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Determinants of moth diversity and community in a temperate mountain landscape: vegetation, topography, and seasonality

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Abstract. Macromoth diversity, abundance, and community structure in the topographically complex HJ Andrews Experimental Forest and LTER site was studied on the west slope of the Cascade Range, Oregon. Data on 493 macromoth species (62,221 individuals) was sampled eight times/year at 20 locations from 2004 to 2008 and examined using multivariate statistics and generalized additive models to determine the importance of topography and vegetation on moth community assembly and diversity. Significant differences exist between moth communities at lower and higher elevations. High-elevation moth communities are far more variable inter-annually, whether associated with high-elevation forests, meadows, or clearcuts. Low-elevation young and old gymnosperm forests and riparian forests are more stable and predictable communities having less inter-annual variability. High-elevation communities show more intra-annual variability than low-elevation communities. Low-elevation moth communities are more abundant than high-elevation communities and typically associated with the most common, abundant species of macromoths in the study. High-elevation communities, by contrast, are associated with less abundant, more evenly distributed species, as well as with rare moth species. Macromoth community structure and diversity were related to year or sample period and structural descriptions of vegetation communities, but not related to known host-plant diversity. High-elevation communities are threatened by contraction of montane meadows and climate change which, given the variability in high-elevation communities, could severely impact the biological diversity of the western Cascades landscape. Nocturnal macromoths represent an important potential indicator of ecosystem health and change.

Key words: community structure; community variability; diversity; host-plant; macromoths; rarity; richness; seasonality.

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INTRODUCTION

Nocturnal macromoths are a highly diverse and ecologically important group of insects that play key roles in herbivory, pollination, prey for birds and bats, and are potential indicators of ecosystem health and change across a wide variety of landscapes (Erhardt and Thomas 1991, Kitching et al. 2000, Summerville and Crist 2004). Numerous studies attempting to determine the distribution of individual moth families to changes in vegetation, climate and topography have been conducted in the tropics (Brehm et al. 2003, 2007, Axmacher et al. 2004, 2009, Beck et al.

2006, Hilt and Fiedler 2006, Beck and Chey 2008), but few have examined multi-family diversity and communities. Most of these studies found that both elevation and plant species distributions are important predictors of moth family distributions and diversity patterns. In temperate regions, studies addressing community structure and diversity of nocturnal macromoths have mostly been undertaken in relatively flat topography and/or homogenous vegetation types (e.g., grassland, deciduous forest, riparian forest) (Usher and Keiller 1998, Kitching et al. 2000, Summerville and Crist 2003, 2004, Ober and Hayes 2010, Summerville 2011). Less is known about how nocturnal macromoth community structure and diversity respond to steep vegetational and elevational gradients at the landscape scale in temperate regions.

Macromoths, like many insect herbivores, tend to be specialized, often utilizing a single species or genus as a host-plant (Hammond and Miller 1998, Miller and Hammond 2003, Maier et al. 2004, Duncan 2006). Because of their dependence on host-plants, the abundance and distribution of macromoth species may reflect vegetation distribution patterns as well as plant phenology (Novotny et al. 2005, 2006), although some studies found that plant diversity did not predict macromoth diversity (Brehm and Fiedler 2003, Axmacher et al. 2004, 2009, Beck and Chey 2007, 2008). Nocturnal macromoth species distribution and diversity have been related to the presence of rare habitats (Miller et al. 2003), vegetation disturbance (Holloway 1985, Kitching et al. 2000, Summerville and Crist 2004, Kuussaari et al. 2007), land use and habitat shifts (Erhardt and Thomas 1991, Ricketts et al. 2001, Baur et al. 2006), habitat size and distribution (Usher and Keiller 1998, Summerville and Crist 2004, Ober and Hayes 2010), and topographic influences on temperature and predation (Brehm and Fiedler 2003, Beck and Chey 2008, Axmacher et al. 2009).

Adult macromoths, which are the more easily trapped life form, emerge in the Pacific Northwest during spring, summer, and fall, and many have estimated life spans of a few weeks, although some live for considerably longer (Miller and Hammond 2000, 2003). The often short adult life spans of many adult moths produce temporal partitioning, with high species turnover in a few weeks. Temporal turnover of moth species exceeded spatial turnover within eastern deciduous woodlands of North America (Summerville and Crist 2004) and in the forests of northern Japan (Hirao et al. 2007), where early and late season moth communities were compositionally very different. Intra-annual or seasonal variability in moth community structure may be as high as or higher than spatial variability. Seasonal variability could also interact with spatial factors, such as vegetation and elevation, to create unique patterns in varied parts of the landscape.

We examined relationships among community structure, abundance, richness, and diversity of nocturnal macromoths in the western Cascades of Oregon, USA. The data consisted of 493 nocturnal macromoth species (62,221 individuals) collected approximately 8 times/year in 20 locations over a five-year period (2004–2008) in the 64-km^2 HJ Andrews Experimental Forest and long-term ecological research (LTER) site, a mountainous conifer forest ecosystem (Appendix: Table A1). The west slope of the Cascade Range is characterized by clearly defined vegetation communities—high and low-elevation conifer forest, riparian forest, and montane meadows—which would be expected to be associated with distinct moth communities. We asked the following questions:

1. What variables explain moth alpha diversity patterns?
2. How do site-level ecological patterns differ, if any, for rare versus common moth species?
3. Are there conservation implications resulting from rare moth distribution patterns?
4. How are moth communities distributed in relation to vegetation communities and topography?
5. How do moth communities ecologically vary seasonally and inter-annually?
6. Are moth communities associated with different vegetation types differentially affected by seasonality?

MATERIALS AND METHODS

Study location

This study was conducted in the HJ Andrews Forest and LTER site (hereafter referred to as

Andrews Forest) within the Willamette National Forest, Lane County, OR (Appendix: Fig. A1), located on the west slope of the Oregon Cascade Range approximately 80 km east of Eugene, OR. The Andrews Forest (6400 ha) occupies the entire Lookout Creek watershed. Elevation ranges from 425 to 1620 m. Annual precipitation averages 230 cm/yr; 80% of rain or snow falls between December and March. Mean monthly temperature typically range from 3°C in January to 20°C in July and August at the low-elevation meteorological station, but seasonal snowpacks persist from November to June above 1000 m.

Approximately 95% of the Andrews Forest is forested, and open ridgetop meadows occupy the remaining 5%. Below 1,000 m, forests are dominated by a 60–80 m overstory of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), with understory species including maple (*Acer* spp.), willow (*Salix* spp.), and alder (*Alnus* spp.). Above 1,000 m, subalpine forest is dominated by Pacific silver fir (*Abies amabilis*) and noble fir (*Abies procera*) with understory species including huckleberry (*Vaccinium* spp.) and ocean spray (*Holodiscus discolor*). Open montane meadows, on broad ridgetops, are dominated by herbaceous plants and grasses, such as lupines (*Lupinus* spp.) and fescues (*Festuca* spp.) (Franklin and Dyrness 1988).

Sampling protocol and moth data preparation

Moths were collected at 20 sites during the late spring, summer, and early autumn of 2004 through 2008 at the Andrews Forest (Appendix: Fig. A1), using UV light traps (Bioquip model number 2851 trap, 22-watt circle light bulbs, 12-volt batteries, and insecticide impregnated strips). Traps were placed at each site for a single night, excluding a seven-day period bracketing the occurrence of a full moon, and collected the following day. Only sampling dates in which all intended traps were deployed were used for this analysis. Sampling events in which some traps were unavailable due to snow blockage were discarded for this study, leaving a total of 800 individual trapping events. All nocturnal macromoths were collected, identified, counted, and recorded according to date and location of collection. No micromoths were considered in this study. Mounted voucher specimens of all species are kept in the Oregon State Arthropod Collection Museum at Oregon State University. All moths used in this study were identified to species level. Moth abundance refers to the number of individuals caught in a single trap for a single night, or the total number of individuals in any group of trapping events. Host plants for caterpillars were determined by field collecting caterpillars and rearing them to adulthood using the vegetation on which they were found (Miller 1995, Miller and Hammond 2003).

Two subsets of the moth dataset were identified from a representative subset of the traps: common and rare moths (Pham et al. 2011). Using a non-metric multidimensional scaling (NMDS) ordination of the fully aggregated moth data (Fig. 1), we identified the two traps in each structural vegetation category that were closest to the centroid of that category and designated those two traps as representative of the moth communities associated with that vegetation category. We then designated common moths as those moth species ($n = 20$) for which more than 300 individuals were captured over the 5-year sampling period. Rare moths ($n = 65$) were defined as those moth species ($n = 65$) for which only 5–10 individuals were captured over the 5-year sampling period.

Explanatory variables

The following explanatory variables, hereafter termed covariates, were used to explain the abundance, richness, Simpson's diversity, Pielou's evenness, and community structure of moths at the Andrews Forest: calendar day (consecutive day of year), sampling period (first or last half of a given month), known host-plant richness, structural vegetation category, watershed, slope, aspect (the horizontal direction to which the slope is facing), elevation, distance to road, distance to stream, and percent vegetational cover within a 100 m radius of the trap site of stream, road, mature/old-growth forest, young forest, open vegetation, and shrub (Appendix: Table A2). For known host-plant richness (assessed during July 2010), plant species not assessed to be host-plants were not recorded. Fifty-two plant species known to be host-plants for Pacific Northwest moths were observed within 100 m of at least one of the 20 trap sites (Appendix: Table A3). Moth trapping sites had

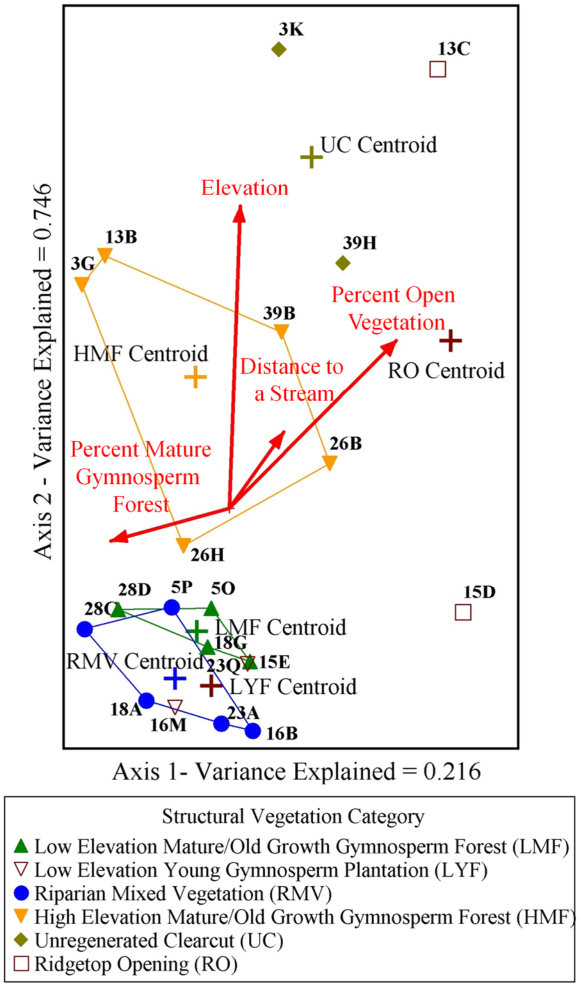

Fig. 1. 2-D non-metric multidimensional scaling (NMDS) ordination graph of fully aggregated moth communities using structural vegetation categories showing the centroid and convex hull polygon for each vegetation category moth community and trap IDs.

between 1 to 5 gymnosperm tree species, 3 to 9 woody-angiosperm species, and 1 to 11 forb and grass species, with an average species richness of 13. Common species included two gymnosperm trees (*Pseudotsuga menziesii* and *Tsuga heterophylla*), three woody-angiosperm trees or shrubs (*Acer circinatum*, *Gaultheria shallon*, and *Rhododendron macrophyllum*), and five ferns-forbs-grasses (*Polysticum munitum*, *Pteridium aquilinium*, *Rubus* spp., *Lupinus* spp., and unidentified grasses). Rarer species included *Abies lasiocarpa*, *Tsuga mertensiana*, *Alnus rubra*, *Arctostaphylos nevadensis*, *Castilleja* sp., *Delphinium* sp., and *Epilobium angustifolium*.

Structural vegetation categories (low-elevation mature/old-growth gymnosperm forest, high-elevation mature/old-growth gymnosperm forest, young gymnosperm forest plantations, open meadows, unregenerated clearcuts, and riparian mixed vegetation) were defined for each moth trap location based on vegetation physiognomy and distance to streams within a 100 m radius of the trap location. These vegetational categories were interpreted from 2005 aerial photography and validated by field visits during the summers of 2008 and 2009. Mature/old-growth gymnosperm forests were subdivided into low-elevation (<1000 m) and high-elevation (>1000 m) categories following Franklin and Dyrness (1988). All young gymnosperm forest plantations were low-elevation (<1000 m) and all unregenerated clearcuts were high-elevation (>1000 m). Riparian mixed vegetation were designated by proximity to streams (<50 m), regardless of the dominant vegetation.

The elevation, aspect, and slope of each moth trap site were calculated using a 10 m Digital Elevation Model (DEM) in ArcGIS 9.3. Aspect and slope raster layers were generated from the DEM using the Spatial Analyst function in ArcGIS.

Statistical analyses

Data were analyzed using repeat-measures analysis of variance (ANOVA), hierarchical agglomerative cluster analysis (HACA), multi-response permutation procedure (MRPP), non-metric multidimensional scaling ordination (NMDS), and generalized additive mixed model (GAMM). HACA, MRPP, and NMDS were conducted using PC-Ord 6.0 (McCune and Mefford 2011). GAMMs were conducted with the mgcv package in R, using Akaike information criterion (AIC) to determine the best model (R Development Core Team 2011, Wood 2011). Analyses were conducted at seasonal and annual time scales. The seasonal analysis (n = 800) included all sampling events at all trap sites for all years (5 years × 20 traps × 10 trapping dates per year, minus 200 sampling events that were not sampled early in the season due to snow or occurrence at low-elevation sites on the same dates that high-elevation sites were not accessible). The yearly analysis ($n = 100$) used total moth abundance or richness from an individual trap site in each year (5 years × 20 traps), including only sampling events from sample periods in which all 20 traps were set.

The abundance and richness of common and rare moths was related to structurally defined vegetation categories using repeat-measures ANOVA and post-hoc Tukey tests. Moth richness, abundance, Simpson's diversity, and Pielou's evenness (dependent variables) were related to biotic and abiotic covariates implemented by a GAMM using Trap ID as a random variable to account for the repeated measures (Zuur et al. 2009). A NMDS was used to quantify community structure of moth species, and to test the effect of the identified covariates on community structure. As with the GAMMs, two versions of the entire moth dataset were created to examine seasonal and yearly patterns with NMDS. A rank-transformed MRPP was used to test the significance of vegetation and topographic variables.

Moth and plant species that were present in <5% of all sample units were omitted from NMDS analyses. Moth abundance data were cube-root transformed before conducting the NMDS to reduce skewness and limit the impact of very abundant species. NMDS analyses were conducted using a Sorensen/Bray-Curtis similarity matrix with a flexible beta linkage (−0.25). For the NMDS analyses, the following procedure was employed: (1) a random starting configuration was chosen, (2) 250 runs were made for a Monte Carlo test, (3) dimensionality was selected based on a better than random solution as determined by the results of the Monte Carlo test and reduction in stress, (4) up to 250 iterations were allowed for calculating a stress stability of <0.000001 over the last 15 iterations, (5) the NMDS plots were overlaid with the environmental variables, and (6) the ordination was rotated to maximize the correlation between the major axis and the most highly correlated environmental variable (Kruskal 1964, McCune and Grace 2002). Using the "convex hull" option in PC-Ord 6.0, convex hull polygons were designated in some ordinations to identify the space occupied by different categorically defined communities (McCune and Mefford 2011).

RESULTS

Alpha diversity

A total of 62,221 individual moths from 493 species were captured in the 800 sampling events from 2004 to 2008 (Appendix: Table A1). Slightly more than 85% of the moths had known host-plants. Most species were rare, as 61 (12%) of the 493 moth species were represented by only 1 individual, and 30 (6%) were represented by 2 individuals. The 15 most common species accounted for 49.9% of the total, while the most common moth species (*Macaria signaria*, a gymnosperm-feeding caterpillar) accounted for 10.7% of total moth abundance.

When aggregated by year to examine inter-annual seasonal patterns, the most significant explanatory variables were year, elevation, and structural vegetation categories (Fig. 2; Appendix: Table A1). Richness was best explained by year ($p < 0.001$), elevation ($p < 0.001$), distance to stream ($p < 0.001$), and percent young forest ($p < 0.001$) ($R^2 = 0.60$). Moth abundance was best explained by year ($p < 0.001$) and structural vegetation categories ($R^2 = 0.63$). Simpson's diversity was best explained by year ($p < 0.001$) and structural vegetation categories ($R^2 = 0.39$). Pielou's evenness was best explained by elevation ($p < 0.001$), year ($p = 0.03$), and structural vegetation categories ($R^2 = 0.74$). Aggregated richness generally decreased from 2004–2008, with a peak in 2005 and slight increase in 2007 from 2006. Aggregated richness decreased with increasing elevation, increased with distance from a stream, and decreased with higher percentages of young gymnosperm forest. Aggregated abundance generally decreased from 2004–2008 with a peak in 2005. Simpson's diversity generally decreased from 2004–2008 with a peak in 2005 and slight increase in 2007 from 2006. Pielou's evenness was fairly consistent from 2004–2008, though with a slight dip in 2006 and slight peak in 2008. Pielou's evenness varied greatly with elevation, with a peak near 1300 m and trough near 800 m.

When moth data were examined for all sampling periods individually (not aggregated) to examine intra-annual seasonal patterns, the most significant explanatory variables were sample period, calendar day, year, and structural vegetation categories (Fig. 3; Appendix: Table

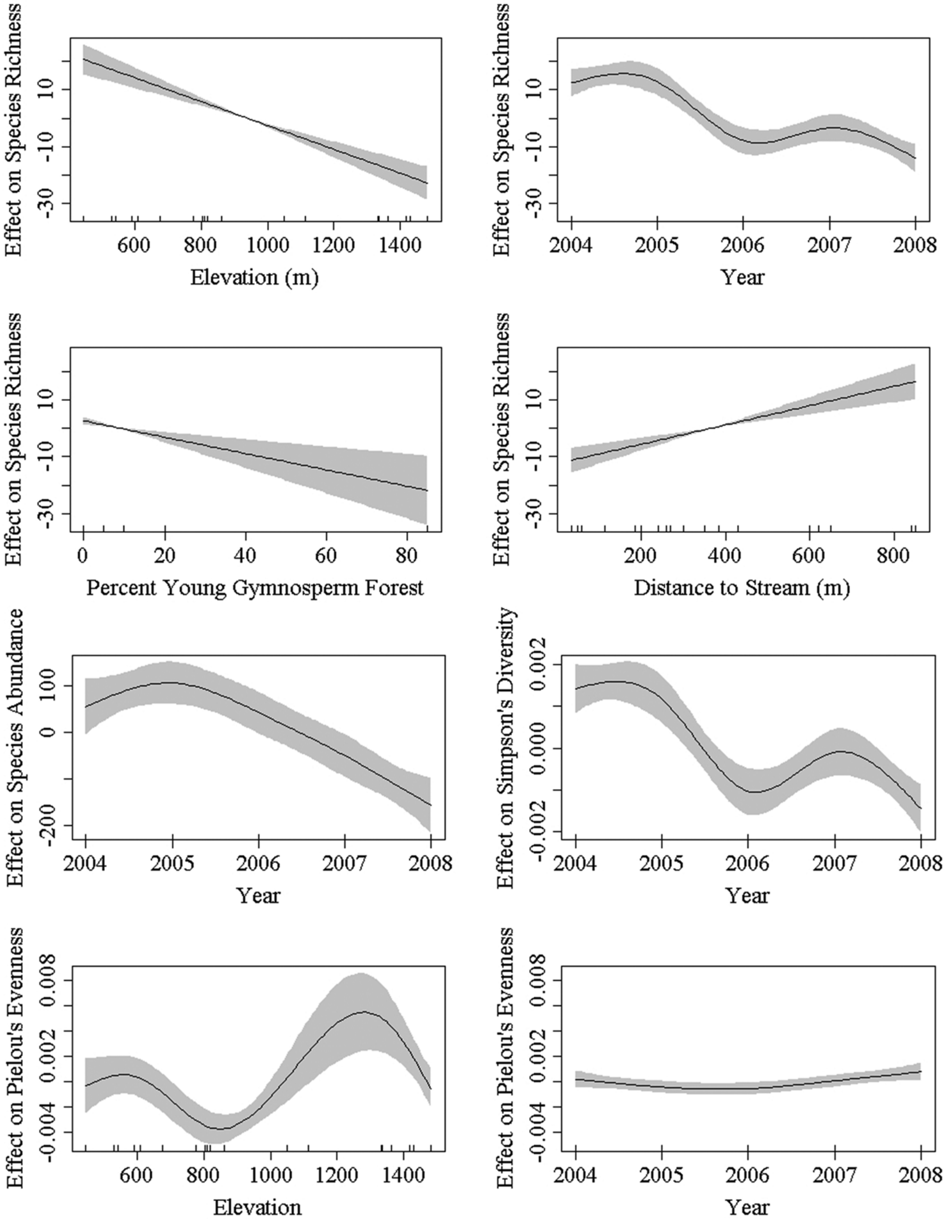

Fig. 2. Plots showing the responses of the yearly aggregated values for species richness, abundance, Simpson's diversity, and Pielou's evenness, to year, elevation, distance to stream, and percent young gymnosperm forest in the best-fit GAMM models. In all plots, the x-axis is the covariate value and the y-axis is the anomaly from the mean response of the dependent variable, with the overall mean response designated as 0.0, showing positive and negative effects on the dependent variable.

A2). Species richness was best explained by sample period ($p < 0.001$), year ($p = 0.004$), and structural vegetation ($R^2 = 0.54$). Moth abundance was best explained by sample period ($p < 0.001$), year ($p = 0.004$), and structural vegetation ($R^2 = 0.45$). Simpson's diversity was best explained by calendar day ($p < 0.001$), year ($p = 0.002$), and structural vegetation ($R^2 = 0.29$). Pielou's evenness was best explained by calendar day ($p < 0.001$) and year ($p = 0.001$). Richness

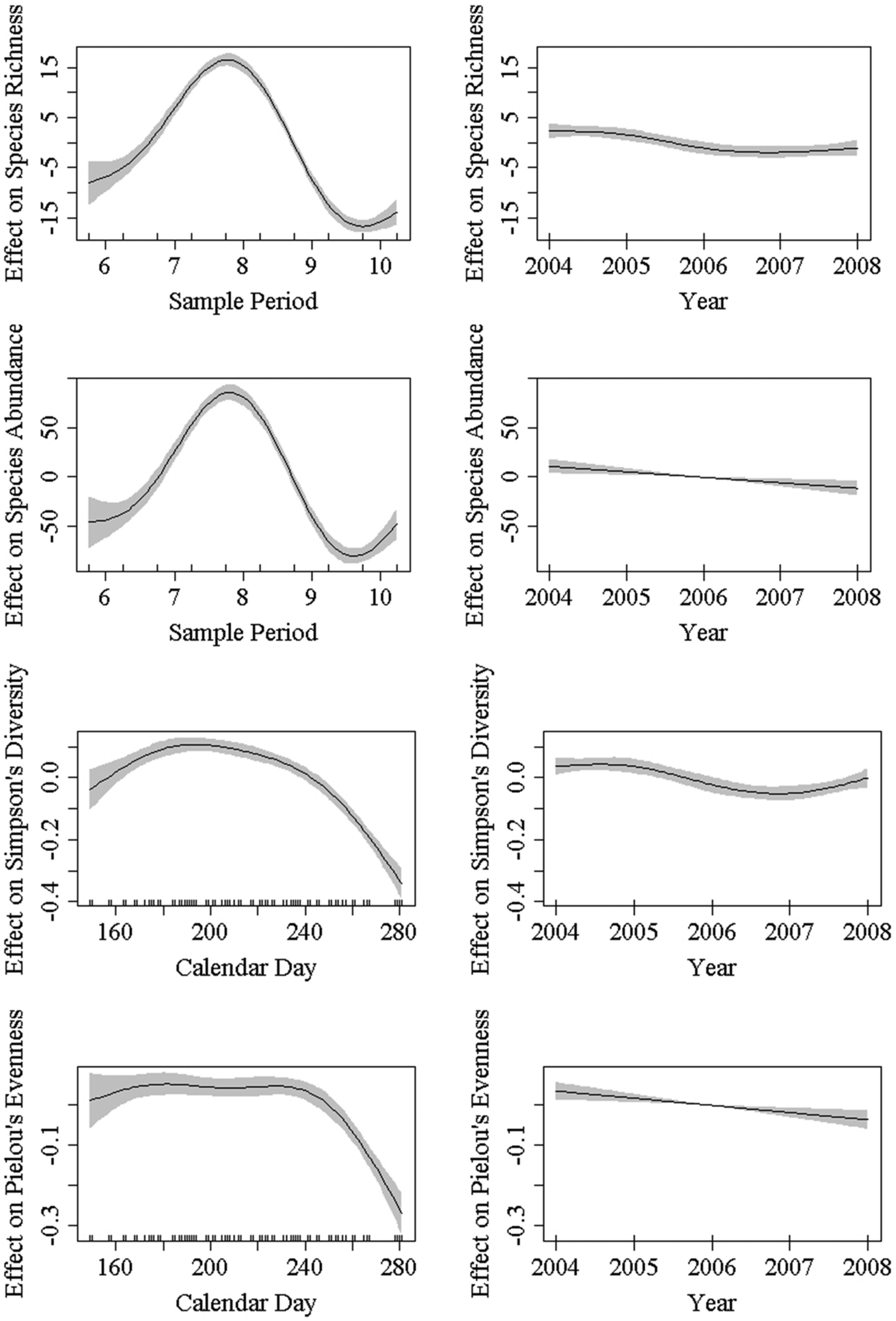

Fig. 3. Plots showing the responses of the unaggregated values for species richness, abundance, Simpson's diversity, and Pielou's evenness to calendar day, sample period, and year in the best-fit GAMM models. In all plots, the x-axis is the covariate value and the y-axis is the anomaly from the mean response of the dependent variable, with the overall mean response designated as 0.0, showing positive and negative effects on the dependent variable.

and abundance peaked in late July and slightly decreased from 2004–2008. Simpson's diversity and Pielou's evenness exhibited less pronounced seasonal peaks, with peaks near calendar day 180 (late June/early July) but also with a gently sloping plateau from near calendar day 180 to 240. Simpson's diversity and Pielou's evenness also showed an overall decrease from 2004–2008, but with a slight increase in 2008 for Simpson's diversity.

Community structure: spatial influences

Yearly aggregated moth community structure was largely explained by different vegetation communities partially associated with elevational differences. A HACA graph shows that the first major split in the overall cluster of aggregated moth community samples largely falls along the 1100 m elevation boundary (Fig. 4). Moth communities also differed significantly among elevation categories with the highest category being the most different, with strong explanatory value (MRPP $A = 0.338$, $p < <0.05$). Vegetation categories also significantly explain moth community structure at the annual time scale. Moth communities differ significantly among structural vegetation categories, with strong explanatory value (MRPP $A = 0.343$, $p < <0.05$). When only moth communities defined by gymnosperm vegetation categories were considered, did elevation categories explain moth community differences better than vegetational categories, although both were significant (MRPP $< <0.05$) and with strong explanatory value (MRPP $A = 0.369$ and 0.264, respectively).

Elevation and the amount of open vegetation within 100 m were strongly associated with moth community structure based on aggregated annual data, and distance to stream also was important (NMDS final stress 14.217, final instability 0.0000) (Fig. 5a). NMDS axes 1 and 2 explained 27.0% and 62.1%, respectively, of the variance in the data. Elevation was most associated with axis 2 of the moth community structure ordination (Pearson correlation $r^2 = 0.805$), followed by percent open vegetation (Pearson correlation $r^2 = 0.472$) and distance to stream (Pearson correlation $r^2 = 0.168$).

Convex hull polygons, connecting the outermost samples of the moth communities, were associated with the different vegetation categories, and also showed that high-elevation communities occupied more ordination space and were therefore more variable and exhibited greater changes from year to year in their species composition and abundance (Fig. 5b). Low-elevation communities occupied far smaller amounts of ordination space and were much more similar from year to year, showing a highly consistent community structure. Successional vectors show that high-elevation communities associated with high-elevation mature/old-growth forests, ridgetop meadows, and unregenerated clearcuts were far more variable from year to year than lower elevation communities associated with low-elevation gymnosperm forests (mature/old-growth or plantation) and riparian mixed vegetation (Fig. 5c). When the successional vectors were reduced to their origin, the higher variability in the higher elevation communities is more evident and comparable with those from the lower elevation communities (Fig. 5d).

Community structure: temporal influences

When moth assemblages were grouped into two-week sampling periods, intra-annual seasonal changes in moth communities overwhelmed other influences on community structure. Moth communities, defined by two-week periods, differed significantly by structural vegetation categories, aspect, slope, and elevation categories (MRPP $p < 0.05$) but only sampling period had high explanatory value (MRPP $A = 0.411$), whereas structural vegetation categories had very weak explanatory values (MRPP $A = 0.062$), as did elevation, aspect, and slope categories (MRPP $A = 0.059$, 0.029, and 0.019, respectively). The 3-D NMDS solution had a final stress of 19.526 and a final instability of 0.00000 (Fig. 6a). Axis 1 explained 20.0%, axis 2 explained 28.0%, and axis 3 explained 23.8% of the variance, for a total of 71.8%. Mean calendar day was the only variable that was strongly correlated (Pearson correlation $r^2 = 0.678$) with any of the three axes. When the samples were coded by sampling period, clusters are evident, especially in late June through early August (Fig. 6a). Clustering is visibly less strong in the spring (late May and early June) and fall (September and October) periods.

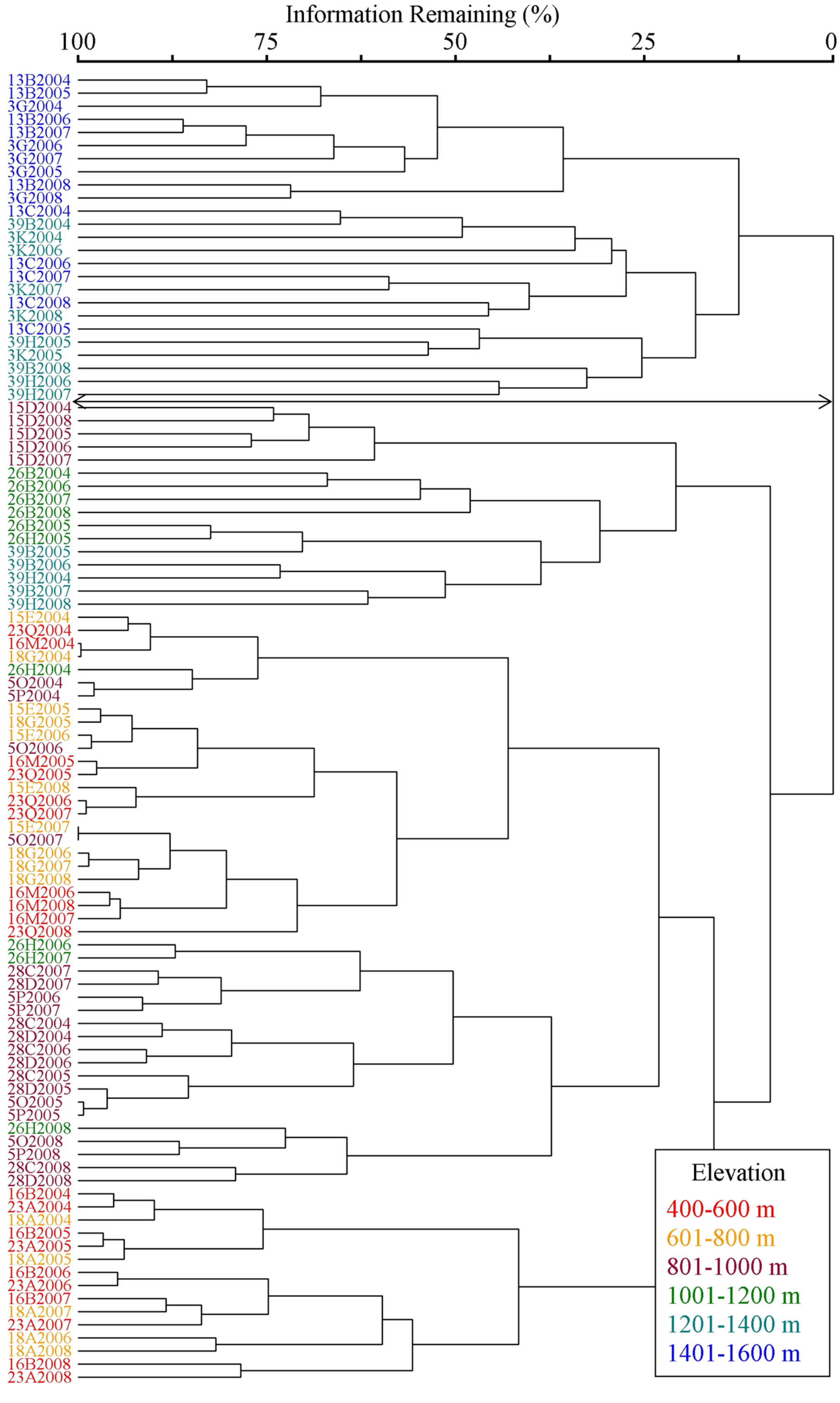

Fig. 4. Hierarchical Agglomerative Cluster Analysis (HACA) showing the grouping of yearly aggregated moth communities. The first and most evident division in the graph, identified by the arrow, is largely along elevationally defined community lines.

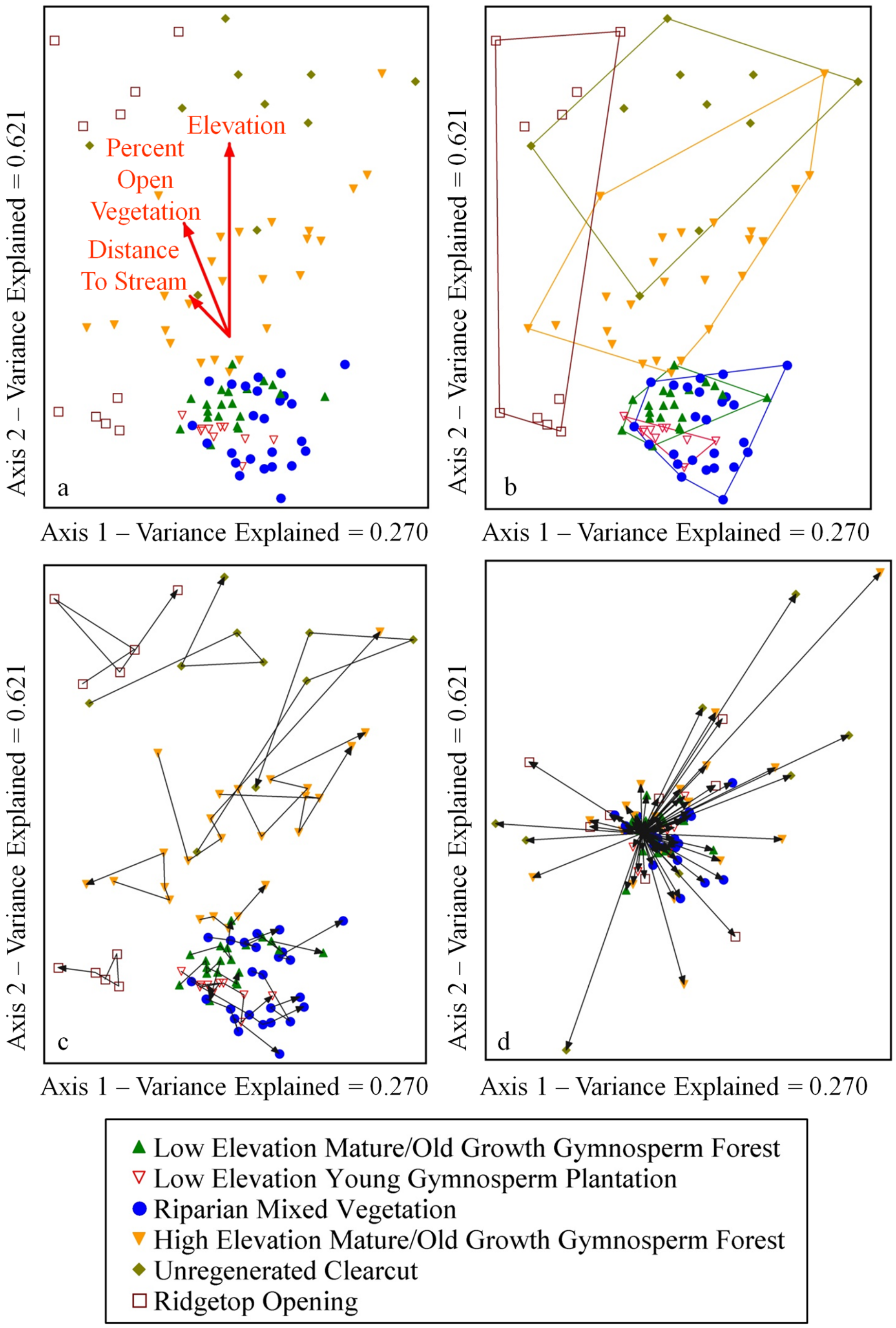

Fig. 5. Two-dimensional non-metric multidimensional scaling (NMDS) ordination graphs of yearly aggregated moth communities using structural vegetation categories showing (a) overall raw pattern, (b) overall pattern with convex hull polygons identifying all points within each vegetation category, (c) overall pattern with successional vectors identifying the direction and magnitude (distance) of community change from one year to the next for each trap, and (d) the successional vectors reduced to origin, showing the comparative magnitude of change of each trap from one year to the next. The high-elevation trap sites exhibit higher inter-annual variation as shown by the larger convex hull polygons and longer successional vectors.

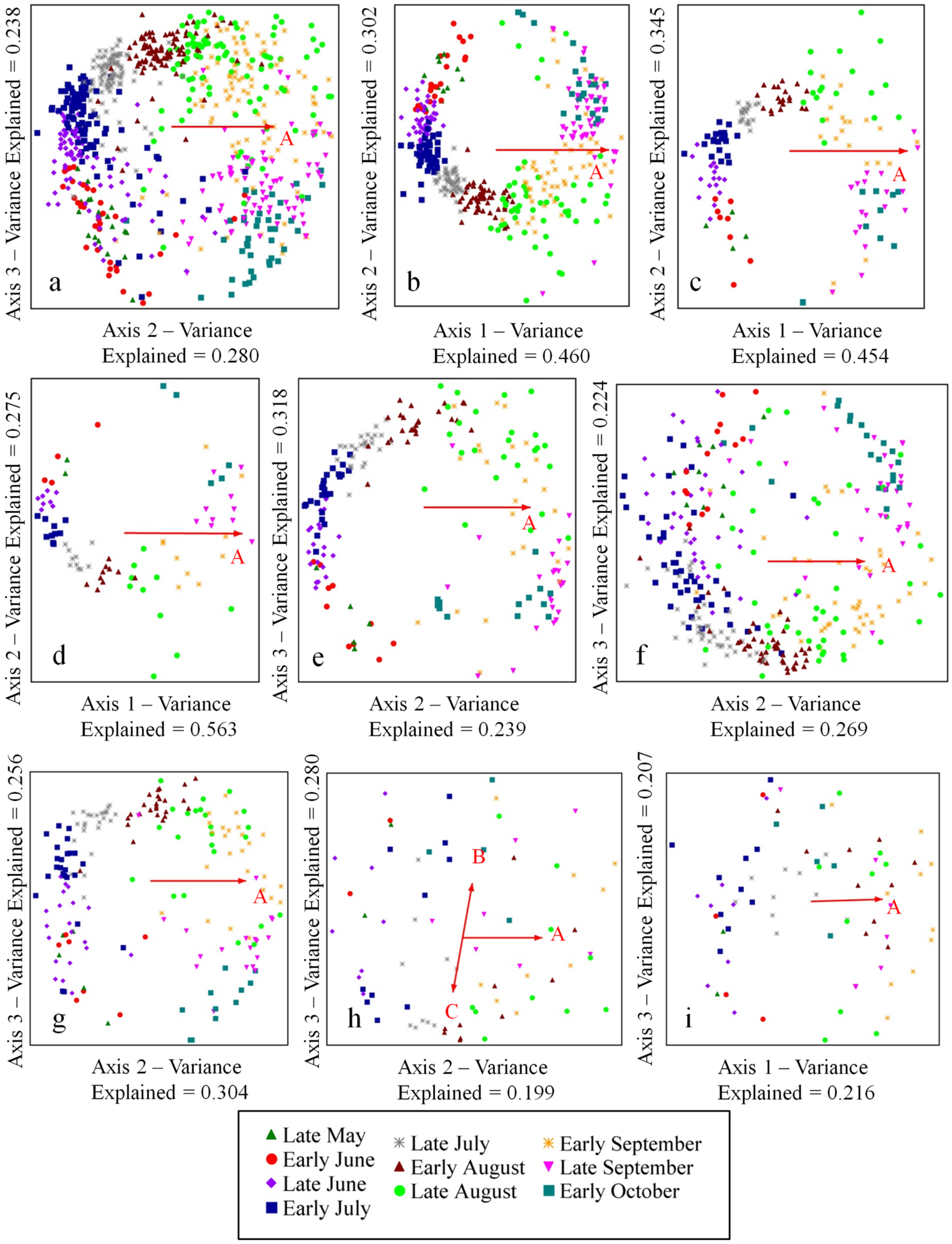

Fig. 6. Graph showing axes 2 vs. 3, the dominant axes, from a 3-D NMDS ordination graph of unaggregated moth traps using sample period categories as the grouping variables for (a) all moths; graphs showing axes 1 vs. 2 from 2-D NMDS ordination graphs for (b) low-elevation moths, (c) low-elevation mature/old-growth gymnosperm forest moths, and (d) low-elevation young gymnosperm plantation moths; and graphs showing axes 2 vs. 3, the dominant axes, from a 3-D NMDS ordination graph for (e) riparian mixed vegetation moths, (f) high-elevation moths, (g) high-elevation mature/old-growth gymnosperm forest moths, (h) ridgetop opening, (i) unregenerated clearcut moths. The designating letters are in the lower left corners of the ordinations. The red letters in the graphs represent different correlated covariates, including calendar day (A), elevation (B), and slope (C).

Community structure: spatial-temporal interaction

Moth communities associated with specific vegetation categories exhibit different seasonal community changes. Aggregated low-elevation moth communities associated with low-elevation gymnosperm forests (young and old) and riparian mixed vegetation exhibit very consistent seasonal patterns, as seen by the tight clustering in the low-elevation seasonal NMDS ordination (Fig. 6b). Late June through early August exhibits very consistent and tight clustering, with late summer and early fall (late August through September) exhibiting increased variation. The 2-D NMDS solution had a final stress of 20.557 and a final instability of 0.00000. Axis 1 explained 46.0% and axis 2 explained 30.2% of the variance, for a total of 76.2%. Mean calendar day was the only variable that was strongly correlated (Pearson correlation $r^2 = 0.774$) with either of the two axes. When examined separately, moth communities associated with low-elevation mature/old-growth gymnosperm forests, young gymnosperm plantations, and riparian mixed vegetation communities all show patterns consistent with the overall low-elevation moth community (Fig. 6c, d, e). All three have consistent, tight clusters from late June through early August and more variable communities from late August through September.

Aggregated high-elevation moth communities associated with high-elevation gymnosperm forests, ridgetop meadows, and clearcuts exhibit far less consistent seasonal patterns than their low-elevation counterparts, as seen by the looser clustering in the high-elevation seasonal NMDS ordination (Fig. 6f). All sample periods show moderate seasonal variability with no tight clustering. The 3-D NMDS solution had a final stress of 21.299 and a final instability of 0.00020. Axis 1 explained 14.6%, axis 2 explained 26.9%, and axis 3 explained 22.4% of the variance, for a total of 63.9%. Calendar day was the only variable that was strongly correlated (Pearson correlation $r^2 = 0.600$) with any of the three axes. When examined separately, moth communities associated with high-elevation mature/old-growth gymnosperm forests, ridgetop meadows, and unregenerated clearcuts have very different seasonal patterns from one another and from the low-elevation communities (Fig. 6g, h, i). High-elevation mature/old-growth gymnosperm forests show the most seasonal consistency of the three communities, with moderate clustering evident in early July through early August and loose but identifiable clustering in the other sample periods. Unregenerated clearcuts show some loose clustering during most sample periods, with only early July exhibiting moderately consistent clustering. Ridgetop meadows show only loose clustering in some sample periods with no clustering evident in other periods. While calendar day is the only variable strongly correlated (Pearson correlation $r^2 > 0.2$) with the high-elevation gymnosperm forest and unregenerated clearcut ordinations, the ridgetop meadow ordination is correlated with calendar day, elevation, and slope (Pearson correlation $r^2 > 0.2$).

Rare and common occurrence patterns

The richness and abundance of common moth species (more than 300 individuals trapped over the five year study) was highest in low-elevation gymnosperm forests followed by low-elevation riparian mixed vegetation and lowest in high-elevation gymnosperm forests, ridgetop meadows, and high-elevation regenerating clearcuts. Common species of moths were more abundant in young gymnosperm plantation forests and mature/old gymnosperm forests at low-elevation than in other vegetation categories (repeat measures ANOVA, $F = 39.7$, $df = 5$, $p < 0.001$; Appendix: Table A3). On average, 308 individuals of common moth species were caught per trap site per year from 2004–2008, but on average 600 individuals were captured in trap sites in young gymnosperm plantations and 588 individuals were captured in trap sites in mature/old-growth gymnosperm forests at low-elevation, and 336 individuals were captured in trap sites in riparian mixed vegetation. Average abundance of common moths was lowest in ridgetop meadows (101 individuals per trap site per year) and high-elevation unregenerated clearcuts (62 individuals per trap site per year), and in high-elevation gymnosperm forests (161 individuals per trap site per year). Similarly, more species of common moths were captured in young and old low-elevation gymnosperm forests and riparian mixed vegetation than in high-elevation vegetation categories (repeat measures ANOVA, F =

15.7, df = 5, p < 0.001; Appendix: Table A3). On average, 16 species of common moths were caught per trap site per year from 2004–2008, but on average all 20 species of common moths were caught in young and old low-elevation gymnosperm forests and 18 were caught in riparian areas. In contrast, on average 14 common moth species were caught in high-elevation gymnosperm forests and ridgetop openings, and only 11 were caught, on average, in unregenerated clearcuts.

Common moths were more likely to be gymnosperm-feeders than woody angiosperm- or herb and grass-feeders. Common moths that feed on gymnosperms or angiosperms were significantly more abundant than moths that feed on herbaceous plants or a mix of plant types (ANOVA, F = 10.8, df = 4, p < 0.001; Appendix: Table A4). Of the 18,482 common moths captured, over half (10,329) were gymnosperm feeders and over a third were woody angiosperm feeders (6364), while 923 were mixed feeders, 866 fed on unknown plant types, and none were known herb and grass-feeders.

Rare species of moths had a richness and abundance of only five to ten individuals trapped in all sites over five years that was highest on ridgetop openings and unregenerated clearcuts and lowest in low-elevation young and old gymnosperm forests. The abundance of rare moth species was highest at ridgetop openings and unregenerated clearcuts, lowest in low-elevation young and old gymnosperm forests, and moderate in riparian areas and high-elevation gymnosperm forests (repeat measures ANOVA, F = 6.2, df = 5, p = 0.0002; Appendix A: Table A5). On average, 20 individuals of rare moth species were caught in trap sites per year in ridgetop meadows and 16 in unregenerated clearcuts, whereas on average 13 individuals were caught in high-elevation gymnosperm forests, 12 in riparian mixed vegetation, nine in low-elevation young gymnosperm plantations, and eight in low-elevation mature/old-growth gymnosperm forests. In terms of species richness, more species of rare moths were captured in ridgetop openings and unregenerated clearcuts than in all four categories of forested areas (repeat measures ANOVA, F = 6.4, df = 5, p = 0.0001; Appendix: Table A5). On average, ten species of rare moths were caught per trap from 2004–2008, but on average 15 species were caught in ridgetop openings, 12 in unregenerated clearcuts, 11 in high-elevation gymnosperm forests, 10 in areas of riparian mixed vegetation, eight in low-elevation young gymnosperm plantations, and seven in low-elevation mature/old-growth gymnosperm forests.

Rare moths more likely were woody angiosperm or herb and grass-feeders than gymnosperm-feeders. Rare moth species that feed on woody-angiosperm and herbaceous species were significantly more abundant than rare moths that feed on gymnosperms, a mix of plant types, or unknown plant types (ANOVA, F = 39.9, df = 4, p < 0.001; Appendix: Table A6). Of the 484 rare moths captured, nearly half were woody angiosperm-feeders (236), with herb-feeders accounting for over a third of the rare individuals captured (176), unknown-feeders accounting for 64 individuals, and gymnosperm-feeders accounting for only eight individuals.

DISCUSSION

Diversity and abundance

Spatial and temporal factors explained moth diversity, but the relationships were complex and dependent on multiple factors. While some studies have reported that overall plant diversity is not a good indicator of overall moth diversity (Axmacher et al. 2004, 2009, Brehm et al. 2007), others have suggested that plant diversity is a good predictor of macromoth diversity (Novotny et al. 2006). Known host-plant diversity was not a good predictor of macromoth richness, diversity, evenness, or abundance in this study, but a more general physiognomic description of the vegetation communities were good predictors, akin to the findings of Axmacher et al. (2009). Known host-plants in this area carry different loads of caterpillars. Some plants (*Ceanothus* spp., *Arctostaphylos* spp., *Symphoricarpos albus*) host a large number of caterpillars, while others (*Rhododendron macrophyllum*, *Polysticum munitum*) host a much lower number of caterpillar (Miller and Hammond 2000, 2003). While Novotny et al. (2006) showed that tree richness predicted the richness of caterpillars feeding on them, the majority of macromoth caterpillars in this region feed on angiosperm shrub species, which host highly varying numbers of caterpillars.

The overall structure of the vegetation community explains much macromoth diversity, abundance, and evenness in space. Models that include structural features of the vegetation as a factor result in the elimination of elevation as a significant variable and ultimately explain more variance. Vegetation-based communities are the major spatial drivers of moth diversity and abundance in this landscape. Generally, mature/old-growth low-elevation gymnosperm forests are positively associated with macromoth abundance and richness, at an annual scale. At the same time, high-elevation vegetation communities are negatively associated annually with macromoth richness and abundance. High moth abundance in low-elevation gymnosperm forests is consistent with the idea that insect abundance depends on plant biomass (Knops et al. 1999), although high-elevation forests are high in plant biomass, but not macromoth abundance. In this study area, gymnosperms are the host plant for the most common moth, *Macaria signaria*, which accounts for nearly one-tenth of the entire moth abundance in the study, and they also host many of the other most common moth species in the study landscape. Species richness on a yearly scale is negatively associated with elevation and percent cover of young gymnosperm forest, but positively associated with distance to a stream. As our lowest trap site is 446 m, this pattern is potentially consistent with other studies showing a mid-domain effect (Brehm et al. 2007). In this system and in any given year, low-elevation old-growth gymnosperm forests are the most moth species rich vegetation community, especially for those that occur away from streams. Although it is often assumed that riparian forests have high nocturnal moth richness (e.g., Ober and Hayes 2010), riparian habitats had only moderate moth richness and abundance in the study landscape. The moderate diversity of moth communities in the narrow linear riparian zones in the study area suggests that nocturnal moths do not perceive major distinctions between these forests and the vegetation types (gymnosperm forests) that border them, nor do the unique plants associated with the riparian habitats, such as western red cedar (*Thuja plicata*), serve as major host-plants for moths not served by other, non-riparian plant species. Riparian associated plants, like *Alnus rubra*, that serve as a host to many macromoth species also occur in non-riparian portions of this landscape, such as disturbed areas.

When aggregated over the entire five years, average richness peaks at the higher elevations, with the two richest traps being located in mature/old-growth high-elevation gymnosperm forests and the highest average richness occurring in ridgetop openings. This pattern contrasts with the pattern shown by the yearly aggregations. Because the species associated with the high-elevation vegetation communities are not captured consistently every year due to their high inter-annual community variation, these habitats have lower yearly richness values. While elevation was not typically a significant variable in explaining Simpson's diversity, Pielou's evenness exhibited a bimodal elevation pattern, peaking at 600 and 1300 m, with a trough at 900 m. The peak at 1300 m is likely due to the presence of meadows and clearcuts, plant communities with the greatest evenness, but it is unclear what is causing the trough at 900 m.

Over time, moths are highly seasonal and possess a distinct seasonal peak in richness and abundance, and a less distinct but still identifiable peak in diversity and evenness. All four measurements have their peaks in July, but while richness and abundance peak in late July, diversity and evenness peak in June or early July and maintain high levels through early September. From 2004 to 2008, abundance, diversity and richness have all decreased, but with a peak in 2005. This is likely the result of an overall cooling trend that has occurred in the region over the study period. Evenness, unlike the other measurements, did not decrease from 2004–2008, as a decrease in highly abundant species would cause a decrease in Simpson's diversity, species richness, and abundance, it would not cause a decrease in evenness and is the likely reason for this pattern.

Moth-plant community coupling at the landscape scale

Most previous moth community studies in temperate climates are short term ($\leq$2 yr) and conducted in relatively homogenous (eastern deciduous forest) landscapes (Summerville and Crist 2003, 2004, Summerville et al. 2005), homogenous habitats (riparian forest) (Ober and Hayes 2010), or cool temperate forests in

Japan (Hirao et al. 2006, 2007). This study revealed a major distinction between nocturnal moth communities associated with low- vs. high-elevation vegetation types typically diverging around 1100 m—the usual winter snowline in the study area. Low-elevation vegetation types included low-elevation old-growth and young gymnosperm forests and riparian vegetation. Low-elevation gymnosperm forests, which dominate the western Cascades landscape, are the most productive habitats for moths in the study area and contain the most stable communities, though not necessarily the richest over the long-term. The least year to year variability is found in low-elevation gymnosperm forests in this landscape (consistent with Hammond and Miller 1998), as well as the highest abundance of macromoths. Riparian moth communities consistently grouped with the low-elevation gymnosperm forest communities and exhibited minimal community differentiation from the low-elevation gymnosperm forests.

High-elevation vegetation types included gymnosperm forests and non-forest openings (meadows and clearcuts). Moth communities of high-elevation gymnosperm forests are far less consistent from year to year than those of lower elevation gymnosperm forests and riparian areas. High-elevation gymnosperm forests appear to be habitats for moth species that are of intermediate abundance or rare. While not necessarily true in all regions (Maier et al. 2004, Duncan 2006), our observations based on our empirical data suggests that most macromoths that feed on gymnosperms as caterpillars in this region possess broad host ranges at the species level particularly involving the Pinaceae (Miller and Hammond 2000, 2003). Nevertheless, in this study the moth communities of high vs. low-elevation gymnosperm forests are very different. Most nocturnal moth species of high-elevation gymnosperm forests consequently depend on understory plants in these forests; these sites are highly variable with respect to both plants and moths. Additionally, the importance of elevation suggests that high-elevation moths are adapted to a partial existence under the snowpack, a life-habit that low-elevation moths are unable to do.

Seasonal and intra-annual moth community variability

Very few studies have examined the inter-annual and intra-annual turnover of moth species. Summerville and Crist (2003) found that species turnover between early and late seasons at a site exceeded spatial turnover among distant patches of eastern deciduous forests of North America. In our study site, bi-weekly to monthly turnover was higher than spatial turnover between different but nearby habitat types. Low-elevation communities also were more consistently formed into tight species groups than high-elevation communities, showing that the intra-annual patterns of moth communities at high-elevations are more variable than those from low-elevations. This is consistent with the finding that low-elevation moth communities are less variable than high-elevation communities at the inter-annual scale. In addition, different communities of moths associated with different vegetation categories exhibited very different patterns of temporal turnover. In the four forest vegetation categories, moth communities associated from July through early August were relatively consistent and tightly grouped over all five years. Spring and fall samples are much more variable and less tightly grouped. In the meadows and clearcuts, there was little to no grouping by sample period, suggesting that these communities are the most variable inter- and intra-annually.

Moths are temperature sensitive and their maturation is partially influenced by weather (Raimondo et al. 2004). The fluctuations in the length of snow pack at the higher elevations and the beginning or ending of winter and spring are likely causes for the higher variability in spring and early summer communities as well as higher elevation communities. Diapause behavior by some summer species awaiting precipitation may cause the drastic increase in variability in late August and September. As this region follows a Mediterranean precipitation pattern, late summer rains after a dry early summer and late spring may be a temporally varied but important influence in late summer moth communities. Therefore, climate change could cause a pronounced and disruptive shift in the already highly variable moth communities at the higher elevations of the study site, which are expected to experience more rapid warming than lower elevations (Daly et al. 2010), and are experiencing a reduction in habitat area (Takaoka and Swanson 2008, Highland 2011). Because the higher elevation moth and plant communities are unique and contain most of the rare species, such changes in climate coupled with changes in habitat size and distribution could significantly impoverish the biodiversity of the region and similar mountain systems.

Rare macromoths

High-elevation nonforested clearings are ecologically important parts of the landscape. While these openings generally have lower moth abundance than forested areas, they have high richness and evenness when summed over many years and are important habitats for rare moth species. While other studies have found that rare species of moths are distributed evenly across feeding guilds (Novotny and Basset 2000), rare moth species in our region are mostly angiosperm–shrub or herb/grass-feeders as caterpillars. Moth communities of high-elevation openings are tightly coupled to the habitats containing high-elevation herbs, grasses, and angiosperm shrubs. However, disturbed openings (unregenerated clearcuts) bore different plant and moth communities than the natural openings, and overall were less abundant and diverse, but still contained many rare moths. High-elevation, unregenerated clearcuts appear to provide some habitat for moths requiring open habitats, including many rare moths, but do not fulfill all of the requirements for meadow specialist moths, as clearcuts are less diverse overall. Therefore, while clearcuts provide some conservation value for macromoths associated with high-elevation clearings, they cannot fully replace meadows and should not be considered their equivalent for conservation purposes.

CONCLUSIONS

This five-year study illustrates the remarkable variety, plasticity, adaptability, specialization of moth communities in heterogenous mountain landscapes. The topographic and vegetative heterogeneity of this steep, western forest landscape helped to reveal the dynamic and spatially complex characteristics of nocturnal moth communities. Further studies of nocturnal moths, which are ubiquitous and diverse, may reveal climate change and land use effects on ecosystems. Because nocturnal moths are closely tied to plant species diversity and structure and, presumably, phenology, they also are useful indicators of overall diversity at the landscape scale (Summerville et al. 2004, Rákosy and Schmitt 2011). Rare moth species are linked to rare habitats, specifically high-elevation openings in the Andrews Forest. This suggests that small, rare habitats in other mountain landscapes also may be islands of moth biodiversity. In our study area, meadow habitats are rare and contracting (Miller and Halpern 1998, Takaoka and Swanson 2008, Highland 2011), so management for preservation and restoration of these habitats is a priority. Furthermore, the high interannual variability in moth communities in these habitats suggest that large areas of habitat may need to be preserved to maintain populations in the face of environmental stochasticity. Also, management approaches may need to be adaptive to account for the high interannual variability of these species.

Nocturnal moths also are good indicators of changing climate conditions in local and regional landscapes because many species have relatively discrete distributional boundaries associated with the distribution of their host-plants and climatic limits. Because moths respond to fluctuations in temperatures from year to year via accelerated or delayed maturation, they are effective biological indicators of climate change effects. Changes in moth maturation can affect food webs, especially in the spring when migratory birds and bats rely heavily upon caterpillars and adult moths for food. Moths additionally are known to be important in pollination networks, such that decoupling of moth and plant maturation due to out-of-phase environmental cues (temperature vs. photoperiod) could disrupt pollination networks. While macromoths do require extensive expertise in taxonomy and require specific environmental conditions, such as the absence of a near-full moon, wind or precipitation, their ubiquity and sensitivity to biotic and abiotic environmental conditions do make them potentially good indicators. Therefore, more attention should be focused on the taxonomy and ecology of this diverse and functionally important group of insects.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Summary of the results of the Generalized Additive Mixed Models of yearly aggregated moth species richness, abundance, Simpson's diversity index value, and Pielou's evenness value, 2004 to 2008, at 20 moth trapping sites in the Andrews Forest, including the variables in the final model and their p-values.

Response variable	Predictor variables included in final model	p
Richness ($R^2 = 0.60$)	Year	<0.001 (−)
	Elevation	<0.001 (−)
	Distance to Stream	<0.001 (+)
	Percent Young Forest	<0.001 (−)
Abundance ($R^2 = 0.63$)	Year	<0.001 (−)
	Factor: Structural Vegetation:Low elevation mature/old growth gymnosperm forest	<0.001 (+)
	Factor: Structural Vegetation:Low elevation young gymnosperm plantation	<0.001 (+)
	Factor: Structural Vegetation:Riparian Mixed Vegetation	0.05 (+)
	Factor: Structural Vegetation:High elevation mature/old growth gymnosperm forest	>0.05
	Factor: Structural Vegetation:Ridgetop Meadow	>0.05
	Factor: Structural Vegetation:High elevation unregenerated clearcut	0.04 (−)
Simpson's Diversity ($R^2 = 0.39$)	Year	<0.001
	Factor: Structural Vegetation:Low elevation mature/old growth gymnosperm forest	>0.05
	Factor: Structural Vegetation:Low elevation young gymnosperm plantation	>0.05
	Factor: Structural Vegetation:Riparian Mixed Vegetation	>0.05
	Factor: Structural Vegetation:High elevation mature/old growth gymnosperm forest	>0.05
	Factor: Structural Vegetation:Ridgetop Meadow	>0.05
	Factor: Structural Vegetation:High elevation unregenerated clearcut	0.03 (−)
Pielou's Evenness ($R^2 = 0.74$)	Elevation	<0.001
	Year	0.03
	Factor: Structural Vegetation:Low elevation mature/old growth gymnosperm forest	>0.05
	Factor: Structural Vegetation:Low elevation young gymnosperm plantation	0.05 (−)
	Factor: Structural Vegetation:Riparian Mixed Vegetation	>0.05
	Factor: Structural Vegetation:High elevation mature/old growth gymnosperm forest	>0.05
	Factor: Structural Vegetation:Ridgetop Meadow	<0.001 (+)
	Factor: Structural Vegetation:High elevation unregenerated clearcut	0.05 (+)

Table A2. Summary of the results of the Generalized Additive Mixed Models of unaggregated moth species richness, abundance, Simpson's diversity index value, and Pielou's evenness value, 2004 to 2008, at 20 moth trapping sites in the Andrews Forest, including the variables in the final model and their p-values.

Response variable	Predictor variables included in final model	p
Richness ($R^2 = 0.54$)	Sample Period	<0.001 (var)
	Year	0.001 (−)
	Factor: Structural Vegetation:Low elevation mature/old growth gymnosperm forest	>0.05
	Factor: Structural Vegetation:Low elevation young gymnosperm plantation	>0.05
	Factor: Structural Vegetation:Riparian Mixed Vegetation	>0.05
	Factor: Structural Vegetation:High elevation mature/old growth gymnosperm forest	0.008 (−)
	Factor: Structural Vegetation:Ridgetop Meadow	<0.001 (−)
	Factor: Structural Vegetation:High elevation unregenerated clearcut	0.02 (−)
Abundance ($R^2 = 0.45$)	Sample Period	<0.001 (var)
	Year	0.002 (−)
	Factor: Structural Vegetation:Low elevation mature/old growth gymnosperm forest	>0.05
	Factor: Structural Vegetation:Low elevation young gymnosperm plantation	>0.05
	Factor: Structural Vegetation:Riparian Mixed Vegetation	<0.001 (−)
	Factor: Structural Vegetation:High elevation mature/old growth gymnosperm forest	<0.001 (−)
	Factor: Structural Vegetation:Ridgetop Meadow	<0.001 (−)
	Factor: Structural Vegetation:High elevation unregenerated clearcut	<0.001 (−)
Simpson's Diversity ($R^2 = 0.29$)	Year	<0.001 (−)
	Calendar Day	<0.001 (var)
	Factor: Structural Vegetation:Low elevation mature/old growth gymnosperm forest	>0.05
	Factor: Structural Vegetation:Low elevation young gymnosperm plantation	>0.05
	Factor: Structural Vegetation:Riparian Mixed Vegetation	>0.05
	Factor: Structural Vegetation:High elevation mature/old growth gymnosperm forest	0.02 (−)
	Factor: Structural Vegetation:Ridgetop Meadow	0.008 (−)
	Factor: Structural Vegetation:High elevation unregenerated clearcut	>0.05
Pielou's Evenness ($R^2 = 0.15$)	Year	0.001 (−)
	Calendar Day	<0.001 (var)

Table A3. Summary of the results of the repeat measures ANOVAs analyzing the vegetation association of common moths. Values followed by the same superscript letter are not significantly different from one another at $p < 0.05$ according to a post-hoc Tukey test.

			Common moths			
Structural vegetation category	No. traps†	No. years sampled	Total abundance	Average abundance	Total richness	Average richness
Low elevation						
Mature/old growth gymnosperm forest	2	5	5883	588.3^{a} (±40.04)	197	19.7^{a} (±0.15)
Young gymnosperm forest plantation	2	5	5995	599.5^{a} (±72.07)	197	19.7^{a} (±0.15)
Riparian mixed vegetation	2	5	3357	335.7^{b} (±45.30)	182	18.2^{a} (±0.42)
High elevation						
Mature/old-growth gymnosperm forest	2	5	1614	161.4^{c} (±30.80)	143	14.3^{b} (±0.92)
Unregenerated clearcut	2	5	620	62^{c} (±18.75)	110	11^{c} (±1.25)
Ridgetop meadow	2	5	1013	101.3^{c} (±21.77)	135	$13.5^{b,c}$ (±1.37)

† No. traps is the number of traps per vegetation category.

Table A4. Summary of the results of the repeat measures ANOVAs analyzing the host-plant preference of common moths. Numbers followed by the same letter are not significantly different from one another at $p < 0.05$ according to a post-hoc Tukey test.

Host plant category—common moths	No. traps†	No. years sampled	Abundance of guild members	
			Total	Average
Gymnosperm	12	5	10329	0.7^{d} (±0.26)
Woody angiosperm	12	5	6364	19.7^{a} (±1.90)
Herb and grass	12	5	0	14.7^{b} (±2.30)
Unknown	12	5	64	5.3^{c} (±0.76)
Mix	12	5	923	0.0

† No. traps is the number of traps per vegetation category.

Table A5. Summary of the results of the repeat measures ANOVAs analyzing the vegetation association of rare moths. Values followed by the same letter are not significantly different from one another at $p < 0.05$ according to a post-hoc Tukey test.

Structural vegetation category	No. traps†	No. years sampled	Rare moths			
			Total abundance	Average abundance	Total richness	Average richness
Low elevation						
Mature/old growth gymnosperm forest	2	5	56	5.6^{c} (±1.12)	47	$4.7^{b,c,d}$ (± 0.86)
Young gymnosperm forest plantation	2	5	49	4.9^{c} (±0.74)	42	4.2^{d} (± 0.47)
Riparian mixed vegetation	2	5	79	$7.9^{b,c}$ (±1.14)	60	$6^{a,b,c}$ (±0.70)
High elevation						
Mature/old-growth gymnosperm forest	2	5	68	6.8^{b} (±1.31)	54	$5.4^{b,c,d}$ (±1.07)
Unregenerated clearcut	2	5	98	$9.8^{a,b}$ (±2.63)	62	$6.2^{a,b}$ (±0.94)
Ridgetop meadow	2	5	117	11.7^{a} (±1.22)	77	7.7^{a} (±0.72)

† No. traps is the number of traps per vegetation category.

Table A6. Summary of the results of the repeat measures ANOVAs analyzing the host-plant preference of rare moths. Values followed by the same letter are not significantly different from one another at $p < 0.05$ according to a post-hoc Tukey test.

Host plant category—rare moths	No. traps†	No. years sampled	Guild members	
			Total abundance	Average abundance
Gymnosperm	12	5	8	0.7^{d} (± 0.26)
Woody angiosperm	12	5	236	19.7^{a} (±1.90)
Herb and grass	12	5	176	14.7^{b} (±2.30)
Unknown	12	5	64	5.3^{c} (±0.76)
Mix	12	5	0	0.0e

† No. traps is the number of traps per vegetation category.

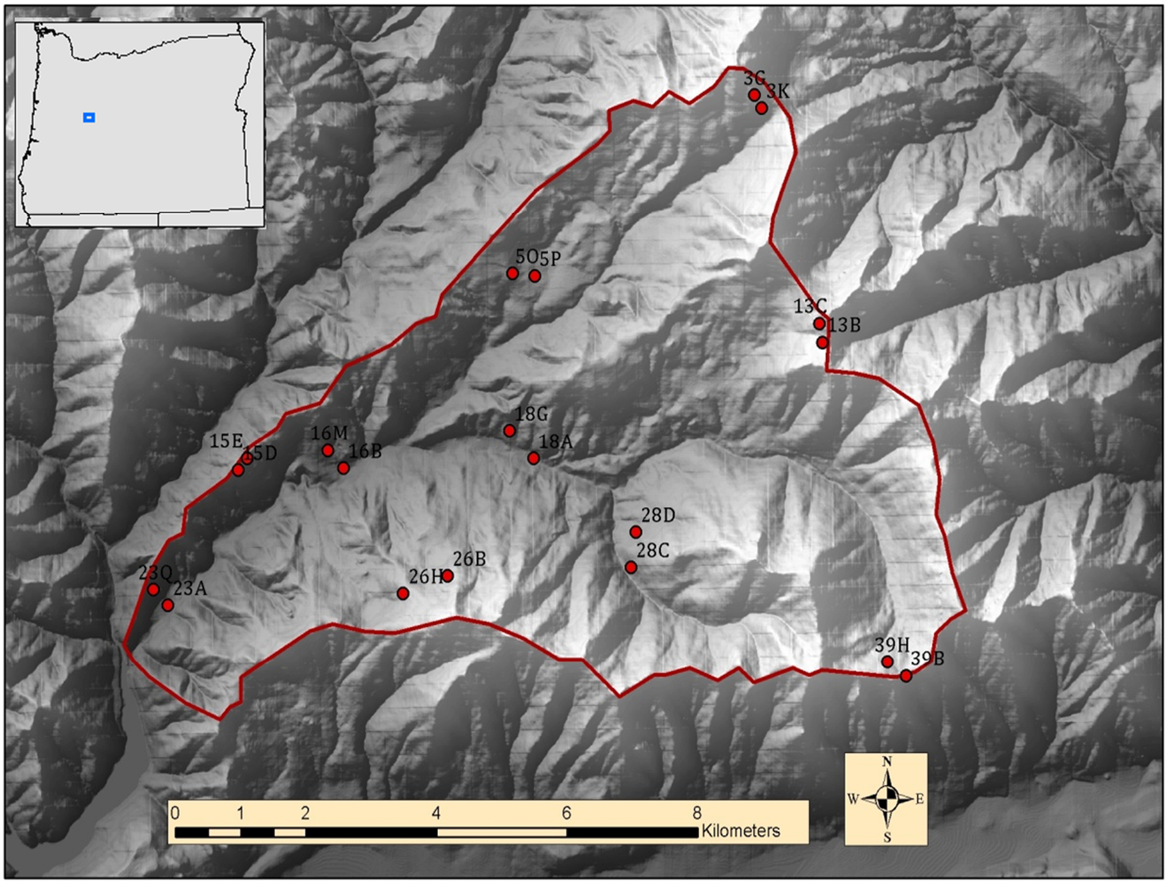

Fig. A1. Locations of the Andrews Forest (red line) and the 20 moth trap sites (red dots) sampled from 2004 to 2008 in the Andrews Forest.

SUPPLEMENT

Tables listing all captured moth species, known host-plant species, and environmental and ecological values for the 20 trap sites utilized in this study (*Ecological Archives* C004-012-S1).