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ORIGINAL PAPER

Extinction debt in naturally contracting mountain meadows in the Pacific Northwest, USA: varying responses of plants and feeding guilds of nocturnal moths

Steven A. Highland · Julia A. Jones

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Abstract Fire suppression and climate change are leading to habitat fragmentation in temperate montane meadows across the globe, raising concerns about biodiversity loss. Restoration strategies may depend on the rate and nature of species response to habitat loss. We examined the effects of habitat loss and fragmentation on plants and nocturnal moths in natural montane meadows in the western Cascades, Oregon, USA, using generalized additive mixed models, non-metric multidimensional scaling, and multiple response permutation procedure. Historic (1949) rather than current (2005) meadow size explained species richness of herbaceous plants and herb-feeding moths and meadow plant community structure, indicating that loss of meadow species may be delayed by many decades following loss of meadow habitat, resulting in an extinction debt. In contrast, abundance of herb-feeding moths and species richness and abundance of woody plant-feeding moths were related to recent meadow configuration: as meadows are invaded by woody plants, abundance of meadow species declines, and woody plants and associated moths increase. Despite decades of fire suppression and climate change, montane meadows in many temperate mountain landscapes may still be amenable to restoration.

Keywords Extinction debt · Meadow-dependent species · Montane meadows · Conservation · Biodiversity · Nocturnal moths

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S. A. Highland (✉) · J. A. Jones
College of Earth, Ocean and Atmospheric Sciences, Oregon State University, 104 CEOAS Administration Building, Corvallis, OR 97330, USA
e-mail: highlans@geo.oregonstate.edu

J. A. Jones
e-mail: jonesj@geo.oregonstate.edu

Introduction

Habitat loss and fragmentation are primary drivers of global loss of biodiversity (Fahrig 2003; Tilman et al. 2001). After habitat loss, populations in remnants may survive for some time before local extinction occurs (Brooks et al. 1999; Hanski and Ovaskainen 2002; Lindborg and Eriksson 2004; Helm et al. 2006; Vellend et al. 2006; Krauss et al. 2010). This lag, or 'extinction debt' (Tilman et al. 1994; Kuussaari et al. 2009) poses major challenges and opportunities for biodiversity conservation. Extinction debt refers to the number of extant specialist species of a habitat expected to become extinct as the community approaches a new equilibrium after a disturbance (Kuussaari et al. 2009). While extinction debt assumes that equilibrium was present prior to disturbance, proving equilibrium in an historic landscape is difficult and typically assumed, not proven, if mentioned at all (e.g. Öckinger et al. 2010; Bommarco et al. 2014). However, while some groups of species experience extinction debt, other species may be favored by changes in the landscape.

Extinction debt has been documented in human-generated and -maintained (agricultural, managed pasture, and urban) landscapes in Europe that begin to undergo natural succession, once they are no longer actively managed by humans for agricultural or other purposes (Helm et al. 2006; Lindborg 2007; Sang et al. 2010; Polus et al. 2007; Sitzia and Trentanovi 2011). However, it is unclear how extinction debt might be expressed in natural habitats that were not originally created by humans and are undergoing fragmentation from natural processes, such as forest succession and tree invasion. Habitat, here, refers to vegetation communities identifiable from aerial photographs that potentially contain specific species of plants that can serve as host-plants to specific moth species. Montane meadows are common in western North America and have dramatically reduced in size and fragmented over the past century due to tree invasion. Therefore, in these meadows, woody plants are colonizers while herbaceous plants and grasses are persisting and, potentially, being driven locally extinct. While the extent of management and manipulation of these meadows by native peoples is unknown, fire suppression, climate change, or cessation of short-term grazing may contribute to meadow contraction (Miller and Halpern 1998). Meadow contraction provides an opportunity to seek evidence of extinction debt in plant and insect species that occur in natural, largely unmanaged landscapes. Also, extinction debt studies typically avoid landscapes with multiple fragments in close proximity (Öckinger et al. 2010) and fragmenting and contracting montane meadows provide a case study for this type of landscape. Additionally, montane meadows represent islands of open habitats in otherwise forested mountains that contain unique assemblages of organisms, including plants that do not persist under forested conditions and require open, non-forested areas to survive (Haugo and Halpern 2007). Many of these plants serve as host-plants to moth species and contribute greatly to the overall biodiversity of mountain landscapes in the western US. Thus, understanding the rates of species loss in these habitats is critical for biodiversity conservation.

Vulnerability to extinction debt varies according to life history and trophic relationships. Long-lived species may experience delayed extinction as individuals die off and are not fully replaced (Helm et al. 2006; Lindborg 2007; Vellend et al. 2006). In contrast, short-lived species such as butterflies provide mixed evidence for delayed extinction (Krauss et al. 2010; Öckinger et al. 2010; Sang et al. 2010), perhaps due to differences in tolerance to reductions in host-plants by generalists and specialists, or due to differences in dispersal abilities. Nocturnal moths, which are very diverse and closely tied to key food plants, offer an ideal study organism for testing the effects of meadow loss and fragmentation on extinction of plants and moths that depend on those plants. Most of the moths in this study have smaller wing lengths than butterflies and, therefore, smaller dispersal distances (Nieminen 1996; Hambäck et al. 2007; Öckinger et al. 2010). Wingspan and body size in nocturnal moths have been shown to affect species responses to fragmentation and habitat isolation and loss, with smaller wingspans and thinner bodies indicating a higher sensitivity to local fragmentation, isolation, and habitat loss (Nieminen 1996; Hambäck et al. 2007; Öckinger et al. 2010). Therefore, if moths are responding to general changes in the size of their habitat overall without regard to the maintenance of specific plants, they should reach equilibrium fairly quickly and not show evidence of extinction debt. On the other hand, if moths are responding to changes in food plant distribution, they should reach equilibrium more slowly and show evidence of extinction debt if their food plants also show evidence of extinction debt. Feeding guilds of nocturnal moths, including herbaceous and woody plant feeders also may respond differently to changes in the landscape.

In this study, we examined how herbaceous plants, nocturnal macromoths that feed on herbaceous plants, and woody-plant feeding macromoths are related to landscape configuration in naturally contracting mountain meadows in the western Cascade Range of Oregon. These changes are thought to have begun contracting due to changes in landscape management associated with the arrival of Euro-American culture and exploration, including fire suppression, grazing, and cessation of Native American foraging and management (Miller and Halpern 1998; Highland 2011). Prior to these changes in landscape management, these meadows are assumed to have been stable and at equilibrium for at least a few 100 years. We hypothesized that

1. species richness of plants in montane meadows, and species richness and abundance of moths that feed on those meadow plants, would be more closely related to past than to present meadow configuration
2. species richness and abundance of moths dependent on woody plants would be related to the present configuration of woody plants.

We interpreted relationships with past meadow configuration as evidence for extinction debt following Kuussaari et al. (2009) and considered the implications for biodiversity conservation.

Materials and methods

Study area

This study was based on vegetation and moth data collected during the summer and fall of 2008, 2009, and 2010 on the high eastern ridge of the HJ Andrews Experimental Forest and Long Term Ecological Research (LTER) site (hereafter Andrews Forest) within the Willamette National Forest, Lane County, OR, USA (Fig. 1). Approximately 95 % of the Andrews Forest is forested, and meadows occupy slightly <5 % of area, along high elevation ridgetops. Plant communities below 1,000 m elevation are dominated by an overstory of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) that create a canopy 60–80 m high. Plant communities above 1,000 m consist of a mix of subalpine forests, shrub fields, and montane meadows. Subalpine forests are dominated by an overstory of 50–70 m Pacific Silver fir (*Abies amabilis*) and noble fir (*Abies procera*) with an understory of various woody-angiosperm trees and shrubs such as huckleberry

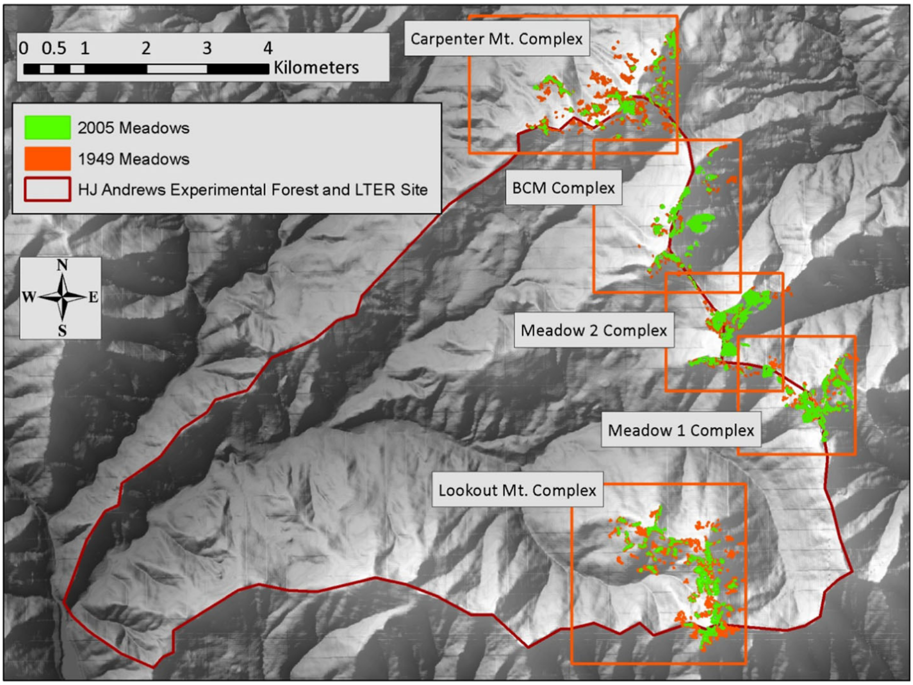

Fig. 1 Overview of the HJ Andrews Experimental Forest, location of the meadows, shape and configuration of meadows in 1949 and 2005, and location of the five meadow complexes

(*Vaccinium* spp.) and ocean spray (*Holodiscus discolor*). Open montane ridgetop meadows are dominated by herbaceous plants and grasses, such as lupines (*Lupinus* spp.) and fescues (*Festuca* spp.). The meadows originated prior to Euro-American settlement and have been undisturbed, apart from sheep grazing for a few decades in the late nineteenth and early twentieth century (Miller and Halpern 1998; Takaoka and Swanson 2008). Similar meadows occur on the high ridges of the western Cascades throughout the Pacific Northwest (Franklin and Dyrness 1988).

Meadow metrics

All meadows (non-forest, non-shrub vegetation) larger than 0.01 ha were mapped using aerial photographs from 1949 to 2005. A 2005 one-meter resolution image of Lane County, OR from the National Agricultural Imagery Program (NAIP) was used as the basis for digitizing the 2005 meadow layer. Aerial photographs from 1949 (black and white, 1:20,000) were acquired and scanned at the U.S. Forest Service Pacific Northwest Research Station, then georectified using permanent or semi-permanent landscape markers. The perimeter and area of each meadow in 1949 and 2005 were digitized, excluding all identifiable trees and tree clusters in meadows. Elevation, aspect, and slope were calculated for each meadow using a 10-m digital elevation model (DEM). The change in area and perimeter of each meadow from 1949 to 2005 was determined. Distances from the edges of each meadow to the nearest neighboring meadow and nearest road were calculated. Meadows were grouped into five “meadow complexes”: spatial clusters containing meadow fragments ranging in size and isolation that formed intuitive landscape groupings (Fig. 1). The total meadow area within each complex was calculated. Spatial data analysis was conducted using ArcGIS 9.3.

Vegetation sampling

Vegetation was sampled in the summer of 2008 at fifteen meadows and two low density forests in saddles adjacent to meadows. Three plots were located in each of the five meadow complexes: one each in the largest meadow, a medium or small fragment of a formerly large meadow (in 1949), and a medium or small meadow that was isolated in 1949. Sampled meadows ranged in size from 0.4 to 10.7 ha in 1949 and from 0.2 to 4.7 ha in 2005. A modified-Whittaker plot [a $20 \times 50\ \mathrm{m}^2$ plot within which are nested one central $5 \times 20\ \mathrm{m}^2$ subplot, two corner $2 \times 5\ \mathrm{m}^2$ subplots, and ten $0.5 \times 2\ \mathrm{m}^2$ subplots distributed around the inside edge of the large plot (Stohlgren et al. 1995)] was sampled in each meadow. This nested vegetation plot design is appropriate for studies of biological diversity because it captures more species of plants in a smaller amount of time than many other techniques (Stohlgren et al. 1995). Percent cover of all plant species was recorded in each nested subplot. The remaining portion of the full plot was examined for plant species not identified in the subplots. Total percent cover by species and total richness for all subplots were used in statistical analyses. Most sampled plots in meadows were within 50 m of a forest edge, from 10 to 920 m from roads, and 25 to 288 m from the nearest neighboring meadow. All plants were identified to species and identified as perennial or annual following Hitchcock and Cronquist (1973). Plants were defined as “meadow specialists” if they required open, non-forested habitats to survive, using habitat descriptions provided by Hitchcock and Cronquist (1973) and the USDA Plants Database (http://plants.usda.gov/).

Moth sampling

Moth sampling utilized a stratified systematic design with trap locations stratified by vegetation type and meadow size (0.5–4.7 ha), and sampling was distributed uniformly over the summers (July to September) of 2008, 2009, and 2010 (Fig. 5 in Appendix). Of the total of 98 moth traps, 65 were in meadows and 33 were in other vegetation types (forests, clearcuts, and roads at high-elevation sites), and 44, 43, and 11 traps were sampled in 2008, 2009, and 2010, respectively. Moths were collected using UV light traps. Each trap consisted of a 5-gallon bucket on which is mounted a circular ultraviolet blacklight and which contained an insecticide-impregnated strip (Bioquip model #2851 trap Rancho Dominguez CA, USA). Moth traps were placed in a given location for a single night (excluding periods of near full moon) and collected the following day. Moth abundance refers to the number of individuals caught in a single trap in a single night, or the total number of individuals in any aggregated assemblage of trapping events. All moths were identified to species when possible and genus level otherwise, following Miller and Hammond (2000, 2003, 2007). Host plants for moths, if known, were based on Miller (1995), who captured caterpillars in the field and successfully reared them to adulthood using the vegetation on which they were found, or further work documented in Miller and Hammond (2000, 2003, 2007). Using host plant information, each moth species was assigned to a feeding guild following Miller and Hammond (2000, 2003, 2007): herb-feeders, woody-angiosperm-feeders, or gymnosperm-feeders. “Herb-feeders” eat herbaceous plants and grasses, “woody-angiosperm-feeders” eat parts of angiosperm shrubs and trees, and "gymnosperm-feeders" eat parts of coniferous trees, during the caterpillar stage. Herb-feeders are "meadow specialists" in this landscape because non-meadow vegetation types contain few herbaceous plants. Very few moths in this system belong to multiple feeding guilds, and few species are specialists on individual plant species (Miller and Hammond 2000, 2003, 2007). Instead, most moth species appear to be somewhat flexible within their feeding guild in that gymnosperm-feeders can likely feed on multiple species of gymnosperm trees and grass-feeders can likely feed on multiple grass species. Therefore, our attribution of feeding guilds to different moth species is reliable, even if all host plants for a given moth species are not known.

Statistical analysis

Data were analyzed using three statistical techniques: (1) generalized additive mixed models (GAMMs), (2) rank-transformed multi-response permutation procedure (MRPP), and (3) non-metric multidimensional scaling ordination (NMDS). PC-ORD version 5.31 was used for the MRPP and NMDS analyses (McCune and Mefford 2006).

Generalized additive mixed models using the Poisson distribution family and log link function tested the relationship between contemporary vegetation and plant richness, moth richness and moth abundance (response variables) and the spatial distribution of meadows, forest, and roads in 1949 and 2005 (predictor variables), using meadow complex as a random variable. Response variables included plant species richness (total and meadow specialist perennial), species richness of the three moth feeding guilds, and species abundances of the three moth feeding guilds. Predictor variables included meadow area and perimeter in 1949 and 2005; forest area increase (new forest) 1949–2005; 1949 meadow complex area; 2005 meadow complex area; 2005 fragment area (total area of meadow fragments that had been one meadow in 1949); distance from sample location to the nearest forest (in 1949 and 2005), road, and next meadow; calendar day of sample; and meadow complex association. GAMM models were run for all combinations of predictor and response variables using un-biased risk estimator criterion (UBRE) scores to assess variable inclusion in the larger models, considered the preferred method when using the Poisson distribution family (Wood 2006, 2011). For the plants, models were run with meadow area and perimeter in 1949 and 2005; forest area increase (new forest) 1949–2005; 1949 meadow complex area; 2005 meadow complex area; 2005 fragment area individually to identify the one with the lowest UBRE score, lowest p value, highest adjusted R^2, and highest deviance-explained. Then, the three distance variables (to road, nearest meadow, or forest) were added to the best model and the distance variable that provided the greatest model improvement was included in the final model. For the moths, models were run with calendar day as the first variable, to account for the high degree of seasonality in the moth data, then each meadow measurement individually to identify the one with the lowest UBRE score, lowest significant p value (<0.05), highest adjusted R^2, and highest deviance-explained. A second set of models were run using only the 65 samples taken in meadows to test whether including forest samples altered the results. Moths in this region have a dramatic increase, peak, and decrease in richness and abundance from spring through fall (Highland et al. 2013; Fig. 6 in Appendix), and the data used here followed the same trend. GAMM analyses were conducted using the mgvc package in R (R Development Core Team 2013; Wood 2011). Plants and moths were determined to have experienced extinction debt if their contemporary richness or abundance values were better explained by 1949 landscape metrics than 2005 landscape metrics, following the methods established by multiple prior extinction debt studies (Kuussaari et al. 2009; Lindborg and Eriksson 2004).

Multi-response permutation procedure is a nonparametric procedure for testing the hypothesis of no difference between two or more groups (McCune and Grace 2002; Mielke 1984; Mielke and Berry 2001). Results of MRPP are evaluated based on a *p* value and an A-statistic. The A value is a chance-corrected within-group agreement that measures the effect size, with a value of 0.1 indicating moderate effect and a value of over 0.2 indicating a moderate to high effect (McCune and Grace 2002). This analysis was designed to supplement and support the NMDS analysis to test for evidence of extinction debt in the community structure, not just richness and abundance, of plants and moths. For plants, MRPP was used to test whether a priori habitat size groups based on 1949 meadow area or based on 2005 meadow area better explained plant community structure. Moth community structure was not analyzed using MRPP due to the high degree of stress in the moth community data. MRPP was conducted using PC-ORD version 6.

Non-metric multidimensional scaling ordination was used to describe plant community structure and to identify correlated environmental variables in montane meadows. The NMDS followed procedures recommended by Kruskal (1964) and McCune and Grace (2002). Plant abundance data (percent cover) were arcsine square root transformed. NMDS was conducted separately for herb-, woody-angiosperm-, and gymnosperm-feeder groups of moths. Moth abundance data was transformed using Beal's Smoothing (McCune 1994). Moth community structure was not analyzed due to high stress in the data.

Results

Meadow contraction

Montane meadows in the study site contracted by more than 45 % from 1949 to 2005 (145.8 to 79.8 ha). Meadow size ranged from 0.05 to 10.7 ha in 1949 and 0.04 to 4.7 ha in 2005. From 1949 to 2005, large meadows became fragmented by tree invasion, and small meadows disappeared, resulting in an overall decrease from 419 patches in 1949 to 261 meadow patches in 2005 (Highland 2011).

Plant richness

A total of 148 plant species, including herbaceous plants, woody-angiosperm shrubs, and coniferous trees, was recorded in the 17 0.1-ha sample plots distributed throughout the five meadow complexes. A few species dominated cover in most plots, and most species were rare and had low (<5 %) cover. Meadow specialists—herbaceous plants that require open, non-forested conditions—represented two thirds (99 species) of species recorded, including 66 perennial herb and 33 annual species. An average of 35 plant species (range 21–49), 25 meadow specialists (range 9–44), and 20 specialist perennials (range 8–30) occurred in the plots.

Meadow area in 1949 and distance to road or distance to nearest meadow explained most variation in plant species richness, and meadow area in 1949 explained more variance and deviance than any other predictor variable (Table 1). Although meadow area in 2005 was also a significant predictor variable, models including meadow area in 2005 explained less variance and deviance, had higher UBRE scores and higher (less significant) *p* values than those including meadow area in 1949. Distance to road was the second most

Table 1 Summary of the results of the GAMM models of plant richness by degree of specialization, and moth richness and abundance by feeding guild, including the total variance explained, deviance explained (GAMM), and the variables (*p* values in parentheses) included in the best fit models

Dependent variable	Adjusted R^2	Deviance explained (%)	Explanatory variables in the best fit model
Total plant richness	0.725	80.8	1949 meadow area (ha) (0.001) Distance to road (m) (0.009)
Meadow specialist perennial plant richness	0.771	82.9	1949 meadow area (ha) (0.0002) Distance to nearest meadow (m) (0.04)
Herb-feeding moth richness	0.184	23.1	Calendar day (<0.001) 1949 meadow perimeter (m) (0.0007) Distance to road (m) (0.04)
Herb-feeding moth abundance	0.318	42.9	Calendar day (<0.001) Percent open vegetation (<0.001) Distance to forest 2005 (<0.001)
Gymnosperm-feeding moth richness	0.353	38.9	Calendar day (<0.001) New forest (ha) (0.002) Distance to nearest meadow (m) (0.03)
Gymnosperm-feeding moth abundance	0.208	40.8	Calendar day (<0.001) New forest (ha) (<0.001) Distance to road (m) (<0.001)
Woody angiosperm-feeding moth richness	0.429	46.8	Calendar day (<0.001) 2005 Meadow perimeter (0.0002) Distance to road (m) (<0.001)
Woody angiosperm-feeding moth abundance	0.453	52.0	Calendar day (<0.001); 2005 Meadow perimeter (<0.001); Distance to road (m) (<0.001)

For the moths, the best fit models were limited to include only calendar day and one meadow size measurement

significant variable after 1949 meadow area in the best-fit model for all plant species (trees, shrubs, and herbaceous plants). Distance to nearest meadow was the second most significant variable after 1949 meadow area in the best-fit model for meadow specialist perennials.

Plant species richness was nonlinearly related to meadow area. Total richness dropped at a faster rate than the mean response in meadows of 0–3 ha and increased at a faster rate in meadows of 8–11 ha (no sampled meadows were in the range of 4–8 ha) (Fig. 2). Plots closer to roads had higher plant richness. Richness of meadow specialist perennials also increased with meadow size (richness increased steeply in meadows from 0 to 4 ha) and was negatively related to distance to the nearest meadow (richness was higher for meadows close to another meadow).

Plant community structure

Meadow area in 1949 explained more variation in plant community structure in montane meadows than other variables, including meadow area in 2005. Meadow area in 1949, slope, distance to forest, meadow area in 2005, and aggregated 2005 fragment area explained variation in plant community structure (Pearson's $r^2 > 0.3$) in the final three-dimension NMDS ordination (NMDS final stress 9.59309, final instability 0.00000) (Fig. 3). NMDS axes 1 and 2 explained 73 and 16 % of the variance, respectively, for a

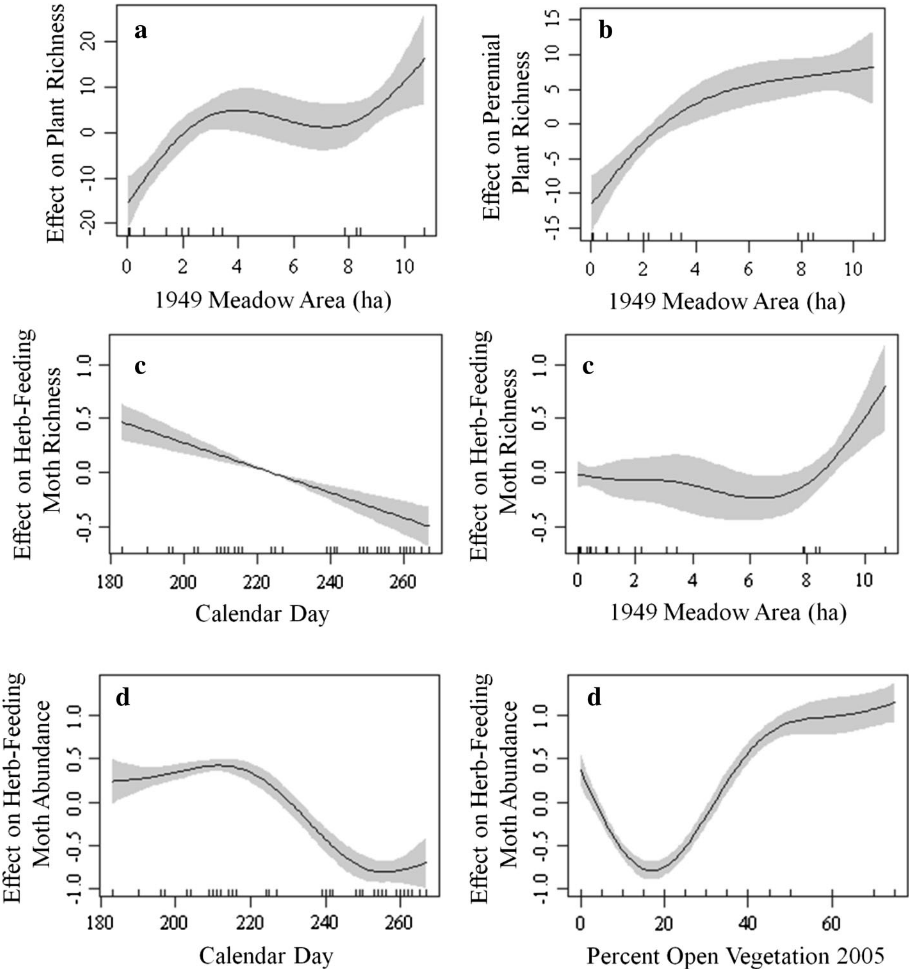

Fig. 2 Predicted anomalies (±95 % confidence interval) of **a** all meadow plant richness related to meadow area in 1949 (ha), **b** perennial meadow plant richness related to meadow area in 1949 (ha), **c** herb-feeding moth richness related to calendar day and meadow area in 1949 (ha), and **d** herb-feeding moth abundance related to calendar day and percent open vegetation in 2005

total r^2 of 89 %. Meadow area in 1949 was strongly correlated with plant community structure ($r^2 = 0.611$ with Axis 1, the dominant axis). Distance to forest, 2005 meadow area, and aggregated 2005 fragment area also were correlated with Axis 1 ($r^2 = 0.377$, 0.428, and 0.361, respectively), the dominant axis. Slope was correlated with Axis 2 ($r^2 = 0.564$), the minor axis. Overall, as meadows become smaller, their plant communities become more similar to non-meadow, forested communities.

Plant community structure in 2009 was more related to meadow area in 1949 than meadow area in 2005, according to the MRPP analysis. The 1949 meadow area category had a higher effect ($A = 0.349$, $p \ll 0.05$) than the 2005 area category ($A = 0.285$, $p \ll 0.05$).

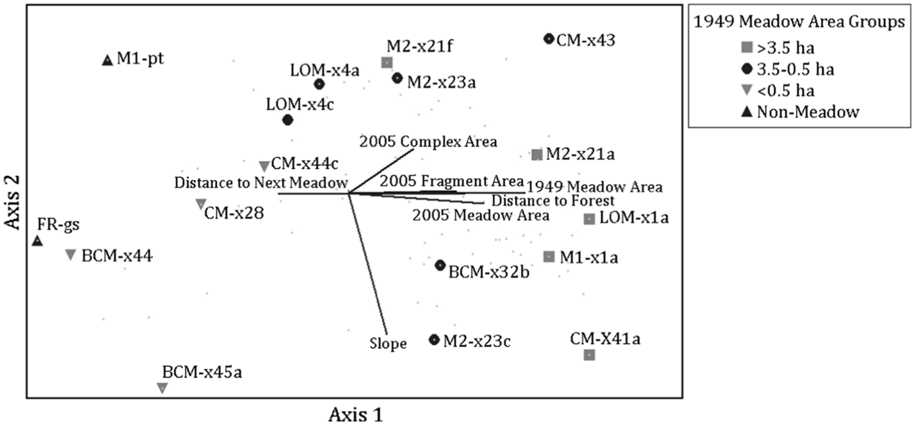

Fig. 3 3-D non-metric multidimensional scaling ordination of vegetation plots along axis 1 and axis 2 using grouping variables derived from 1949 meadow area

Nocturnal moth richness and abundance

A total of 2,923 individuals from 232 moth species were recorded in 65 samples in montane meadows over 3 years (2008–2010). The number of individuals caught in a single sample varied from 4 to 146, with an average of 45 individuals. Overall species richness varied from 3 to 40 per sample, with an average of 17. All three major feeding guilds were well represented and included abundant to rare species. The seasonal trends represented by these traps are consistent with those demonstrated by a 5-year study in the same region using similar techniques (Highland et al. 2013; Fig. 6 in Appendix).

Factors explaining richness and abundance of moths varied among herb-feeding, woody-angiosperm-feeding, and gymnosperm-feeding moth guilds (Table 1; Fig. 4). Calendar day was the only variable included in all of the best-fit models; this accounts for the rapid turnover of moth species over the summer. Richness and abundance of herb-feeding moths peaked earlier in the summer than for woody angiosperm- and gymnosperm-feeding moths. Richness of herb-, gymnosperm-, and woody-angiosperm-feeding moths peaked on days 185, 210, and 210, respectively, while abundance of herb-, gymnosperm-, and woody-angiosperm-feeding moths peaked on days 220, 185, and 215, respectively. All best-fit models also included some measure of habitat area or perimeter. Best-fit models for richness of herb-feeding moth species included meadow area in 1949, but the best-fit model for herb-feeder abundance included the 2005 percent open vegetation within 100-m of the trap (Fig. 4a, b). According to the GAMM model, herb-feeding moth richness was equivalent to the mean response in meadows with a 1949 area of up to approximately 6 ha, then increased more steeply relative to the mean in meadows with a larger 1949 area. Herb-feeding moth abundance decreased relative to the mean when the percent open vegetation was <20 %, then increased steeply when the percent open vegetation was 20–50 %, then was consistent with the mean response when the percent open vegetation was over 50 %. Best-fit models for richness and abundance of woody-angiosperm-feeding moth species included the 2005 meadow perimeter. Best-fit models for richness and abundance of gymnosperm-feeding moth species included the area of new forest added from 1949 to 2005, which is the amount of meadow lost to forest encroachment. Woody-angiosperm-feeding moth richness and abundance decreased in meadows with perimeters smaller than

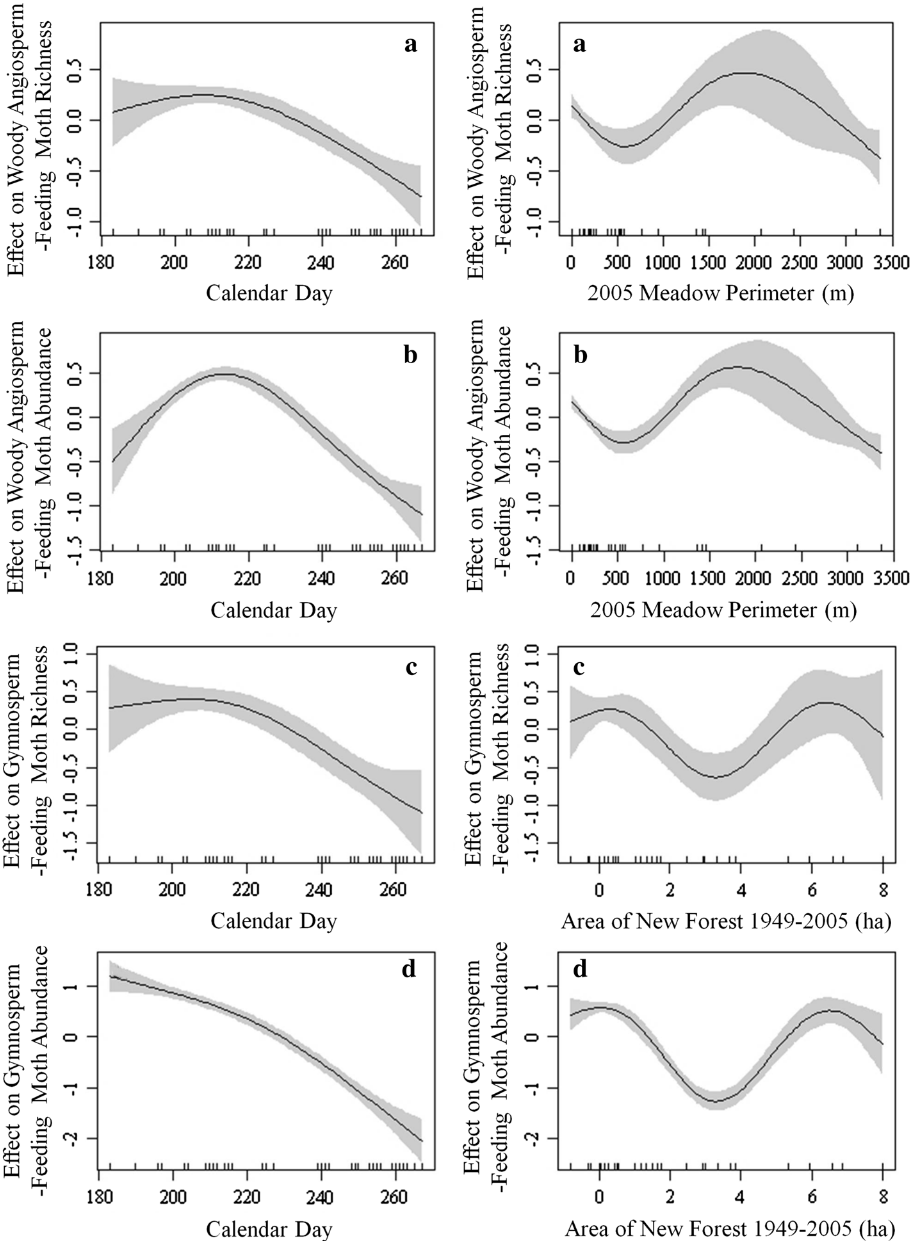

Fig. 4 Predicted anomalies (±95 % confidence interval) of **a** woody angiosperm-feeding moth richness related to calendar day and meadow perimeter in 2005 (m), **b** woody angiosperm-feeding moth abundance related to calendar day and meadow perimeter in 2005 (m), **c** gymnosperm-feeding moth richness related to calendar day and area of new forest 1949–2005 (ha), and **d** gymnosperm-feeding moth abundance related to calendar day and area of new forest 1949–2005 (ha)

500 m, but increased in meadows with perimeters 500–2,000 m (Fig. 4c, d). Gymnosperm-feeding moth richness and abundance decreased where 0–3.5 ha of meadow converted to forest from 1949 to 2005, but increased where more than 3.5 ha of meadow converted to forest from 1949 to 2005 (Fig. 4e, f).

Discussion

Plant and moth specialists in naturally contracting montane meadows in Oregon appear to be subject to an extinction debt. Both richness of plant and moth specialists and community structures of montane meadow plant species displayed a lagged response to landscape change; variation in richness was better explained by historic rather than present meadow configuration. These results are similar to multiple studies in northern Europe, which showed that the patch size of semi-natural agricultural grasslands decades prior to the date of the study explained grassland plant specialist perennial richness better than current grassland patch size (Cousins and Vanhoenacker 2011; Cristofoli et al. 2010; Helm et al. 2006; Krauss et al. 2010; Lindborg 2007; Sang et al. 2010). However, Adriaens et al. (2006), found no evidence of an extinction debt in calcareous grassland remnants in Belgium. Our study provides the first evidence that the richness of short-lived insect species and their host-plants may exhibit a lagged response to the loss of their preferred habitat, while their abundances do not and that this phenomenon is partly dependent upon a mosaic of habitat patches of varying qualities, making it a response of the meta-community at the landscape level.

Meadow size in the western Cascades of Oregon in 1949 explained more variation in overall plant richness, richness of meadow-specialist plants, and meadow plant community structure than meadow area in 2005. In other words, the greatest plant species richness today occurs in meadow fragments that were parts of large meadows in 1949, rather than in the meadow fragments that are largest today. This lagged relationship was observed not only for meadow-specialist perennials, as typically theorized (Kuussaari et al. 2009; Vellend et al. 2006), but also for meadow specialist annuals and invading tree species. While extinction debt has been shown to occur in patches that are responding to rapid change, as from a clearcut leaving an isolated remnant, patches experiencing gradual change with multiple nearby other fragments have been little studied. This study shows that extinction debt also occurs in patches that are experiencing gradual change and have other nearby fragments. Hence, gradual tree invasion of montane meadows has exerted pronounced, delayed effects on local extinction and meadow plant community structure. Moreover, the smallest meadow fragments in 1949 had lowest diversity in 2009, while plant richness was higher for meadow fragments near roads, possibly due to the corridor effect of roads on ruderal species, and other meadows, as expected from island biogeography theory (e.g., Diamond 1972). As meadows become smaller, their plant communities become more similar to forested plant communities, with the smallest sampled meadows being more similar to forested areas than to large meadows.

Like meadow specialist plants, moth richness also displayed a lagged relationship with meadow configuration, consistent with extinction debt, even though moths are short-lived and might respond rapidly to habitat loss. After accounting for seasonal species turnover, richness of meadow specialist moths was highest in areas that had been large meadows in 1949, rather than areas that are large meadows today, consistent with extinction debt. However, herb-feeding moths are more abundant in meadows that are large today. Thus, as a meadow fragments contracts, moth abundance decreases to the point that the species becomes extirpated. We hypothesize that moth species are able to persist due to the persistence of their long-lived perennial host-plants, leading to a lagged response to habitat loss in the largest meadows, though moth richness appears to decrease faster than plant richness in moderate to small-sized meadows.

Our findings indicate stronger evidence for extinction debt in meadow-specialist nocturnal moths than has been documented for butterflies or diurnal moths in European grasslands. In Estonia, both past and present-day area of contracting calcareous grasslands explained the richness of butterflies and meadow specialist diurnal moths (Sang et al. 2010). In a broader-scale study, contemporary habitat patch size explained more variation in diversity of European butterflies than historic habitat sizes (Krauss et al. 2010). While most of the moths in our study have smaller wing lengths and body sizes than butterflies and, therefore, smaller dispersal distances (Nieminen 1996; Hambäck et al. 2007; Öckinger et al. 2010), they exhibited evidence of extinction debt while the European butterflies did not. This suggests that moths in our study were able to survive due to the persistence of their host plants and, perhaps, due to patches of usable habitat within the forest mosaic surrounding the meadows. Also, this landscape is a mosaic of meadows and forest, unlike most of the European grassland patches that were mostly surrounded by agricultural or urban landscapes. The matrix of forest potentially possesses isolated host plants and, therefore, occasional dispersal opportunities. Dispersal of moths between meadows is possible and likely occurs with some species, though some meadows are very isolated and most of the moth species in this study are relatively small-bodied with small wingspans (Highland et al. 2013). Moths with small bodies and small wingspans have been shown to have very limited dispersal capabilities (Nieminen 1996; Öckinger et al. 2010), suggesting that moth dispersal and migration from one meadow to another likely accounts for only a small portion of moth assemblages identified in the different meadows through this study. In addition, if larger meta-community population assemblage and richness was the driver for the observed patterns, meadow complex area for 1949 or 2005 would have explained moth richness better than local meadow metrics. Because historic local meadow metrics and not a landscape level metric explained moth richness better, local populations are the primary drivers in the moth assemblages that we have sampled, with migrants or “tourists” comprising only a minor part. Additionally, in a previous study, we found that these meadows had highly distinctive moth assemblages that contrasted greatly with the surrounding forests, which dominate the western Cascades mountain range (Highland et al. 2013). Therefore, little immigration of tourist species is occurring from other parts of western Oregon to these meadows. This suggests that extinction debt, in a relatively natural landscape of habitat mosaics, is a landscape meta-community level phenomenon dependent on multiple landscape characteristics that provide not only large habitat patches but also small, isolated habitat patches potentially useful for connectivity but still largely dominated by local landscape characteristics and populations (Dennis et al. 2013).

As meadows in the western Cascades of Oregon have contracted, the diversity of meadow specialist herbaceous plants and the moth species that feed on these plants has declined, while retaining a memory of past meadow sizes. At the same time, moth species that feed on woody flowering plants and conifer trees apparently have increased as trees have invaded and fragmented formerly large continuous meadows. As trees invade contracting meadows, the moths that feed on those species gradually invade the former meadow as well, while the moth species that formerly inhabited the meadow persist in relict meadow fragments. Because extinction debt delays the disappearance of species whose habitat is declining, while species diversity has increased in expanding habitat types, meadow invasion by trees produces a transient local biodiversity surplus.

Montane meadows in the Cascades of Oregon have been shrinking in size and fragmenting for several centuries (Halpern et al. 2010; Highland 2011). Montane meadows are declining throughout much of the western US (e.g., Norman and Taylor 2005; Zier and Baker 2006). Because montane meadows occupy <5 % of the landscape, but contribute a unique assemblage of species, their preservation and potential restoration represent an important goal for biodiversity conservation. The apparent lagged extinction of plants and moth species in montane meadows of the western Cascades may be representative of extinction debt in montane meadows throughout the western US and provides an opportunity for restoration that will promote landscape-level biodiversity in forested mountain landscapes in the western US. Ongoing research suggests a combination of woody plant removal, specifically, and potentially fire applications could assist in the maintenance and restoration of these meadows (Halpern et al. 2012). Such restorations could potentially lead to a increase and recovery of some plant and insect populations currently threatened with local extinction though present in small numbers.

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Appendix

See Figs. 5 and 6.

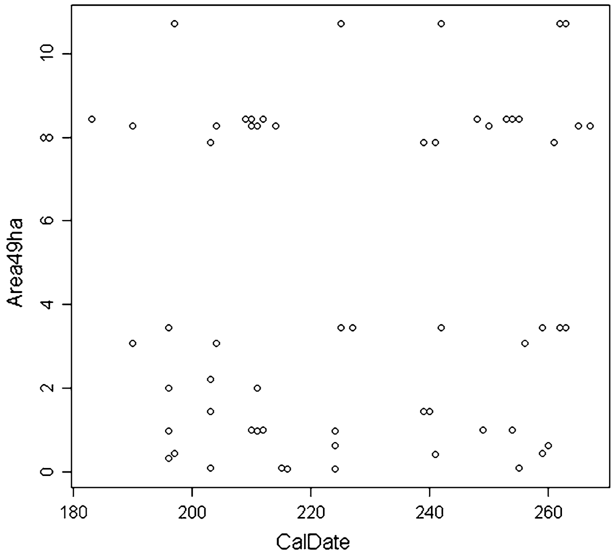

Fig. 5 Scatterplot showing the distribution of samples by calendar day (*x-axis*) versus 1949 meadow area (*y-axis*). Note that samples were taken in large and small meadows throughout the sampling season

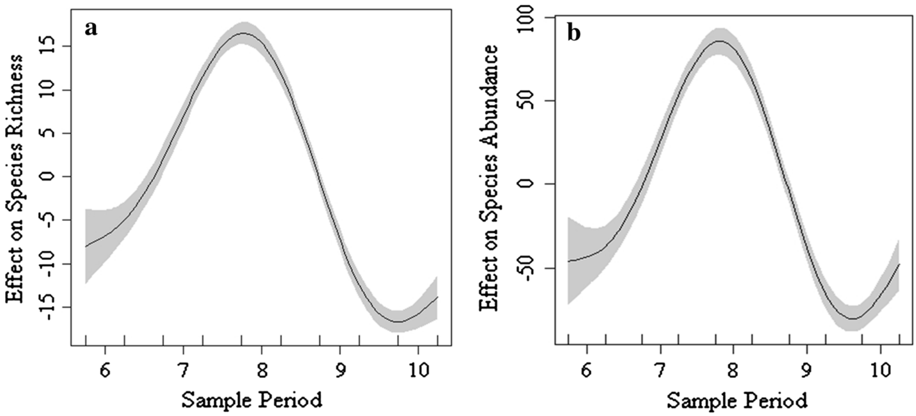

Fig. 6 GAMM plot showing the trend in richness (**a**) and abundance (**b**) of nocturnal moths in the Andrews Forest using a 5-year dataset. Sample period number refers to the month in which the sample was taken (ex: sample period 7 = July). Figures taken from Highland et al. (2013)

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