


Landscape patterns and diversity of meadow plants and flower-visitors in a mountain landscape

Julia A. Jones  · Rebecca Hutchinson · Andy Moldenke · Vera Pfeiffer · Edward Helderop · Elaina Thomas · Josh Griffin · Amanda Reinholtz

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Abstract

Context Wild flowering plants and their wild insect visitors are of great importance for pollination. Montane meadows are biodiversity hotspots for flowering plants and pollinators, but they are contracting due to tree invasion.

Objectives This study quantified flowering plants and their flower-visitor species in montane meadows in the western Cascade Range of Oregon. Species diversity in small, isolated meadows was expected to

be lower and nested relative to large meadows. Alternatively, landform features may influence richness and spatial turnover.

Methods Flowering plants and their visitors were sampled in summers of 2011–2017 in twelve montane meadows with varying soil moisture. All flowering plants and all flower-visitors were recorded during five to seven 15 min watches in ten 3 × 3 m plots in each meadow and year.

J. A. Jones (✉)
Geography, CEOAS, Oregon State University, Corvallis,
OR, USA
e-mail: jonesj@geo.oregonstate.edu

R. Hutchinson
Electrical Engineering and Computer Science, Fisheries
and Wildlife, Oregon State University, Corvallis, OR,
USA

A. Moldenke
Department of Botany, Oregon State University,
Corvallis, OR, USA

V. Pfeiffer
Nelson Institute for Environmental Studies, University of
Wisconsin, Madison, WI, USA

E. Helderop
School of Geographical Sciences and Urban Planning,
Arizona State University, Phoenix, AZ, USA

E. Thomas
Department of Biology, Carleton College, Northfield,
MN, USA

J. Griffin
Electrical Engineering and Computer Science, Oregon
State University, Corvallis, OR, USA

A. Reinholtz
Long Tom Watershed Council, Eugene, OR, USA

Results A total of 178 flowering plant species, 688 flower-visitor species and 137,916 interactions were identified. Richness of flower-visitors was related to meadow patch size, but neither plant nor flower-visitor richness was related to isolation measured as meadow area within 1000 m. Species in small meadows were not nested subsets of those in large meadows. Species replacement accounted for more than 78% of dissimilarity between meadows and was positively related to differences in soil moisture.

Conclusions Although larger meadows contained more species, landform features have influenced meadow configuration, persistence, and soil moisture, contributing to high plant and insect species diversity. Hence, conservation and restoration of a variety of meadow types may promote landscape diversity of wild plants and pollinators.

Keywords Functional connectivity · Species replacement · Spatial turnover · Nestedness · Soil moisture · HJ Andrews Experimental Forest · Meadow restoration

Introduction

Pollination is a key ecosystem service provided by interactions between flowering plants and flower-visitors. Montane meadows are hotspots of biodiversity for flowering plants and pollinators (flower-visitors). Wild flowering plants and their wild insect visitors are of great importance for pollination (Garibaldi et al. 2011, 2014). While many plant–pollinator systems have been greatly disrupted by land use change, montane meadows contain some of the remaining relatively undisturbed plant–pollinator systems. Most studies of the landscape ecology of plants and pollinators have been conducted in landscapes modified by agriculture or development, which are often in topographically homogeneous areas. Although it is well known that mountain landforms influence ecosystem processes in many ways (Swanson et al. 1988), relatively little is known about how mountain landforms and montane meadow landscape configuration affect plant–pollinator interactions. Few long-term studies have examined wild plants and their wild insect visitors in montane meadows. This study addressed this gap by examining how landscape

patterns were related to the diversity of flowering plants and flower-visitors in montane meadows of the western Cascades of Oregon.

Varied effects of landscape patterns on plant and pollinator diversity are reported in the literature. Some studies show that species richness in plant–pollinator networks declines with loss of meadow habitat and reduced meadow connectivity (e.g., Aizen and Feinsinger 1994; Aguilar et al. 2006; Sabatino et al. 2010; Burkle et al. 2013). However, these effects have been documented primarily in systems where very little natural habitat remains (Winfree et al. 2009). Landscape history, landscape configuration, and life history strategies of pollinators likely also influence pollinator diversity (Senapathi et al. 2015, 2017). In the past century or two, trees have gradually encroached on montane meadows in many areas (Vale 1981; Jakubos and Romme 1993; Millar et al. 2004; Coop and Givnish 2007).

Long-term stability of montane meadow complexes, relatively recent meadow contraction, and the heterogeneous topography of montane meadow landscapes raise important questions for landscape ecology about plant–pollinator interactions (see e.g., Montoya and Galiana 2017). To address these questions, this study explored the diversity of plant and pollinator (flower-visitors) species over 7 years in montane meadow complexes of a relatively wild landscape in the western Cascade Range of Oregon. We asked:

- What is the history and current status of meadow size, spacing, and surrounding meadow habitat?
- How do landform features (elevation, slope, aspect) influence the landscape configuration of meadows and meadow soil moisture?
- How are the richness and turnover of flowering plants and flower-visitors in montane meadows related to landscape configuration and landform features as measured by soil moisture?

If forest barriers limit species exchange among meadows, small, isolated meadows would be expected to have lower diversity of plants and flower-visitor species compared to large meadows, and their species would be nested subsets of large meadows (as found by Gilarranz et al. 2015). On the other hand, landscape heterogeneity and meadow persistence may have favored plant and insect species adapted to local conditions, producing meadows with distinct

communities irrespective of size or isolation (as found by Traveset et al. 2016).

This study tested how diversity of plants and flower-visitors would be related to three aspects of landscape pattern in mountain landscapes: the present configuration of meadows, the past configuration of meadows, and landform features.

Methods

The landscape ecology of montane meadows was assessed from a perspective of functional connectivity that considers the physical characteristics of the landscape as well as the behavior of organisms moving through the landscape (Bélisle 2005; Kindlmann and Burel 2008). Connectivity was quantified using meadow patch size and surrounding meadow area arrangement (Taylor et al. 1993; Tischendorf and Fahrig 2000; Fahrig 2003; Hadley and Betts 2012). Landform features included elevation, slope angle and aspect, which control soil moisture. Present and past meadow size and functional connectivity were expected to affect both richness (alpha diversity) and turnover (beta diversity) in the study landscape.

- (1) Richness of plants and flower-visitors were expected to be lower in meadows that
 - a) were small, more isolated, and had experienced greater loss of surrounding meadow area, compared to meadows that were larger, more connected, or had experienced less loss of surrounding meadow.
 - b) had been isolated for many decades, compared to meadows of similar size that were fragments of previously larger meadows.
 - c) had landform features which produce low soil moisture and rapid soil drying, curtailing flowering during the dry summers.
- (2) Beta diversity of plants and flower-visitors was expected to be
 - a) dominated by nestedness, rather than species replacement, and smaller meadows would contain a nested subsample of species in larger meadows,

- b) lower among pairs of meadows that were closely spaced or similar in size compared to pairs that were far apart or differed in size, and
- c) lower among pairs of meadows with similar soil moisture compared to pairs that differed in soil moisture.

Study site

The study was conducted from 2011 to 2017 in twelve montane meadows (elevation 1300 to 1600 m) in the H.J. Andrews Experimental Forest (44.2°N and 122.2°W) in western Oregon, hereafter “Andrews Forest” (Fig. 1). Meadows are located along the crest of the western Cascade Range, in the Willamette National Forest. Mean annual precipitation (at Vanilla Leaf meteorological station, 1273 m) is 2220 mm and mean annual temperature is 6.7 °C. Study areas may be snow-covered from mid-October to late June, and mean annual snow water equivalent exceeds 0.4 m.

The study site is densely forested. Vegetation is mature (100 to 500-years) forest dominated by Douglas-fir (*Pseudotsuga menziesii*), mountain hemlock (*Tsuga mertensiana*), and Pacific silver fir (*Abies amabilis*), with some young Douglas-fir plantation forest growing in patches created in the 1960s. As of 2005, montane meadows represented only 2.5% of the area of the Andrews Forest, and meadows and open rocky areas represented < 5% of the 687,000 km² Willamette National Forest (Dailey 2007). Montane meadows may have persisted as non-forested areas throughout the Holocene, possibly maintained by a combination of Native American burning and early 20th century grazing (Highland 2011). Extirpation of Native Americans in the late 1700s and fire suppression since arrival of Europeans in the late 1800s are associated with significant contraction of meadow habitat throughout the Cascade Range of Oregon (Miller and Halpern 1998). In the Andrews Forest, montane meadows contracted by 45% from 1948 to 2005 (Takaoka and Swanson 2008; Rice 2009; Highland 2011). The nearest town (McKenzie Bridge, unincorporated, population a few hundred people) is about 3 km from the nearest study meadow. The nearest agriculture (blueberries, hazelnuts) is roughly 30 km down-valley to the west.

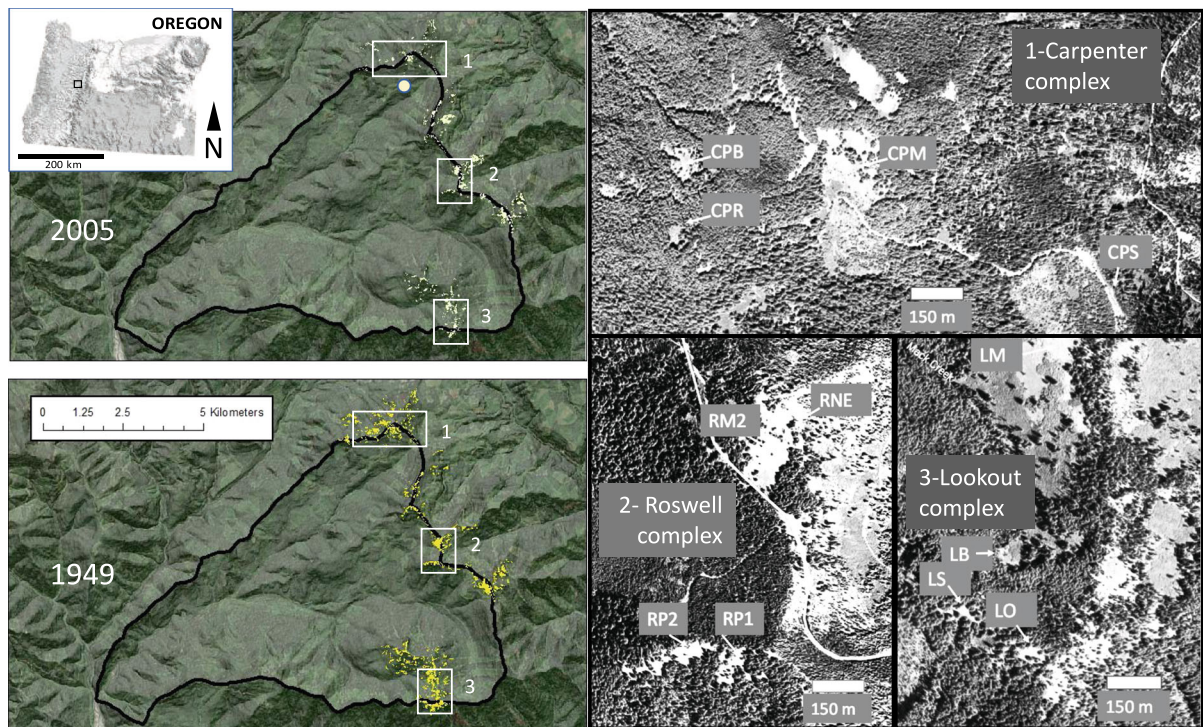


Fig. 1 Locations of study meadows in the H.J. Andrews Experimental Forest, Oregon. The Vanilla Leaf meteorological station is shown as the white dot. Imagery sources: Helderop (2015) and Google Earth

Field methods

Four study meadows were selected in each of three meadow complexes. Each complex consisted of one large meadow, one small meadow near the large meadow, and two small isolated meadows (Fig. 1, Table 1). Study meadows range in size from 0.26 to 4.4 ha, and were separated by 0.1–8.7 km. Meadows range in elevation from 1300 to 1600 m, and range in slope from 30 to over 70% (except for Lookout Bog, 6%). Most of the meadows face SE to SW, but Carpenter basin faces NW (Table 1).

Each meadow contained ten 3×3 m plots, spaced at 15 m intervals along two parallel transects spaced 20 m apart, aligned along the long meadow axis near the center of the meadow. Thus, 90 m² were surveyed in each meadow regardless of meadow size.

At each plot, flowering plants and flower-visitors were surveyed for a 15 min ‘watch’ weekly, over 5–7 weeks from mid-June to mid-August in 2011–2017. Watches were conducted between 900 and 1700 h, on days that were sunny or partly cloudy, had little to no wind, and experienced no precipitation.

At the beginning of each watch, every flowering plant in the plot was identified to species, and flower abundance was counted or estimated (Pfeiffer 2012; Helderop 2015). Individual plants that could not be identified were photographed, and samples were harvested outside plots, pressed, and transported to the lab for identification. Only non-wind-pollinated plants were counted.

Each ‘watch’ consisted of observations for a period of 15 min, which might last up to an hour, including interruptions for note-taking and capture activities. At each minute, the observer recorded all species that visited each flower species. An ‘interaction’ consisted of an individual of a flower-visitor species making contact with the reproductive parts of a flower. Flower-visitors were identified to species in the field or captured using a net after their first visit and euthanized, transported to the lab, given unique ID numbers, and pinned. Identifications were completed by A. Moldenke. A synoptic collection of all the flower-visitors is archived in The Oregon State Arthropod Collection: Andrews Forest LTER Collection.

Table 1 Landform characteristics of montane meadows sampled in the H.J. Andrews Experimental Forest

Meadow	Code	Years	Elevation (m)	Slope (%)	Aspect (deg)	Soil moisture					Index
						2011 Ave Week 3	2011 Ave Week 5	2013 Ave Week 1	2013 Ave Week 4	2013 Ave Week 6	
Carpenter basin	CPB	2011–2017	1341	40	350	9	7	19 ± 7	6 ± 7	5 ± 6	1
Carpenter main	CPM	2011–2017	1509	60	178	39	13	19 ± 4	5 ± 3	4 ± 3	0.3
Carpenter ridge	CPR	2011–2017	1432	58	148	32	12	25 ± 10	6 ± 7	2 ± 4	– 0.1
Carpenter saddle	CPS	2011–2017	1349	31	116	29	17	10 ± 6	2 ± 2	1 ± 1	–0.7
Lookout bog	LB	2013–2017	1457	6	166	–	–	71 ± 10	72 ± 10	70 ± 11	2.5
Lookout main	LM	2011–2017	1475	47	247	< 1	< 1	28 ± 5	5 ± 2	2 ± 1	0.4
Lookout outcrop	LO	2011–2017	1484	81	220	38	10	10 ± 7	1 ± 1	1 ± 1	– 1
Lookout steep	LS	2012–2017	1448	73	213	–	–	19 ± 9	4 ± 3	1 ± 1	– 0.5
Meadow 2	RM2	2011–2017	1479	37	207	41	3	15 ± 5	6 ± 3	1 ± 1	0.3
Northeast	RNE	2013–2017	1518	65	122	–	–	12 ± 8	5 ± 4	3 ± 3	– 0.4
Roswell Point 1	RP1	2011–2017	1444	71	185	< 1	< 1	10 ± 5	2 ± 1	1 ± 1	– 0.5
Roswell Point 2	RP2	2011–2017	1456	61	184	2	< 1	9 ± 6	2 ± 1	1 ± 1	– 0.5

Elevations are of study plots within meadows

Soil moisture was determined gravimetrically (% oven-dry weight) from composited samples collected adjacent to plots during weeks 3 and 5 of 2011 and weeks 1, 4, and 6 of 2013. Landform features (i.e., elevation, slope and aspect) control soil moisture (Table 1). Xeric (dry) meadows, with soil moisture index of – 1.0 to – 0.1, are on steep S- and W-facing slopes (LO, LS, RP1, RP2) or steep ridges (CPR, CPS, NE). Hydric (wet) meadows, with soil moisture index of 1 to 2.5, are on gentle to moderately steep N to SE-facing slopes (CPB, LB). Mesic (moderately moist) meadows, with soil moisture index of 0 to 1, are on steep S and SW-facing slopes. In an average year (2013), soil moisture in most meadows ranged from 10 to 25% at the beginning of the summer and declined to less than 5% by early August (Table 1). Lookout Bog remained wet all summer. Thus, soil moisture was used an integrated measure of landform features in statistical analyses.

Data analysis

Altogether five to seven weekly watches were conducted in ten plots in twelve meadows from 2011 to 2017, producing a total of > 4200 meadow-plot-watches. For this study, data were summarized by meadow (totals for ten plots per meadow) and year,

producing 67 meadow-years of data. Plant richness was defined as the number of plant species in anthesis. Flower-visitor richness was defined as the number of species observed to visit the reproductive parts of flowers. Total interactions were defined as the number of unique pairings of a flower-visitor individual with an individual plant, and unique interactions were defined as the number of unique pairings of a flower-visitor species with a plant species.

Daily temperature data and digital elevation data were obtained from the Andrews Forest data repository (<https://andrewsforest.oregonstate.edu>, datasets GI002 and MS001).

Meadow size and isolation were calculated from digitized aerial ortho-photographs (e.g., Figure 1) obtained in 2005 (1 m resolution) and 1949 (1:20,000) using the Arcpy module from ArcGIS version 10.2.2 in Python version 2.7.9. The perimeters of all meadows (non-forest, non-shrub vegetation) larger than 0.01 ha were digitized, excluding all identifiable trees and tree clusters in meadows. Elevation, aspect, slope, and topographic convergence of each meadow were calculated using a 10-m digital elevation model (Highland 2011; Pfeiffer 2012). Meadow isolation was measured by the surrounding meadow area, defined as the proportion of non-forest area within each of a set of concentric rings established

at varying distances ranging from 50 to 3000 m from the centroid of each study meadow (Pfeiffer 2012; Helderop 2015). Values of surrounding meadow area > 1000 m were less than 5% and varied little among the meadows, so only values < 1000 m were used in the analysis.

A soil moisture index was calculated for study meadows based on (1) gravimetric soil moisture measurements from five dates in summers of 2011 and 2013 and (2) a topographic convergence index for each meadow (Pfeiffer 2012), and (3) qualitative rankings of meadow moisture based on the abundance and timing of flowering. Each meadow was ranked for each variable, the ranks were normalized, and the index was the average of these ranks. The moisture index ranges from driest (low values) to wettest (high values) (Table 1).

Spatial dissimilarity (pairwise comparisons among meadows in a given year, e.g., Carstensen et al. 2014) was determined using beta diversity (Sørensen distance) for all pairs of meadows, for both plant and flower-visitor species in each year, 2011–2017. The Sørensen index is one of the oldest and most widely used indices for assessing compositional dissimilarity based on species incidence data (Chao et al. 2005). Sørensen distance is less affected than other indices of beta diversity by differences in total abundances between the two compared sites (Legendre and De Cáceres 2013). The Sørensen distance can be partitioned into species replacement or spatial turnover (two sites have different species) and nestedness (when species at one site are a subset of species at another) (Baselga 2010). Spatial turnover implies the replacement of some species by others and is interpreted as a consequence of environmental sorting or spatial and historical constraints. In contrast, nestedness of species assemblages occurs when the biotas of sites with smaller numbers of species are subsets of the biotas at richer sites, and is interpreted as reflecting a non-random process of species loss (Baselga 2010). Sørensen species replacement values (β_{sim}) are a measure of the fraction of the total species in two sites which are replaced from one site to another, and ranges from 0 (no species replacement) to 1 (all species replaced).

Sørensen values were partitioned into species replacement and nestedness following Baselga (2010). Pairwise Sørensen dissimilarity (β_{sor}),

dissimilarity due to species replacement (β_{sim}), and dissimilarity due to nestedness (β_{sne}) were calculated as:

$$\beta_{sor} = (b + c)/2a + b + c \quad (1)$$

$$\beta_{sim} = \min(b, c)/a + \min(b, c) \quad (2)$$

$$\beta_{sne} = \beta_{sor} - \beta_{sim} \quad (3)$$

where a is the number of species common to both sites, b is the number of species unique to the first site, and c is the number of species unique to the second site. The multiple-site Sørensen dissimilarity and its components also were calculated following Baselga (2010), using the betapart package in R (Baselga and Orme 2012).

Statistical models were fitted to plant richness and flower-visitor richness as a function of landscape configuration (meadow size, surrounding meadow), and soil moisture, which is controlled by landform features including elevation, aspect, and slope (Table 1). Predictor variables were selected which were least correlated with one another. Hence richness was predicted by meadow size in 2005, surrounding meadow habitat at 750–1000 m in 1949, and soil moisture index. R^2 and AICc were used to discriminate the best models. Linear models also were fitted to predict pairwise plant species replacement and flower-visitor species replacement as a function of landscape configuration (difference in meadow size, distance between meadows) and landform features (as measured by difference in soil moisture). All analyses were performed in R, version 3.5.1 (R Core Team 2018).

Results

Diversity, abundance, and timing of interactions

A total of 178 flowering plant species, 688 flower-visitor species and a total of 137,916 interactions between individuals of plant and flower-visitor species were identified. Thirteen flowering plant species and seven flower-visitor species accounted for 50% of the total interactions, and many flower-visitor species were observed on only one occasion. Of the flower-visiting species, roughly one third are neighboring forest-dwelling species for the rest of their lives, only

coming to the meadow flowers to mate; one third are meadow-dwellers who may move between meadows; and one third are meadow-dwellers who remain within 100 m of the nest site.

Frequently visited plant species accounted for 50% of total interactions, and *Apis mellifera* (the European honeybee) accounted for 31.3% of all interactions (Table 2). Frequently visited plant species occurred in subsets of the meadows, and no plant species occurred in all meadows (Table 2). The most frequently visited plant, *Gilia capitata*, was observed to flower in only six of the twelve meadows. *Boykinia major* was observed primarily in only the wettest meadow (LB). In contrast, *Sedum oreganum* was observed only in steep, rocky ridgetop meadows in the Carpenter complex. Peak flowering dates also varied with soil moisture: on average (2011–2017) flowering peaked

10 days later in the wettest meadow (LB) compared to dry, steep, rocky meadows (CPS, LO, NE, RP1, RP2).

Meadow plant flowering and flower-visitor visits began as soon as the snowpack melted, peaked in late July, and ceased by mid-August. Daily maximum temperature ranged from 10 to 20 °C in late June, but from 30° to more than 40 °C in late July and August. Air temperature was higher on exposed, rocky, south- and west-facing meadows, and cooler on north-facing meadows or those surrounded by tall forest (CPB, LB).

Historical changes in meadow configuration

Study meadows became smaller and less connected from 1949 to 2005. Meadow patch sizes ranged from 0.36 to 6.37 ha in 1949 and 0.26 to 4.44 ha in 2005. Surrounding meadow area declined from 55 to 100%

Table 2 Numbers of meadows involved in 22 most frequent interactions and three rare interactions in twelve meadows in the H.J. Andrews Experimental Forest, 2011–2017

% frequency of this interaction as percent of all 137,916 interactions observed, *Rank* rank of this interaction out of 3600 interactions observed, *FV* the number of meadows in which this plant flowered and was visited by this pollinator, *F* the number of meadows in which this plant flowered and was not visited by this pollinator

Flower-visitor species	Plant species	%	Rank	FV	F	all
Common interactions						
<i>Apis mellifera</i>	<i>Angelica arguta</i>	1.1	17	4	2	6
<i>Apis mellifera</i>	<i>Boykinia major</i>	1.5	7	1	2	3
<i>Apis mellifera</i>	<i>Erigeron foliosus</i>	1.2	14	7	2	9
<i>Apis mellifera</i>	<i>Eriogonum compositum</i>	0.9	22	7	3	10
<i>Apis mellifera</i>	<i>Eriogonum umbellatum</i>	1.2	13	7	4	11
<i>Apis mellifera</i>	<i>Eriophyllum lanatum</i>	5.6	2	9	2	11
<i>Apis mellifera</i>	<i>Gilia capitata</i>	16.3	1	6	1	7
<i>Apis mellifera</i>	<i>Ligusticum grayi</i>	2.3	4	9	2	11
<i>Apis mellifera</i>	<i>Sedum oreganum</i>	1.1	16	2	0	2
<i>Bombus bifarius</i>	<i>Orthocarpus imbricatus</i>	1.4	11	7	0	7
<i>Bombus mixtus</i>	<i>Delphinium nuttallianum</i>	1.2	15	8	2	10
<i>Bombus mixtus</i>	<i>Hypericum perforatum</i>	1.3	12	5	2	7
<i>Bombus mixtus</i>	<i>Orthocarpus imbricatus</i>	1.5	10	6	0	6
<i>Bombus mixtus</i>	<i>Sedum oreganum</i>	1.5	9	2	0	2
<i>Bombus vosnesenskii</i>	<i>Hypericum perforatum</i>	1	20	3	4	7
<i>Bombylius major</i>	<i>Gilia capitata</i>	3	3	6	0	6
<i>Bombylius major</i>	<i>Penstemon procerus</i>	1	19	6	6	12
<i>Epicauta puncticollis</i>	<i>Eriophyllum lanatum</i>	1.9	6	8	3	11
<i>Epicauta puncticollis</i>	<i>Gilia capitata</i>	1.5	8	6	0	6
<i>Eristalis hirtus</i>	<i>Eriophyllum lanatum</i>	1.1	18	8	3	11
<i>Eristalis hirtus</i>	<i>Ligusticum grayi</i>	2	5	6	5	11
<i>Euphilotes enoptes</i>	<i>Gilia capitata</i>	0.9	21	3	0	3
Selected rare interactions						
<i>Bombus mixtus</i>	<i>Aquilegia formosa</i>	0.02	477	2	2	4
<i>Chrysotoxum fasciatum</i>	<i>Aquilegia formosa</i>	0.02	421	1	3	4
<i>Selasphorus rufus</i>	<i>Aquilegia formosa</i>	0.01	647	2	1	3

of the area within 150–200 m in 1949 to only 7 to 100% in 2005. Surrounding meadow area declined from 10 to 33% of the area within 750–1000 m in 1949 to 6 to 15% in 2005 (Table 3). Thus, most meadow patches contracted by 22–63% from 1949 to 2005 (Table 3). Surrounding meadow area also contracted by 22–77% within 150–200 m, by 48–70% within 300–500 m, and by 49–70% within 750–1000 m. Meadow patch size at CPS and surrounding meadow area in the Roswell complex increased slightly because of openings created by road construction in the 1960s (Table 3, Fig. 1). Changes in meadow size and surrounding meadow area were not related to soil moisture (Tables 1, 3).

Species richness

Plant richness was positively related to flower-visitor richness ($r = 0.79$) (Table 4). Richness of plants and flower-visitors were positively correlated to meadow size and surrounding meadow area (r ranging from 0.57 to 0.79, Table 4). Richness was not related to loss of surrounding meadow habitat at any distance. Meadow size and surrounding meadow fraction were positively correlated, both in 1949 and 2005 (Table 4). The more surrounding meadow there was within

750–1000 m in 1949, the greater was the percent loss from 1949 to 2005 ($r = 0.71$). Meadow size and connectivity were not related to soil moisture (Table 4). In the best-fit linear models, plant richness and flower-visitor richness were related only to meadow size in 2005 (Figs. 2, 3, Table 5).

Species turnover

Beta diversity was dominated by species replacement. The mean yearly species replacement component of multiple-site Sørensen dissimilarity was 78% for flowering plants and 81% for flower-visitors. In other words, nestedness accounted for less than a quarter of beta diversity in plants and less than a fifth of beta diversity for flower-visitors. Nestedness was not related to meadow spacing or differences in meadow size.

Plant species replacement ranged from 0.22 to 0.78 for the 66 meadow pairs, with a mean value of 0.44 ± 0.13 , and flower-visitor species replacement ranged from 0.26 to 0.65 with a mean value of 0.49 ± 0.05 . In other words, on average, 44% of plant species and 49% of flower-visitor species were unique to the less-species-rich meadow in each pair. For over 95% of meadow pairs, flower-visitor species

Table 3 Plant and flower-visitor richness and landscape configuration of montane meadows sampled in the H.J. Andrews Experimental Forest

Meadow	Code	Plant		Flower		Meadow size			Surrounding meadow area					
		Ave	SD	Ave	SD	1949	2005	%chg	150–200 m			750–1000 m		
									1949	2005	%chg	1949	2005	%chg
Carpenter basin	CPB	36.4	9.2	57.3	16.9	1.95	0.72	– 63	0.98	0.23	– 77	0.23	0.07	– 70
Carpenter main	CPM	38.1	7.8	60.7	14.4	3.23	2.52	– 22	1.00	0.73	– 27	0.23	0.07	– 70
Carpenter ridge	CPR	15.9	6.1	26.7	8.0	0.57	0.26	– 54	0.68	0.17	– 75	0.21	0.06	– 70
Carpenter saddle	CPS	22.9	6.3	46.7	17.4	0.36	0.39	8	0.20	0.07	– 64	0.13	0.06	– 49
Lookout bog	LB	18.2	2.6	39.6	11.9	0.54	0.29	– 47	0.45	0.12	– 74	0.24	0.11	– 52
Lookout main	LM	29.9	4.1	66.3	18.7	5.59	3.89	– 30	1.00	1.00	0	0.33	0.15	– 54
Lookout outcrop	LO	33.1	3.6	66.3	20.2	3.50	1.95	– 44	1.00	0.77	– 23	0.20	0.10	– 52
Lookout steep	LS	31.5	3.6	57.2	13.8	1.77	1.68	– 5	1.00	0.77	– 23	0.24	0.11	– 52
Meadow 2	RM2	33.0	4.4	74.3	19.1	6.37	4.44	– 30	1.00	1.00	0	0.14	0.16	14
Northeast	RNE	29.2	6.1	62.2	18.6	0.65	0.43	– 33	0.89	0.92	3	0.14	0.16	20
Roswell Point 1	RP1	25.6	5.0	59.1	12.5	1.09	0.61	– 44	0.55	0.43	– 22	0.12	0.12	3
Roswell Point 2	RP2	23.0	4.8	55.9	7.6	0.83	0.63	– 24	0.57	0.35	– 39	0.11	0.12	2

Average richness was calculated for 2011–2017

Table 4 Bivariate correlations among richness of plants and flower-visitors and measures of landscape configuration

	1	2	3	4	5	6	7	8	9	10	11	12
1. Plant richness	1.00											
2. Flower-visitor richness	0.79	1.00										
3. Meadow size (1949)	0.59	0.71	1.00									
4. Meadow size (2005)	0.57	0.70	0.98	1.00								
5. % Loss of meadow size, 1949–2005	– 0.05	– 0.15	0.01	– 0.15	1.00							
6. Surrounding meadow 150–200 m, 1949	0.77	0.60	0.67	0.63	0.25	1.00						
7. Surrounding meadow 150–200 m, 2005	0.62	0.80	0.74	0.77	– 0.14	0.77	1.00					
8. % loss of surrounding meadow 150–200 m	– 0.47	– 0.80	– 0.59	– 0.65	0.25	– 0.53	– 0.93	1.00				
9. Surrounding meadow 750–1000 m, 1949	0.21	– 0.04	0.37	0.36	0.21	0.48	0.21	0.05	1.00			
10. Surrounding meadow 750–1000 m, 2005	0.10	0.58	0.41	0.43	– 0.03	0.29	0.69	– 0.79	– 0.07	1.00		
11. % loss of surrounding meadow 750–1000 m	0.05	– 0.44	– 0.04	– 0.06	0.10	0.09	– 0.34	0.58	0.71	– 0.74	1.00	
12. Soil moisture index	– 0.13	– 0.25	0.03	0.00	0.41	– 0.05	– 0.26	0.39	0.45	0.01	0.28	1.00

Correlations > 0.5 are in bold font, correlations < – 0.5 are in italicized bold font

replacement ranged between 0.4 and 0.6, indicating that 40–60% of the flower-visitor species in each meadow were unique to that meadow.

Species replacement was positively correlated between plants and flower-visitors ($r = 0.59$). Species replacement values were not related to meadow spacing or difference in meadow size. Of 15 pairs of meadows with the lowest plant species replacement values, two were in the same complex; these pairs (RP1 and RP2, LO and LS) were fragments of two larger meadows from 1949 (Fig. 1). Other pairs of meadows that were widely separated also had species replacement < 0.27, e.g., LS versus RP1, LS versus RP2, LO versus RP1, LO versus RP2, and CPM versus LM. Flower-visitor species replacement was lowest for one pair of meadow fragments (RP1 and RP2) but average for the other (LO and LS). Fourteen of the 15

pairs of meadows with the lowest flower-visitor species replacement involved two different complexes.

Relationships with soil moisture

Species replacement was positively related to soil moisture difference for plants ($y = 0.11x + 0.32$, $R^2 = 0.59$) and flower-visitors ($y = 0.03x + 0.46$, $R^2 = 0.21$) (Fig. 4). The slope coefficients for both models were significant at $p < 0.001$, even when two extreme values were removed from the flower-visitor species replacement data. Thirteen of the 15 pairs with highest plant species replacement and eleven of the 15 pairs with highest flower-visitor species replacement involved wet meadows (LB or CPB). Twelve of the pairs with highest plant species replacement combined

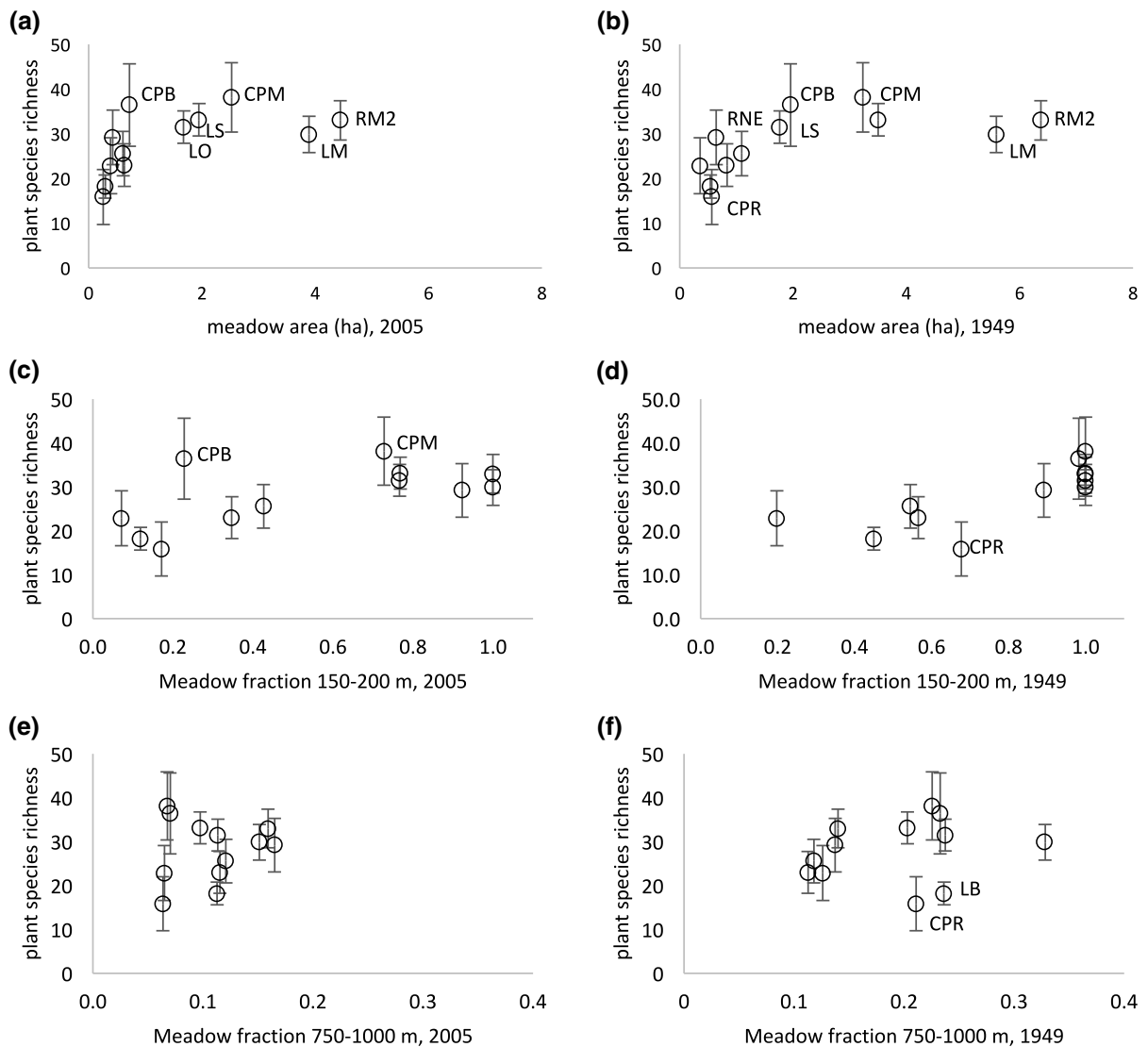


Fig. 2 Plant species richness as a function of **a, b** meadow size in 2005 (**a**) and 1949 (**b**), **c, d** meadow area as a fraction of area in a ring of 150–200 m from meadow center in 2005 (**c**) and

1949 (**d**), and **(e, f)** meadow area as a fraction of area in a ring of 750–1000 m from meadow center in 2005 (**e**) and 1949 (**f**)

wet (LB, CPB) with dry (LO, LS, RP1, RP2, NE) meadows. Nine of the 15 pairs with the lowest plant species replacement were pairs of small, dry, meadows, and three were pairs of large, mesic meadows.

Discussion

The landscape patterns revealed in these twelve montane meadows are robust, as the species data for each meadow was based on 10 plots sampled 25–37

times over a 7-year period. Diversity of flowering plants and flower-visitors is high compared to several recent studies of similar duration. A total of 178 flowering plant species, 688 flower-visitor species, 3600 unique interactions, and 137,916 total individual visits to flowers were noted in this study. In a 6-year study of a desert shrubland nature reserve in Argentina, Chacoff et al. (2017) identified 59 plant species, 196 pollinator species, 1050 unique interactions, and 28,015 interaction events. In an 8-year study of hedgerows in the semi-arid Central Valley of

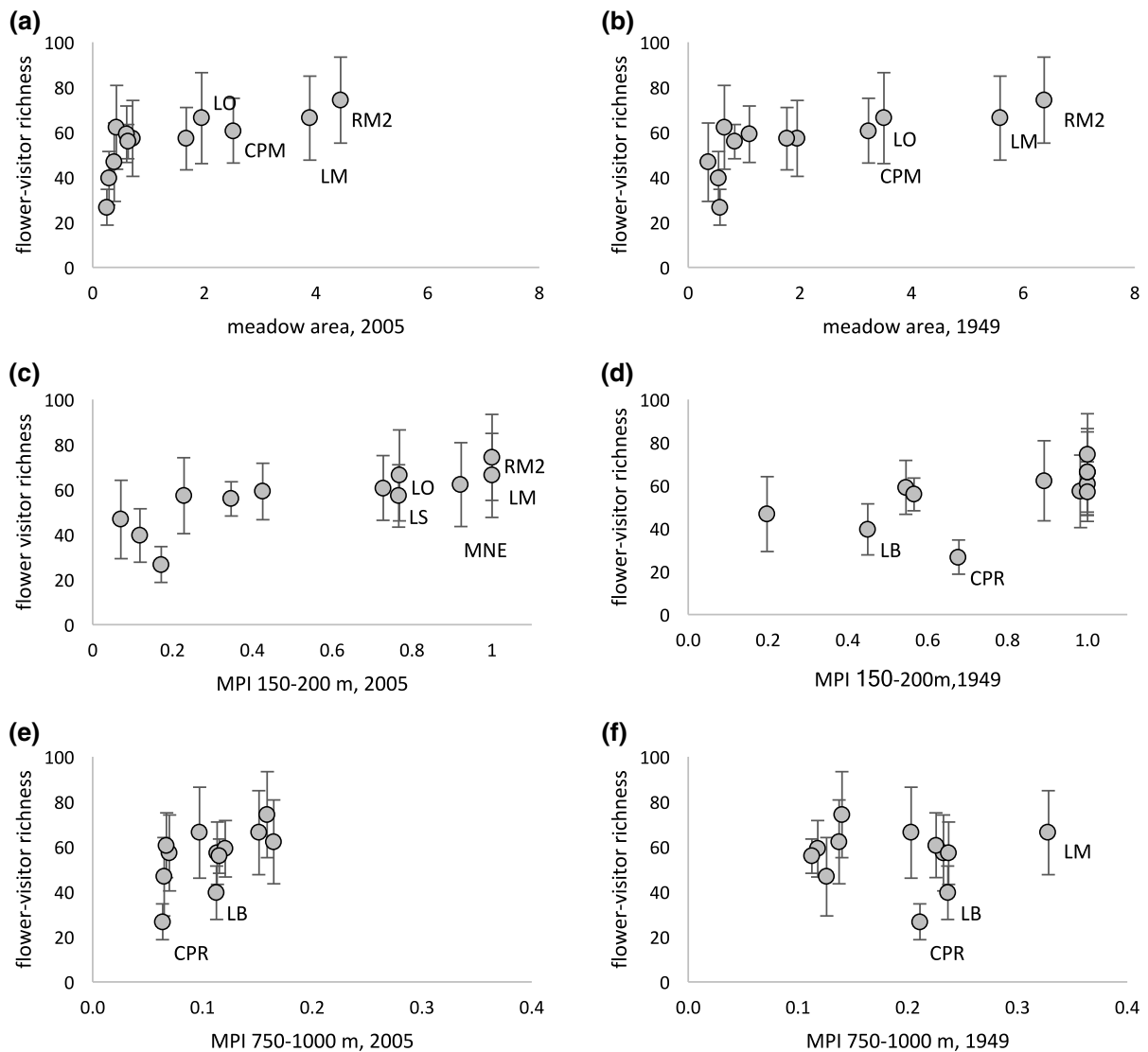


Fig. 3 Flower-visitor species richness as a function of **a**, **b** meadow size in 2005 (**a**) and 1949 (**b**), **c**, **d** meadow area as a fraction of area in a ring of 150–200 m from meadow center in

2005 (**c**) and 1949 (**d**), and **e**, **f** meadow area as a fraction of area in a ring of 750–1000 m from meadow center in 2005 (**e**) and 1949 (**f**)

California, Ponisio et al. (2017) identified 173 species of wild bees and syrphids in 1521 unique interactions. Caradonna et al. (2017) sampled two sub-alpine meadows in the Rocky Mountains of Colorado over 3 years and observed 45 flowering plant species, 74 pollinator species, 566 unique pairwise interactions, and a total of 28,959 individual pollinator visits to flowers.

As in other studies, interactions between plants and flower-visitors in this study were dominated by a few species. In montane meadows in the Sierra Nevada of

California, a few plant species dominated flowering, most species were generalists, and a few species of flower-visitors accounted for the vast majority of flower visits (Moldenke 1975, 1979). The plant and flower-visitor networks in this study are nested (Pfeiffer 2012; Helderop 2015), i.e., specialist species interact largely with generalist species, and all but the most extremely morphologically specialized plants are visited by both generalist and specialist flower-visitor species, as is typical of plant–pollinator systems (e.g., Bascompte et al. 2003; Olesen et al.

Table 5 Coefficients in alternative models predicting plant richness and flower-visitor richness

Size	Surr	SMI	Size × surr	AICc	R ²
Plant richness					
2.7	–	–	–	84.2	0.32
–	18.2	–	–	88.5	0.03
–	–	– 1.0	–	88.6	0.02
2.7	–	– 1.0	–	88.6	0.33
2.8	– 2.2	–	–	88.9	0.32
–	26.8	– 1.6	–	92.6	0.07
2.7	4.2	– 1.1	–	94.9	0.34
3.1	2.3	–	– 1.9	95.2	0.32
Flower-visitor richness					
6.2	–	–	–	95.5	0.48
7.2	– 69.9	–	–	97.4	0.59
6.2	–	– 3.4	–	98.7	0.54
2.6	– 137.7	–	29.1	101.9	0.65
–	–	– 3.4	–	102.6	0.06
7.0	– 58.2	– 2.0	–	103.1	0.61
–	– 16.8	–	–	103.3	0.01
–	1.6	– 3.5	–	107.3	0.06

Predictor variables included meadow size in 2005 (size), surrounding meadow at 750–1000 m in 1949 (surr), and soil moisture index (SMI). Models are listed in order of AICc, smallest (best) to largest (worst). Coefficients in bold font were significant at $p < 0.05$

2008). Overall, our findings are consistent with other studies with comparable sampling effort (see e.g., Chacoff et al. 2012). While not developed in this paper, study meadows also displayed high week-to-week and year-to-year dissimilarity and reassembly of plant pollinator networks noted by many studies (Alarcón et al. 2008; Olesen et al. 2008; Petanidou et al. 2008; Burkle and Alarcón 2011; Caradonna et al. 2017).

Landform features affect meadow configuration and diversity of plants and flower-visitors

The effects of landscape pattern on diversity of plant and flower-visitors in this study landscape, which contains natural meadows in a matrix of native forest, differ from studies of plants and pollinators in human-dominated landscapes. Counter to our prediction, plant richness was not related to any measure of

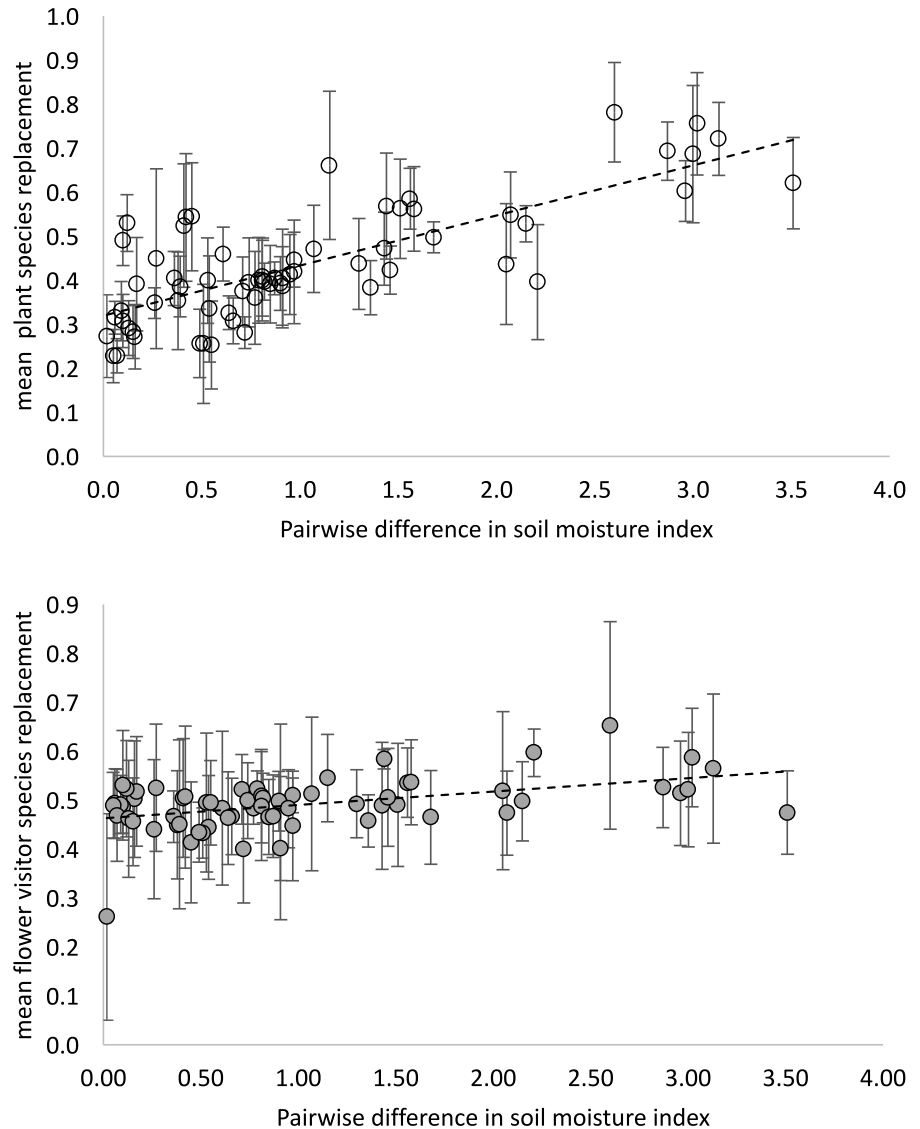
landscape configuration in models including meadow patch size and surrounding meadow area in 2005 and 1949, and flower-visitor richness was related only to meadow size in 2005.

Archaeological and paleoecological evidence suggests that montane meadows (non-forest areas) were present in the landscape since the late Pleistocene era (Gottesfeld et al. 1981). Over the past several thousand years, montane meadows served as summer encampments and hunting grounds for Native peoples, whose low-density, dispersed activities likely had little effect on meadow configuration or species composition (Highland 2011). Most trees in and around the meadows today are relatively young (< 100 years), but these relatively dense stands contain isolated, open-grown trees, whose ages (dated to late 1700s) coincide with the beginning of the extirpation of Native Americans from this landscape (Highland 2011; Jones 2016).

Landform features control meadow locations and their configurations in this mountain landscape, and hence they influence richness of plants and flower-visitors. Montane meadows are located at upper elevation on ridges and mountaintops with steep slopes and shallow or poorly drained soils. Each complex is a cluster of meadows, with the largest and least isolated meadow in the center, and smaller, more isolated meadows in the periphery, so meadow patch size, isolation, and loss of surrounding meadow are strongly correlated. In this study, while present-day meadow patch size explained richness of plant visitors in statistical models, richness appears to be related to inextricable relationships among patch size, connectivity, and historical changes in meadow configuration.

These findings are consistent with studies of extinction debt in plants. In a study of heathlands, past landscape structure explained more of the variability in current plant species richness than the current landscape structure alone (Cristofoli et al. 2010). Piqueray et al. (2011) found that the addition of past landscape configuration did not improve models of plant diversity in calcareous grasslands over those based on current landscape metrics, but fragmented meadows did have distinct diversity patterns compared with stable meadows. In our study, richness and species replacement were not different in small meadows that were fragments of previously larger

Fig. 4 Species replacement among all pairs of meadows for **a** plants ($y = 0.11x + 0.32$, $R^2 = 0.59$) and **b** flower-visitors ($y = 0.03x + 0.46$, $R^2 = 0.21$) as a function of pairwise difference in soil moisture index. Sørensen species replacement index for plant and flower-visitor species are averages and standard errors of the species replacement component of pairwise Sørensen dissimilarity for 2011 to 2016



meadows compared to small meadows that had been long isolated.

Counter to our expectations, very little of beta diversity was explained by nestedness, and nestedness was not related to differences in meadow size or spacing. Instead, more than 78% of beta diversity was species replacement based on multiple-site Sørensen dissimilarity. Species replacement (spatial turnover) is interpreted as a consequence of environmental sorting or spatial and historical constraints (Baselga 2010). The high spatial turnover observed in this study is consistent with intrinsic differences among meadows or barriers due to gradual tree encroachment in the

meadows. For example, a generalist species, *Eriophyllum lanatum* (common woolly sunflower) was observed to flower in eleven meadows, but was visited by common flower-visitors in only seven meadows. *Eriogonum compositum* (arrowleaf buckwheat) was observed to flower in ten meadows, but was visited by common flower-visitors in only seven meadows (Table 2). *Boykinia major*, which was a common flower in a wet meadow, also was observed to flower, but was not visited, in a neighboring dry meadow. In contrast, nestedness is interpreted as the result of non-random processes that selectively filter out certain groups as meadows become smaller or more isolated.

In this study, low levels of nestedness suggests that there is relatively little selective filtering of meadow plant and flower-visitor species in small or isolated meadows. Key flower-visitor species, such as *Apis mellifera*, *Bombus* spp., and *Bombylius major*, were present in all meadows, indicating that individuals of these species may be able to move among meadows in the study area. Colony-nesting bees (honeybees and bumblebees [*Bombus* spp.]) are known to forage over distances of up to several kilometers (Greenleaf et al. 2007; Osborne et al. 2008; Rao and Strange 2012), and are able to access temporally and spatially variable floral resources (Jha and Kremen 2013).

Floral characteristics or pollinator preferences for alternative species also may limit flower visitation. *Penstemon procerus*, a specialist species favored by hummingbirds and bees (Wilson et al. 2004), flowered in all twelve meadows, but was visited by common flower-visitors in only six meadows (Table 2). *Aquilegia formosa* (western columbine), a specialist flower favored by pollinators with long tongues (Whittall and Hodges 2007), accounted for less than 0.04% of total interactions, flowered in only four meadows (CPB, CPM, LM, M2), and was visited in only a subset of these meadows, even by common flower-visitor *Bombus mixtus* (Table 2).

Landform features affect soil moisture and species turnover

Counter to our expectations, richness was not higher in meadows where soil moisture, and therefore flowering, remained high for a longer period during the dry summers. Instead, species turnover was higher among pairs of meadows that differed in soil moisture, for both plants and flower-visitors. Soil moisture differences within and among meadows also explained plant species dissimilarity among subalpine meadows of Colorado (Burkle and Alarcón 2011).

Montane meadows are resistant to tree establishment for a variety of reasons, including microclimate, aspect, elevated water tables, and other factors (Miller and Halpern 1998). The process of meadow invasion by trees may take decades to centuries. Prior studies in this area have shown rapid meadow contraction, especially in mesic meadows and meadows adjacent to forest established after wildfires since the late 19th century (Takaoka and Swanson 2008; Halpern et al. 2010; Rice et al. 2012; Jones 2016). Regional

landform features, and specifically the mountain ridges where these meadows occur, impose moisture and temperature patterns which influence communities of plants and flower-visitors and may confound landscape pattern effects. In agricultural landscapes, regional scale effects confounded landscape scale effects on arthropod communities (Schweiger et al. 2005). In a semi-natural landscape, beetle communities were best explained by simultaneously considering the composition and configuration of habitat (Neumann et al. 2016).

As expected, flower-visitor richness was related to meadow size. However, the very high species replacement of flower-visitors among meadows and the high proportion of species unique to each meadow were unexpected. Soil moisture variation contributes to landscape-scale diversity by influencing the timing of flowering and providing habitats for a variety of plant and pollinator life history strategies (Ogilvie and Forrest 2017). Many flower-visitors also are influenced by edaphic characteristics. For example, the masarid bee-wasp *Pseudomasaris zonalis* is restricted to exposed scree, and most solitary bees are restricted to either very thin non-vegetated soils or rodent tumulus in dense vegetation. Some of the most abundant flower-visitors, the Eristaline hoverflies, are aquatic (standing water) as immatures and could only exist in sustained populations in Lookout Bog. While some flower-visitors observed in this study are native meadow dwellers including solitary bees with short foraging distances (Gathmann and Tscharrntke 2002; Zurbuchen et al. 2010), many of the flower-visitors to these meadows are forest dwellers which move readily across forest-meadow edges, and others (honeybees, bumblebees) are capable of relatively long-distance foraging dispersal (Beekman and Ratnieks 2000; Greenleaf et al. 2007; Osborne et al. 2008). Our findings are consistent with the notion that different flower-visitor species respond differently to the same landscape pattern (Ekroos et al. 2013). The variety of life history requirements of flower-visitors, the semi-permeability of the forest matrix separating meadows, and the diversity of meadow moisture conditions contribute to the high diversity of plants and pollinators in this study.

Non-native pollinator and plant species

The presence and dominance of *Apis mellifera* (European honeybee) in these interaction networks is puzzling. The study site is in the Willamette National Forest, which was unlogged and unroaded until 1948. In the 1950s to 1990, patch clearcutting and road construction occurred extensively in the landscape (total of 25% of the area in the vicinity of these meadows, Jones and Grant 1996). Since the 1970s, road traffic has been very low (mainly by researchers). Anecdotal information from local high school teachers indicates that honeybee hives may have been brought into the Forest in the 1960s or 1970s, when regenerating clearcuts provided abundant fireweed; some of these may have established feral colonies.

Hypericum perforatum (St. John's wort), native to Europe, was also present in the study meadows and is an important late-season floral resource. *Hypericum perforatum* apparently was introduced along logging roads in the 1950s to 1970s and was present throughout the road network in the early 1990s (Parendes and Jones 2000), reaching meadows by wind dispersal.

Meadow management and restoration

Plant and flower-visitor diversity in this study site was related to environmental characteristics as well as changes in the landscape over centuries. Thus, conservation approaches could consider earlier states of the landscape (Aguirre-Gutiérrez et al. 2015), including restoration of former meadow patches.

Although large meadows had higher richness, especially of flower-visitors, the small, diverse montane meadows in this study contributed significantly to landscape-scale diversity. These areas may serve as “stepping stones” for long-distance dispersal of meadow plants and pollinators among montane meadows (e.g., Herrera et al. 2017). Isolated patches of distinct meadow types may benefit solitary bees, which reside in these small meadows, while measures that promote landscape connectivity may benefit their antagonists, such as wasps (Steckel et al. 2014). Maintaining a landscape of disconnected, environmentally distinct montane meadows may also benefit bumblebees, which forage further in pursuit of species-rich floral patches (Jha and Kremen 2013), or hoverflies, whose species richness depends on richness of flowering plants (Meyer et al. 2009).

Our results indicate that it is important to maintain both hot dry and cool wet isolated meadows to promote plant–pollinator diversity in the region. At the same time, management should also protect large, mesic meadows. Large, mesic meadows have lost the greatest amount of area, and they support plant and flower-visitor species not found in steep dry or cool wet meadows. Hence, tree removal from large mesic meadows may play a disproportionate role in the conservation of plant–pollinator diversity in the region.

Conclusion

Despite contraction and loss of connectivity, montane meadows in the forested mountains of western Oregon have very high diversity of flowering plant species and flower-visitors. Large meadows had more surrounding meadow area and greater richness of flower-visitors. However, plant richness was not related to meadow size, and species in small isolated meadows were not nested subsets of larger nearby meadows. Moreover, landform features influenced soil moisture differences, which accounted for high levels of species replacement. Landform features that allow meadows to form and persist as isolated patches in the landscape over millennia apparently have favored diverse plant and insect species adapted to local conditions. Small isolated meadows contribute plant and flower-visitor species not found in large meadows. Landform features, especially differences in slope, aspect, and resulting moisture and temperature conditions strongly influence plant and flower-visitor communities, as well as the landscape configuration of patches in which plants and pollinators interact, and how these patches change over time. Thus, landform features, particularly those that affect moisture and temperature and hence the timing and types of floral resources, should be considered in future landscape ecology studies of plant–pollinator interactions.

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