (Douglas-fir, Arbutus, or Garry oak) as this is obviously an important predictor of species composition. However, vegetation type is very strongly correlated with the percent cover of bare rock (Appendix S1 Figure A3), and therefore we decided to include this variable and not categorical vegetation type. Canopy cover is also an important predictor of plant community composition, but in our dataset it is very strongly correlated with vegetation type and percent cover of rock. By choosing to include percent cover of rock, we acknowledge that any effect of rock cover could also be a result of these correlated factors.

Landscape context factors included past and present road density, total surrounding forest area, and distance to the nearest forest edge. Road density is a measure of land use surrounding a focal plot. In our region, landscapes with high road density have greater amounts of urban or

suburban land use. High-density housing can facilitate invasion by exotic and/or disturbance tolerant species because human activities both transport propagules of disturbance-associated species, and create disturbed conditions that favour these species (Gavier-Pizarro et al. 2010). Total surrounding forest area is an indication of habitat amount, which has been shown to influence species density in a focal site (Fahrig 2013). Distance to the nearest forest edge indicates the relative position of a plot within a naturally vegetated patch. Plots closer to the boundary with human land use may have altered species richness and/or composition due to the influence of edge effects (e.g. Pharo and Zartman 2007). We measured these factors using GIS software, from imported and digitized aerial photos from 1964 (past) and 2005 (present). We included in total forest area all naturally vegetated areas (forests, woodlands, and savannahs), but excluded agricultural lands, built-up areas, and other artificial vegetation (e.g. playing fields, cemeteries). We measured forest area and road length within a buffer distance of 500m around each plot. Previous research has shown that this distance is optimal for testing the effects of landscape context on vascular plant composition on this landscape (Lilley and Vellend 2009). Löbel et al. (2006) and Randlane et al. (2017) both found that landscape context variables at a 500m buffer size correlated with changes in bryophyte and lichen diversity, therefore we used the same buffer distance for both taxonomic groups. There was considerable variation in all three landscape predictors amongst the 184 plots (Appendix S1 Figure A4). All independent and dependent variables are summarized in Appendix S1, Table A1.

Statistical Analyses

We used multiple linear regression to determine which variables were important predictors of total richness, and the richness of non-disturbance-associated species. First, we examined all

pairwise correlation coefficients between the predictor variables (Appendix S1 Table A2). Landscape context factors are highly correlated with each other, especially for the same factor in different years (e.g. road density 1964 and road density 2005); therefore, we included only one landscape context variable per model.

We began by building a linear model based on the local predictor variables only. We standardized all continuous predictor variables by centering and dividing by twice the standard deviation, as recommended by Grueber et al. (2011). Our goal was to find the minimum adequate model based on local variables only, so we used backward stepwise model selection to select the most important local factors. We ensured that all models met the assumptions for linear regression and that no data point exerted undue influence on model fit. We ruled out spatial autocorrelation in model residuals by examining spline correlograms (Bjornstad 2016). If there was evidence for spatial autocorrelation, we included a spatial autocovariate in the model (Dormann 2007; Bardos et al. 2015).

After we determined the minimum adequate model, we added each landscape variable separately, and compared the AIC with and without the landscape predictor included. This allowed us to test whether adding in the landscape predictor could improve our ability to predict species richness after we had accounted for the important local variables. We conservatively considered models including the landscape predictor to be better than the minimum adequate model if $\Delta AIC > 2$ (Burnham et al. 2011). We used a *drop1* test to determine the relative importance of each variable in the model with the lowest AIC (Chambers 1992; R Core Team 2017). We report AIC and F-test results for each comparison in the *drop1* tests. We visualized the final 'best' models with partial regression plots, which show the predicted effect of one variable with all other variables held constant at their median (Breheney and Burchett 2013). We

carried out these analyses in **R** version 3.4.0 (R Core Team 2017). We used packages "MASS" for stepwise model selection (Venables and Ripley 2002), "arm" for standardizing continuous predictor variables (Gelman and Su 2016), "ncf" for correlograms (Bjornstad 2016), "spdep" for constructing spatial autocovariates (Bivand et al. 2013, Bivand and Piras 2015), and "visreg" to plot partial regression plots (Breheney and Burchett 2017).

To test the importance of local and landscape factors on multivariate community composition, we used a similar procedure with the Bray-Curtis resemblance matrix (calculated on square-root transformed abundances) as the response variable. We removed 'unknown' species prior to calculating the resemblance matrix. We used distance-based linear models (DISTLM; McArdle and Anderson 2001; Anderson et al. 2008) to test the effect of local and landscape variables on the multivariate bryophyte or vascular plant species composition of the 184 plots. Essentially, this is a test of the relationship between species composition, as represented by the resemblance matrix, and the corresponding matrix of environmental predictors, with significance determined using permutation (Anderson et al. 2008). We used the program PRIMER for these analyses (Clarke and Gorley 2006). As with the species richness analysis, we started out with the local predictors only, and then used the forward selection procedure in PRIMER to find the most parsimonious model based on local factors only, based on the model AIC. We forced inclusion of latitude and longitude to account for any spatial dependency in the data. We set the number of permutation to 5,000. Once we determined the 'best' local factor model, we then added each landscape context variable one at a time and calculated the difference in AIC compared to the local factor only model. Once again, we considered models including the landscape predictor to be better than the minimum adequate model if $\Delta AIC > 2$. We then performed a *drop1* test on the model with the lowest AIC to

297 determine the importance of each factor in the model, once the others had been accounted for.
298 For the analysis of bryophyte community composition, we removed one plot that had no non-
299 epiphytic bryophytes present.
300 To visualize the gradient of vascular plant species composition across the vegetation
301 types, we used non-metric multidimensional scaling (NMDS) in PRIMER to ordinate all plots
302 based on the Bray-Curtis dissimilarity calculated on the square-root transformed abundance of
303 each vascular plant species in each plot. We used distance-based redundancy analyses (dbRDA;
304 Anderson et al. 2008) to visualize the effect of significant predictors on the community
305 composition of bryophytes and vascular plants, respectively. This analysis is a constrained
306 ordination that is essentially an ordination of fitted values from a given DISTLM model. Vectors
307 overlain on the ordination show the relative influence and direction of predictor variables on the
308 variance in community composition explained by the DISTLM model (Anderson et al. 2008).
309 Dupré and Ehrlén (2002) suggested that the importance of local conditions relative to
310 landscape context increases with the length of the environmental gradient among sampled sites.
311 Therefore, we repeated our statistical tests on the 115 plots surveyed in Douglas-fir dominated
312 vegetation only, which represent the smallest portion of the environmental gradient, but the
313 greatest number of plots in our dataset.
314
315 **Results**
316 We recorded 56 bryophyte taxa in total, including 53 mosses and three liverworts (we combined
317 some difficult species at the level of genus, see Appendix S1 Table A3). The most common
318 bryophyte species recorded was *Kindbergia oregana,* a perennial stayer, which we found in 175
319 out of 184 plots. *K. oregana* was also the most abundant species, with an average cover of 20.8%

320 in plots where it was present. Fifteen species occurred in only one plot. The species richness
321 ranged from one to 10 bryophyte species per plot, with a mean of 4.6 species. Total percent
322 cover of bryophytes ranged from 0% to 98.6% with a mean of 35.4%.
323 There were 237 species of understory plants, including herbs, ferns, grasses, sedges,
324 shrubs, or vines (again, a few species were combined at the level of genus; Appendix S1 Table
325 A4). We removed five 'unknown' species prior to calculating the resemblance matrix. The most
326 frequently occurring species was *Mahonia aquifolia* or *M. nervosa* (163 out of 184 plots),
327 followed by *Symphoricarpos albus* (157 plots), and *Polystichum munitum* (156 plots). The most
328 abundant species was *Gaultheria shallon*, which had an average cover of 20.2% in plots where it
329 was present. Understory vascular plant species richness ranged from 11 to 63 species, with a
330 mean of 29.8 species. Total understory plant cover ranged from 7.9 to 259%, with a mean of
331 96% (note: total cover could exceed 100% due to multiple overlapping layers of vegetation).
332
333 *Species Richness*
334 The minimum adequate model for bryophyte total species richness included slope, elevation,
335 rock cover, and decomposing wood cover (Table 1). These variables explained 31% of the
336 variation in bryophyte richness. All variables correlated positively with species richness (Fig. 1).
337 None of the landscape context variables improved significantly on the minimum model. Road
338 density in 1964 reduced the AIC, but only slightly, and was not significant in the drop1 test
339 (Table 1).
340 The minimum adequate model for vascular plant total species richness included slope,
341 aspect, rock cover, and decomposing wood cover (Table 2). These variables explained 31% of
342 the variation in vascular plant species richness. Richness increased on east and south-facing

aspects, and in plots with more rock cover, and declined with greater cover of decomposing wood (Fig. 2). The present distance to the nearest forest edge was the only landscape variable that improved the model significantly when added to the minimum model. Vascular plant species richness tended to decline with distance from the forest edge (Fig. 2).

The minimum adequate model for species richness of perennial stayer bryophytes included slope, elevation, rock cover, and decomposing wood cover (Table 3). These variables explained 24% of the variation in richness of perennial stayers. The number of perennial stayers tended to be higher on steeper slopes, at higher elevations, and with greater cover of rock and decomposing wood substrate (Fig. 3). This minimum model significantly improved with the addition of past road density, or with past total forest cover (Table 3). The model with past road density had the lowest AIC, with richness of perennial stayers declining in areas that had a greater length of roads within 500m in 1964 (Fig. 3).

The minimum model for species richness of non-disturbance-associated vascular plants included all the local predictors, and required a spatial autocovariate to account for spatial autocorrelation in the residuals (Table 4). Richness of this group of species was highest in east-facing plots, and increased with slope, elevation, and rock cover (Fig. 4). The only landscape factor that improved this model when added was past road density (Table 4). Species richness of vascular plants that are not disturbance-associated declined with higher length of roads within 500m in 1964 (Fig. 4).

Overall community composition

None of the landscape factors improved upon a model of bryophyte species composition based on local factors only, although the model with the lowest AIC included present forest area (Table

5). The most important predictors of bryophyte species composition were slope, percent cover of decomposing wood, and especially rock cover (Table 5, Appendix S1 Figure A5). Past road density and current forest area both improved ability to predict vascular plant species composition when added to a model with local predictors only (Table 6). The model with the lowest AIC was the model with present forest area. The most important predictors of vascular plant species composition were aspect, present forest area, and especially rock cover (Table 6, Appendix S1 Figure A6).

Douglas fir plots only

When we repeated the analyses on the 115 Douglas fir plots only, the results were nearly identical to those for the complete dataset (Appendix S1 Tables A5 through A10).

Discussion

Non-epiphytic bryophyte communities showed less correlation with landscape context at a scale of 500m compared to vascular plants in the same plots. Models of vascular plant total species richness, species richness of non-disturbance-associated species, and overall community composition all improved significantly with the addition of at least one of the landscape context variables. In contrast, the addition of landscape context variables did not significantly improve models for bryophyte total species richness and overall community composition based on local factors only. Several other studies have found that local habitat factors outweigh landscape context for bryophyte species richness (Moen and Jonsson 2003; Pharo et al. 2004; Vanderpoorten et al. 2004; Pharo et al. 2005; Löbel et al. 2006). In particular, the availability of preferred substrates is a crucial determinant of bryophyte species richness (Rambo and Muir

1998; Pharo et al. 2004; Fenton and Frego 2005). Habitat heterogeneity, as represented by the *variability* in substrates available, also increases bryophyte species richness (e.g. Newmaster et al. 2003; Zechmeister et al. 2003; Gignac and Dale 2005; Hylander and Hedderson 2007). Even at broader spatial scales, the size and context of habitat patches may not have a strong influence on bryophyte communities. For example, in a study across a group of Macaronesian Islands, habitat heterogeneity and climatic factors were much more important than island size or distance to the nearest island for predicting bryophyte species richness (Aranda et al. 2014).

The reason for this lower effect of landscape context relative to local habitat conditions could be that bryophytes are not dispersal limited at a scale of 500m. Therefore, the contiguity of natural vegetation at this scale does not affect the ability of a bryophyte species to colonize a particular site, as long as the required substrate and other local conditions are available. Each bryophyte individual can produce thousands to millions of spores, and while most spores do not travel far, a small percentage can travel several kilometers, allowing bryophytes to colonize or re-colonize even distant, isolated patches (Miles and Longton 1992; Hutsemekers et al. 2007). For example, Miller and McDaniel (2004) found that bryophyte species colonized new concrete walls built along a highway in New York State from populations more than 5km away. Barbé et al. (2016) found that bryophyte propagules from sources nearby and 30km away had an equal chance of contributing to local propagule rain. This reasoning seems to match with our finding that the species richness of perennial stayers, which likely have lower dispersal ability due to their larger spores, was the only bryophyte response variable significantly affected by landscape context.

Another reason that landscape context factors may not be important for predicting bryophyte species richness and composition in our system is because the matrix between

412 fragments of forest is not entirely hostile. The matrix between patches in our study region
413 consists of a combination of agricultural fields, fencerows, roads, sports fields, and housing.
414 Some bryophyte species could be surviving in backyards or other "unnatural" habitats that act as
415 stepping-stones for dispersal, thus maintaining populations and richness even in patches that are
416 seemingly isolated. Some species can live on surfaces that may be common in the matrix of our
417 study area. For example, species of *Polytrichum* can live on road banks, *Ceratodon purpureus*
418 can grow on concrete, rooftops, and road banks, and *Plagiomnium insigne* sometimes grows in
419 lawns (Klinkenberg 2017). Therefore, at least some of the bryophytes in our study can survive in
420 the matrix between fragments, shortening the dispersal distance necessary to colonize new sites
421 and sustain populations. In other words, the cover of natural vegetation surrounding a site may
422 not be an accurate measure of the amount of suitable habitat on the surrounding landscape for
423 many of our bryophyte species (see also Zulka et al. 2014). Some research with birds has
424 suggested that a species-centred approach to defining habitat extent on a landscape is necessary
425 to test accurately the effect of habitat amount on species (Betts et al. 2014). This approach could
426 be tested for bryophytes by defining and measuring habitat amount based on models of habitat
427 suitability rather than simply forest vs. non-forest.
428 It is important to note that for both vascular plants and bryophytes our models explained
429 only about one third or less of the variation in the response variables. The unexplained variation
430 is likely due to factors we did not measure, including soil pH and nutrient levels, soil moisture
431 (Raabe et al. 2010), age of the forest (time since last clear-cut or selective timber harvest), and
432 the degree of local disturbance (e.g. from nearby hiking trails). Several studies have found that
433 forest age is an important determinant of bryophyte diversity (e.g. Rambo and Muir 1998;
434 Newmaster et al. 2003; Gignac and Dale 2005). However, while measuring these local

435 predictors could have increased our ability to explain the variation in bryophyte diversity among
436 plots, it would not change the result that landscape context explains little or none of that
437 variation. Even for vascular plants, the addition of landscape context variables added relatively
438 little explanatory power (e.g. increasing R^2 from 0.31 to 0.33; Table 2). This is consistent with
439 the results of Löbel et al. (2006), who found that local habitat quality had a stronger effect on
440 both vascular plant and bryophyte species richness relative to landscape structure. They cite
441 Dupré and Ehrlén (2002) in suggesting that the importance of local conditions relative to
442 landscape context increases with the length of the environmental gradient among sampled sites.
443 However, our tests on Douglas fir plots only did not support this explanation. Perhaps the length
444 of the gradient among Douglas-fir forest plots only is still too long for landscape context to
445 outweigh local factors.
446 Despite the relatively small influence of landscape context, it is noteworthy that
447 landscape context factors that improved models of the richness of non-disturbance-associated
448 vascular plants and perennial stayer bryophytes were those measured 40 years prior to our
449 survey. For both groups, higher road density in 1964 correlated with lower current richness.
450 None of the present-day landscape factors was a significant predictor. This suggests a time lag
451 between an increase in road density and the loss of some of these disturbance-sensitive species.
452 This contrasts with the results of Paltto et al. (2006), who found that red book and indicator
453 bryophyte species density was more strongly correlated with present forest amount, while
454 vascular plant species density was correlated with forest amount 120 years in the past. Other
455 studies have found evidence of time lags leading to 'extinction debt' for both vascular plant and
456 bryophyte communities (Kuussaari et al. 2009). For example, Lindborg and Eriksson (2004)
457 found that vascular plant richness in Swedish grasslands correlated with grassland connectivity

50 and 100 years ago, but not with current connectivity. Löbel et al. (2009) found that for obligate epiphytic bryophytes in Sweden, past habitat connectivity predicted species richness of monoecious species. The density of roads surrounding our plots has increased on average 62%, from a mean of 2.2km of roads within 500m in 1964 to a mean of 3.6 km in 2005. As a result, we may expect further declines in the richness of perennial stayer bryophytes in the future, as the bryophyte community responds. Alternatively, we may have already lost the most sensitive perennial stayers, with the remaining species able to persist even with the increase in road density.

Conclusion

Conversion of natural vegetation to agricultural and residential land use has reduced the area available for both bryophytes and vascular plants globally. Local factors are the best predictors of the diversity and composition of both bryophytes and vascular plants in our study area, despite the high degree of fragmentation. Nevertheless, a significant effect of landscape context is measureable for vascular plant richness and composition, and for the richness of perennial stayer bryophytes. For both groups, the density of roads four decades in the past is a better predictor of species richness than current road density, suggesting a time lag between increased human population density and extirpations within forest patches. At this time, even small patches of natural vegetation in our study area, whether surrounded by suburbs or agricultural fields, can support total species richness of non-epiphytic bryophytes and vascular plants comparable to sites with larger extents of contiguous forest. However, studies like ours provide an important baseline for determining whether this pattern will persist into the future.

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Author Contributions

JLM designed the study and led the data collection. JLM, CJF, and MR analysed the data and drafted the manuscript. LKB provided the bryophyte life history data and helped to revise the manuscript. All authors provided critical feedback on the drafts and gave final approval for publication.

Data Accessibility

Plant and bryophyte community data and plot characteristics are available on Dryad, doi:10.5061/dryad.1rn8pk0rb.

Supporting Information

Appendix S1: supplementary tables and figures

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Figures:

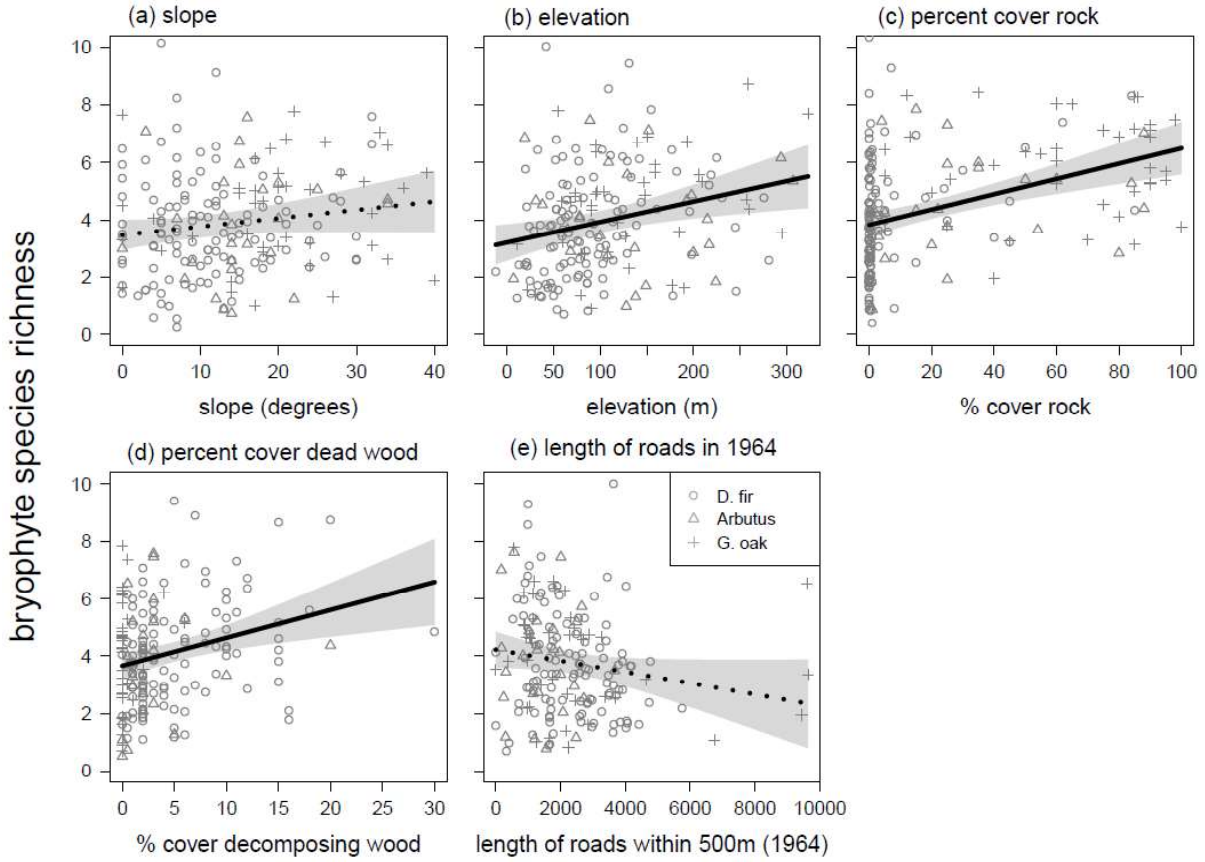

Figure 1. Partial regression plots based on the lowest AIC model for total bryophyte species richness, showing the predicted changes in richness with slope, elevation, percent cover of rock substrate, percent cover of decomposing wood substrate, and length of roads within 500m in 1964. Solid lines indicate the predictor is significant according to a drop1 test. In each case, all other factors are held constant at their median. Symbols represent the vegetation type of each plot. D. fir = Douglas-fir dominated, Arbutus = Douglas-fir with significant component of arbutus trees, G. oak = Garry oak.

Figure 2

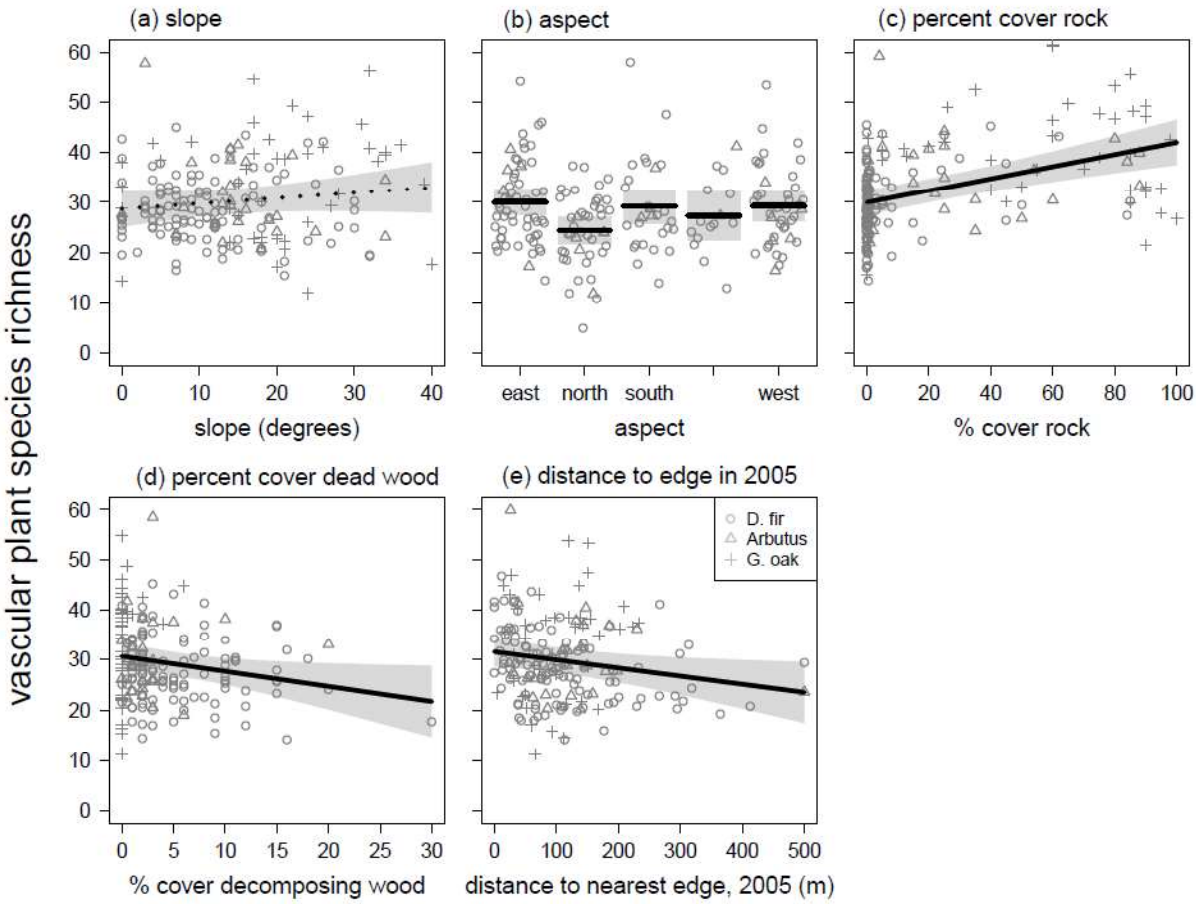

Figure 2. Partial regression plots based on the lowest AIC model for total understory vascular plant species richness, showing the predicted changes in richness with slope, aspect, percent cover of rock substrate, percent cover of decomposing wood substrate, and distance to the nearest forest edge in 2005. Solid lines indicate the predictor is significant according to a drop1 test. In each case, all other factors are held constant at their median. Symbols represent the vegetation type of each plot. D. fir = Douglas-fir dominated, Arbutus = Douglas-fir with significant component of arbutus trees, G. oak = Garry oak.

Figure 3

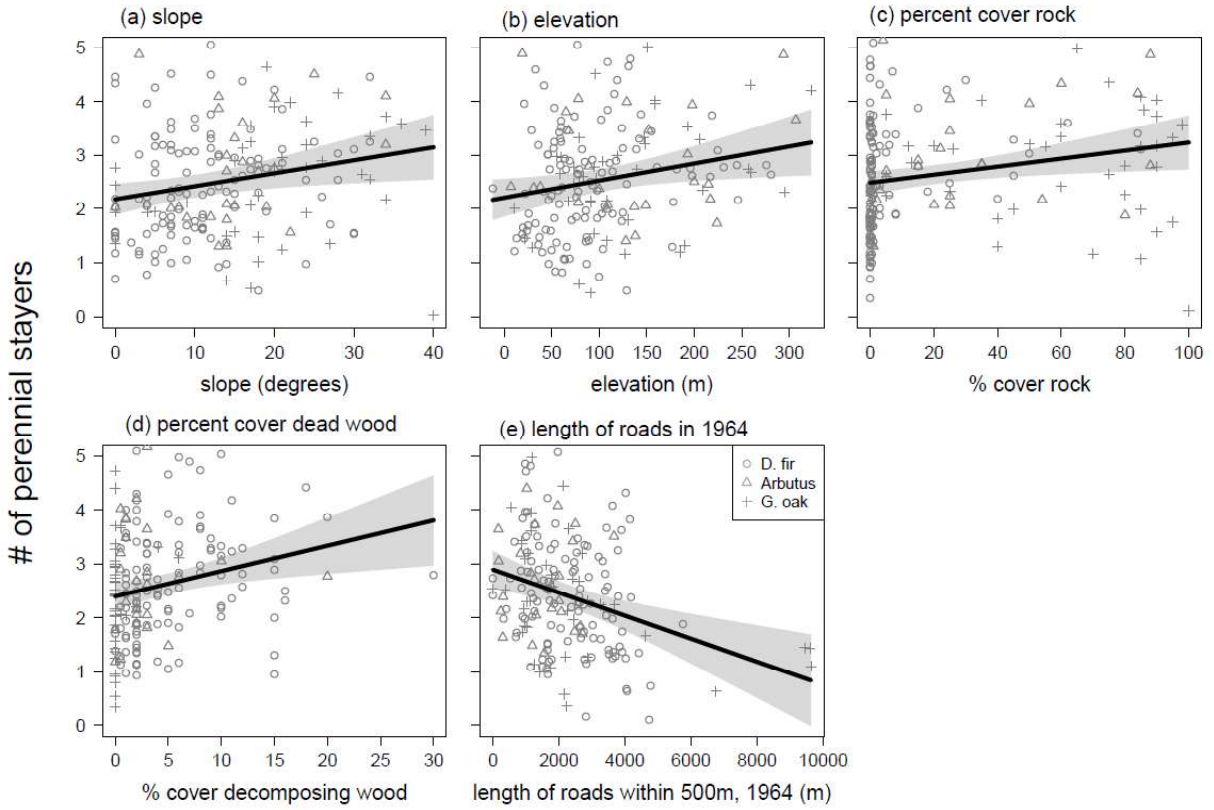

Figure 3. Partial regression plots based on the lowest AIC model for number of perennial stayer bryophyte species, showing the predicted changes with aspect, elevation, percent cover of rock substrate, percent cover of decomposing wood substrate, and length of roads within 500m in 1964. Solid lines indicate the predictor is significant according to a drop1 test. In each case, all other factors are held constant at their median. Symbols represent the vegetation type of each plot. D. fir = Douglas-fir dominated, Arbutus = Douglas-fir with significant component of arbutus trees, G. oak = Garry oak.

Figure 4

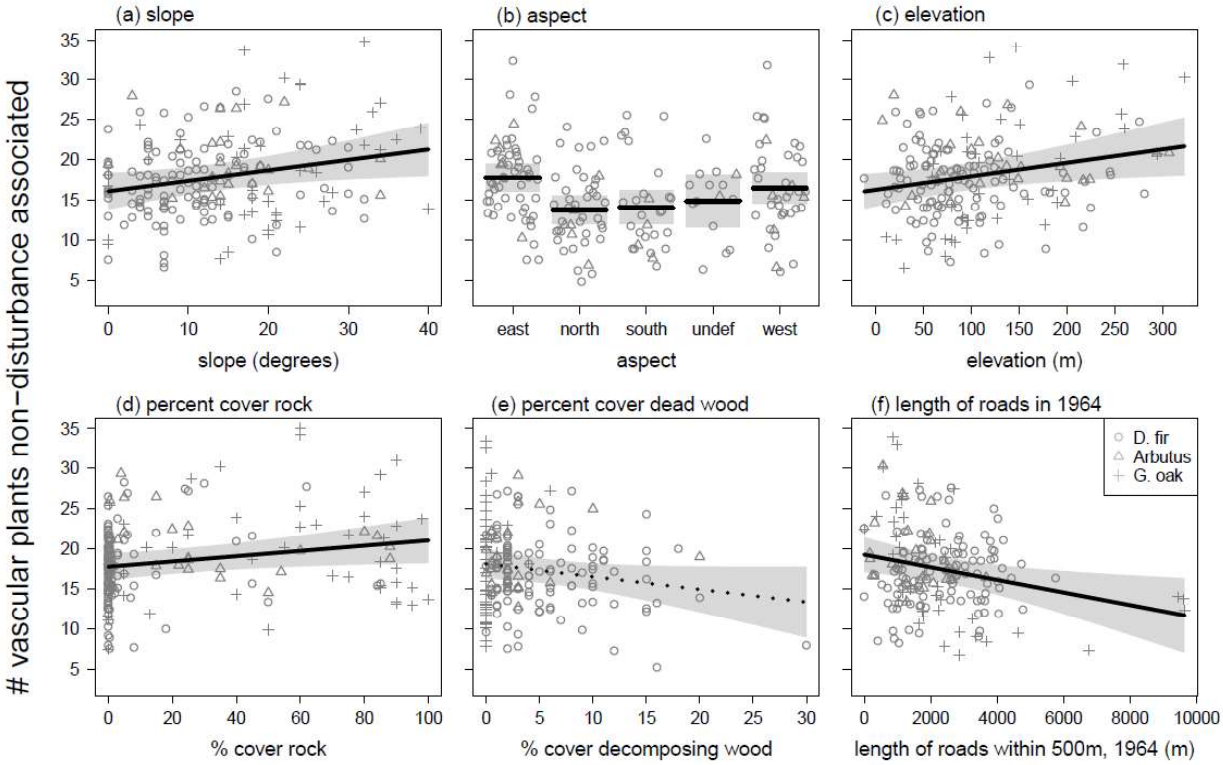

Figure 4. Partial regression plots based on the lowest AIC model for number of non-disturbance-associated vascular plant species, showing the predicted changes with slope, aspect, elevation, percent cover of rock substrate, percent cover of decomposing wood substrate, and length of roads within 500m in 1964. Solid lines indicate the predictor is significant according to a drop1 test. In each case, all other factors are held constant at their median. Symbols represent the vegetation type of each plot. D. fir = Douglas-fir dominated, Arbutus = Douglas-fir with significant component of arbutus trees, G. oak = Garry oak

Tables:

Table 1: (a) model comparisons, and (b) results of drop1 test for each factor included in the lowest AIC model for total bryophyte species richness. Candidate models that outperform the minimum model and/or significant predictors within the lowest AIC model are in bold.

(a) model comparisons MODEL	AIC	ΔAIC[a]	adjusted R^2	
minimum (local factors only)	230.79	0	0.31	
minimum + road density (present)	232.78	-1.99	0.31	
minimum + road density (past)	229.24	1.55	0.32	
minimum + forest area (present)	232.07	-1.28	0.31	
minimum + forest area (past)	231.39	-0.60	0.31	
minimum + distance to edge (present)	231.70	-0.91	0.31	
minimum + distance to edge (past)	232.76	-1.97	0.31	
(b) drop1 test on lowest AIC model FACTOR	coefficient	SE[b]	AIC[c]	p[d]
intercept	4.63	0.14	229.24	n/a
slope	0.54	0.32	230.14	0.094
elevation	**0.97**	**0.33**	**236.04**	**0.004**
% cover rock	**1.67**	**0.34**	**250.21**	**<0.001**
% cover decomposing wood	**0.95**	**0.32**	**237.87**	**0.001**
road density (past)	-0.59	0.32	230.79	0.064

[a] Difference in AIC, minimum model – test model. Values >2 indicate a better model than the minimum model

[b] standard error

[c] AIC of the model including all factors except the one being tested

[d] p value based on an F-test comparing the full model with a model excluding the factor

Table 2: (a) model comparisons, and (b) results of drop1 test for each factor included in the lowest AIC model for total vascular plant understory species richness. The lowest AIC model and/or significant predictors within that model are in bold.

(a) model comparisons MODEL	AIC	ΔAIC[a]	adjusted R^2	
minimum (local factors only)	784.95	0	0.31	
minimum + road density (present)	786.48	-1.53	0.31	
minimum + road density (past)	786.42	-1.47	0.31	
minimum + forest area (present)	784.22	0.73	0.32	
minimum + forest area (past)	786.88	-1.96	0.31	
minimum + distance to edge (present)	**781.58**	**3.38**	**0.33**	
minimum + distance to edge (past)	784.16	0.79	0.32	
(b) drop1 test on lowest AIC model FACTOR	coefficient	SE[b]	AIC[c]	p[d]
intercept	31.75	1.12	781.58	n/a
slope	2.01	1.65	781.12	0.225
aspect (north)	**-5.71**	**1.70**	**786.78**	**0.013**
aspect (south)	**-0.90**	**1.91**		
aspect (undefined)	**-2.80**	**2.81**		
aspect (west)	**-0.78**	**1.73**		
% cover rock	**7.53**	**1.51**	**803.86**	**<0.001**
% cover decomposing wood	**-2.93**	**1.36**	**784.38**	**0.033**
distance to edge (present)	**-2.81**	**1.23**	**784.95**	**0.024**

[a] Difference in AIC, minimum model – test model. Values >2 indicate a better model than the minimum model

[b] standard error

[c] AIC of the model including all factors except the one being tested

[d] p value based on an F-test comparing the full model with a model excluding the factor

* note: coefficients for the categorical predictor aspect are given with respect to the reference level (east). AIC is reported for a model without categorical aspect as a predictor.

Table 3: (a) model comparisons, and (b) results of drop1 test for each factor included in the lowest AIC model for species richness of perennial stayer bryophytes. The lowest AIC model and significant predictors within that model are in bold.

(a) model comparisons MODEL	AIC	ΔAIC[a]	adjusted R^2	
minimum (local factors only)	25.13	0	0.24	
minimum + road density (present)	24.50	0.63	0.25	
minimum + road density (past)	**13.78**	**11.35**	**0.29**	
minimum + forest area (present)	26.03	-0.90	0.25	
minimum + forest area (past)	**21.52**	**3.61**	**0.28**	
minimum + distance to edge (present)	27.13	-2.00	0.24	
minimum + distance to edge (past)	27.13	-2.00	0.24	
(b) drop1 test on lowest AIC model FACTOR	coefficient	SE[b]	AIC[c]	p[d]
intercept	2.73	0.08	13.78	n/a
slope	**0.45**	**0.18**	**18.24**	**0.013**
elevation	**0.44**	**0.18**	**17.55**	0.018
% cover rock	**0.47**	**0.19**	**17.94**	**0.015**
% cover decomposing wood	**0.46**	**0.16**	**19.78**	**0.005**
road density (past)	**-0.65**	**0.18**	**25.13**	**<0.001**

[a] Difference in AIC, minimum model – test model. Values >2 indicate a better model than the minimum model

[b] standard error

[c] AIC of the model including all factors except the one being tested

[d] p value based on an F-test comparing the full model with a model excluding the factor

* note: coefficients for the categorical predictor aspect are given with respect to the reference level (east). AIC is reported for a model without categorical aspect as a predictor.

Table 4: (a) model comparisons, and (b) results of drop1 test for each factor included in the lowest AIC model for species richness of non-disturbance-associated vascular plants. The lowest AIC model and significant predictors within that model are in bold.

(a) model comparisons MODEL	AIC	ΔAIC[a]	adjusted R^2	
minimum (local factors only)	615.09	0	0.29	
minimum + road density (present)	614.75	0.35	0.29	
minimum + road density (past)	**610.32**	**4.78**	**0.31**	
minimum + forest area (present)	617.09	-2.00	0.28	
minimum + forest area (past)	615.58	-0.49	0.29	
minimum + distance to edge (present)	613.82	1.28	0.29	
minimum + distance to edge (past)	613.61	1.48	0.30	
(b) drop1 test on lowest AIC model FACTOR	coefficient	SE[b]	AIC[c]	p[d]
intercept	19.50	1.08	610.32	n/a
slope	**2.42**	**1.04**	**613.94**	**0.022**
aspect (north)	**-4.01**	**1.06**	**620.97**	**0.001**
aspect (south)	**-3.70**	**1.24**		
aspect (undefined)	**-2.91**	**1.81**		
aspect (west)	**-1.31**	**1.12**		
elevation	**2.28**	**0.95**	**614.30**	**0.018**
% cover rock	**2.07**	**0.96**	**613.20**	**0.032**
% cover decomposing wood	-1.56	0.85	611.81	0.070
spatial autocovariate	**0.00**	**0.00**	**612.64**	**0.044**
road density (past)	**-2.40**	**0.94**	**615.09**	**0.012**

[a] Difference in AIC, minimum model – test model. Values >2 indicate a better model than the minimum model

[b] standard error

[c] AIC of the model including all factors except the one being tested

[d] p value based on an F-test comparing the full model with a model excluding the factor

* note: coefficients for the categorical predictor aspect are given with respect to the reference level (east). AIC is reported for a model without categorical aspect as a predictor.

Table 5: (a) model comparisons, and (b) results of drop1 test for each factor included in the lowest AIC model for overall species composition of bryophytes. The lowest AIC model and significant predictors within that model are in bold.

(a) model comparisons MODEL	AIC	ΔAIC[a]	R^2
minimum (local factors only)	1365.3	0	0.32
minimum + road density (present)	1366.3	-1.00	0.32
minimum + road density (past)	1364.5	0.80	0.33
minimum + forest area (present)	1363.9	1.40	0.33
minimum + forest area (past)	1365.6	-0.30	0.33
minimum + distance to edge (present)	1366.8	-1.50	0.32
minimum + distance to edge (past)	1366.4	-1.10	0.32
(b) drop1 test on lowest AIC model MODEL	AIC[b]	ΔAIC[c]	R^2
full model	1363.9	0	0.33
full model - slope	**1366.2**	**-2.30**	**0.32**
full model - aspect	1364.4	-0.50	0.30
full model - elevation	1364.3	-0.40	0.32
full model - % cover rock	**1380.8**	**-16.90**	**0.26**
full model - % cover decomposing wood	**1366.1**	**-2.20**	**0.32**
full model - forest area (present)	1365.3	-1.40	0.32

[a] Difference in AIC, minimum model – test model. Values >2 indicate a better model than the minimum model

[b] AIC of the model including all factors except the one being tested

[c] Difference in AIC of the full model – model with the given predictor dropped out. Values < -2 indicate the model becomes substantially worse if the predictor is dropped.

Table 6: (a) model comparisons, and (b) results of drop1 test for each factor included in the lowest AIC model for overall species composition of understory vascular plants. The lowest AIC model and significant predictors within that model are in bold.

(a) model comparisons MODEL	AIC	ΔAIC[a]	R^2
minimum (local factors only)	1389.7	0	0.31
minimum + road density (present)	1388.3	1.40	0.32
minimum + road density (past)	**1387.0**	**2.70**	**0.33**
minimum + forest area (present)	**1386.2**	**3.50**	**0.33**
minimum + forest area (past)	1388.3	1.40	0.32
minimum + distance to edge (present)	1389.2	0.50	0.32
minimum + distance to edge (past)	1389.7	0.00	0.32
(b) drop1 test on lowest AIC model MODEL	AIC[b]	ΔAIC[c]	R^2
full model	1386.2	0	0.33
full model - slope	1387.4	-1.20	0.32
full model - aspect	**1388.8**	**-2.60**	**0.29**
full model - elevation	1386.5	-0.50	0.32
full model - % cover rock	**1401.0**	**-14.80**	**0.27**
full model - % cover decomposing wood	1387.2	-1.00	0.32
full model - forest area (present)	**1389.7**	**-3.50**	**0.31**

[a] Difference in AIC, minimum model – test model. Values >2 indicate a better model than the minimum model

[b] AIC of the model including all factors except the one being tested

[c] Difference in AIC of the full model – model with the given predictor dropped out. Values < -2 indicate the model becomes substantially worse if the predictor is dropped