PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

The direct and indirect effects of fire on the assembly of insect herbivore communities: examples from the Florida scrub habitat

Tania N. Kim · Robert D. Holt

Abstract Disturbance is a major source of spatial and temporal heterogeneity. In fire-maintained systems, disturbance by fire is often used as a management tool to increase biological diversity, restore degraded habitats, and reduce pest outbreaks. Much attention has been given to how plant communities recover from fire, but relatively few studies have examined post-fire responses of higher order species, such as insect herbivores. Because dynamic feedbacks occur between plants and their consumers, which can in turn influence the response of the entire ecosystem, incorporating higher trophic level responses into our understanding of the effects of fire is essential. In this study, we used structural equation modeling (SEM) to tease apart the direct and indirect effects of fire on insect herbivore assemblages found on three common oak species in the Florida scrub (*Quercus inopina*, *Q. chapmanii*, and *Q. geminata*). We investigated how fire affected herbivore abundance, richness, and community composition both directly and indirectly through environmental heterogeneity at different spatial scales (e.g., leaf quality, plant architecture, and habitat structure). We also investigated how seasonality and landscape heterogeneity influenced post-fire responses of insect herbivores and whether fire effects on herbivore assemblages varied among different host plants. Our general findings were that fire effects were (1) largely indirect, mediated through habitat structure (although direct fire effects were observed on *Q. inopina* herbivores), (2) non-linear through time due to self-thinning processes occurring in the scrub habitat, and (3) varied according to herbivore assemblage as a result of differences in the composition of species in each herbivore community. To the best of our knowledge, this is the first comprehensive study to examine how fire influences the assembly of insect herbivore communities through both direct and indirect pathways and at multiple spatial scales.

Keywords Disturbance · Structural equation modeling · Community assembly · Oak-scrub

Introduction

Disturbance is a major source of temporal and spatial heterogeneity, and its importance in structuring natural communities has long been recognized (Dayton 1971; Connell 1978; Sousa 1984; Pickett and White 1985). In many terrestrial systems, fire is an important source of disturbance, and in some ecosystems it is used as a management tool for increasing biological diversity, restoring degraded habitats, and reducing pest outbreaks (Angelstam 1998; McCullough et al. 1998; Peterson and Reich 2001; Brooks et al. 2004). Although fire disturbance at the local scale is relatively short in duration, the recovery of the ecosystem following fire can span several years or even many decades due to colonization lags, feedbacks between different trophic levels, and other processes that play out over time (Abrahamson 1984; Keeley and Keeley 1988).

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Since prescribed fires are increasingly used to manage fire-dependent systems, following the unfolding effects of fire through time can provide insight into effective habitat management and restoration procedures.

Although a vast body of literature has focused on the effects of fire on plant communities and population dynamics (Collins 1992; Glitzenstein et al. 1995; Menges and Quintana-Ascencio 2004), much less attention has been given to how fire influences species at higher trophic levels, such as insect herbivores. The response of a given consumer species assemblage to fire involves the interplay of multiple processes that directly and indirectly affect in situ survival, recolonization, and within-patch population dynamics. First, fire can directly impact consumer populations through mortality and movement out of the habitat. Some species can tolerate fire locally by seeking refuge or having below-ground storage of eggs or other resting forms, while other species migrate out of the habitat and thereby persist (Swengel 2001). For these species (assuming fires are modest in intensity and scale, and source populations persist nearby), recolonization can be fairly quick, and populations can quickly rebound following fire. However, if fires are severe, intense, or large in extent, herbivores may be locally extirpated, or population sizes may drop substantially. In these cases, the recovery of these species may be slow as their return may require colonization from more distant external refuges not affected by the fire (Sousa 1984). Under all of these scenarios, abundances immediately following fire will be low. Early successional stands should harbor fewer individuals than later successional stands, simply because herbivores have not had enough time to reach or accumulate within the focal habitat. Likewise, the species composition of the herbivore community may be driven by the dispersal ability and/or refuge seeking strategies of the herbivores. Early successional stands may be dominated by highly mobile taxa or those with stronger refuge-seeking behaviors. By contrast, a greater proportion of less mobile or fire-sensitive species should be found to occupy later successional stands (Swengel 2001; Joern 2005; Knight and Holt 2005). If recruitment is entirely dependent on recolonization by herbivores from the surrounding unburned habitat, then landscape features, such as proximity to unburned habitat, the types of unburned habitat within the surrounding landscape, and the amount of edge, may all be important factors to consider as well (Swengel 2001; Panzer 2003; Saint-Germain et al. 2004; Knight and Holt 2005).

Second, because consumers always depend upon resources, disturbance effects on insect herbivores can also be indirect, mediated by temporal changes post-fire in the host-plant and/or the surrounding habitat structure. The short-term indirect consequences of fire for insect herbivores after the fire has passed can include suppressed fecundity and increased mortality due to starvation and heightened exposure to predators and harsh environmental conditions through lost foliage, lost branches, and an overall reduction in plant size. The long-term indirect effects of fire play out in time through dynamic changes in plant individuals, populations, and communities following the fire. For example, a pulse of nutrients released from ash can increase the macronutrient content of the host-plant foliage, and this enhancement in plant quality can attract insect herbivores to a recently burned habitat. These fine-scale changes in host-plant quality have the potential to cause herbivore populations to quickly rebound following a fire (Swengel 2001; Turchin et al. 2003; Helms and Hunter 2005). At larger spatial and temporal scales, fire-mediated changes in host-plant abundance and the overall three-dimensional structure of the habitat can influence insect herbivore recolonization by attracting different herbivore species to specific habitat types and microhabitats. For example, open-habitat specialists may dominate recently burned habitats, with closed-canopy specialists occupying denser stands that develop as vegetation recovery progresses (Swengel 2001). Furthermore, fire-mediated changes in host-plant species abundance and vegetation structure may influence host-plant "apparency", thereby increasing or decreasing colonization rates onto host plants, depending on the density, species composition, and physical structure of non-host plant species in the surrounding neighborhoods (Strong et al. 1984; Basset et al. 2001; Swengel 2001).

Studies examining fire effects on insect herbivores are relatively scarce. Those that do exist on fire-dependent systems have largely attributed the fire effects to be indirect through changes in plant quality and vegetation structure (Whelan and Main 1979; Evans 1984; Bock and Bock 1991; Vieira et al. 1996; Kerstyn and Stiling 1999; Swengel 2001). It could be argued that since herbivores within fire-prone systems have most likely evolved mechanisms to withstand fire (e.g., seeking refuge belowground or the burial of eggs), the direct effects of fire should be minimal, and post-fire recovery should be largely dependent on changes within the plant communities (Brennan et al. 2011). However, if the fires are intense, spatially extensive, and severe, the direct effects of fire have the potential to be equally important in the post-fire recovery of insect herbivores; unfortunately, these are often overlooked (but see Vermeire et al. 2004; Knight and Holt 2005; Vogel et al. 2010). Furthermore, previous studies examining fire effects on insect herbivores have largely focused on environmental heterogeneity at a single spatial scale, possibly overlooking important mechanisms structuring herbivore communities at other scales (Stein et al. 1992; Vieira et al. 1996; Fay 2003; Vogel et al. 2010).

Because different insect herbivore species use different environmental cues to detect and select host-plant individuals, coupled with the fact that multiple herbivore species often share a single host-plant, the responses of herbivore assemblages following fire may depend on several factors operating simultaneously at multiple spatial scales. Lastly, traditional studies examining fire effects have simply compared communities in burned and unburned habitats. However, as population dynamics are likely to change over the course of succession, examining how communities change with time-since-fire (TSF) may elucidate whether fire effects are short-lived, non-linear, or change in strength with time.

The goal of this study was to examine how multiple spatial and temporal factors can influence insect herbivore community structure in a fire-maintained Florida scrub habitat. Using a combination of regression analyses and structural equation modeling (SEM), we examine how multiple factors vary and co-vary with one another as a first step towards an understanding of the recolonization and population dynamics of insect herbivores following fire. Given the many possible interacting pathways of fire effects on insect herbivores described above, SEM is ideally suited for addressing this problem, since it has the ability to tease apart the direct and indirect effects of fire on herbivore assemblages—an approach that previous studies have rarely used. Specifically, we asked (1) what are the effects of TSF on plant quality, plant architecture, and local habitat characteristics; (2) how do these factors, in addition to seasonality, TSF, and landscape heterogeneity, influence three metrics of herbivore community structure (insect herbivore abundance, species richness, and species composition); (3) do the direct and indirect effects of TSF on insect herbivore community structure differ among communities found on three dominant oak species (*Quercus geminata*, *Q. inopina*, and *Q. chapmanii*)? Previous studies have demonstrated an increase in insect species richness and abundance with succession following disturbances such as fragmentation, flooding, and land abandonment, due to increased resource availability, permanence, and resource complexity in later successional stands (Southwood et al. 1979; Brown 1985; Martinko et al. 2006). We therefore predicted similar responses of increased herbivore abundance and species richness as a function of TSF.

Methods

Study site

This study was conducted at the Archbold Biological Station (ABS) in 2005. ABS is a 8,000-acre natural preserve and is located at the southern tip of the Lake Wales Ridge near Lake Placid, Florida [27°11′N, 81°21′W, Highlands Co., FL; Electronic Supplementary Material (ESM) Fig. S1]. There are seven main habitat associations that make up the Florida scrub at ABS, namely, the southern ridge sandhills, sand pine scrub, flatwoods, swale, bayhead, seasonal ponds, and scrubby flatwoods (Abrahamson 1984). Each main habitat association is further subdivided based on the dominant plant species, resulting in 23 different sub-habitat types (Givens et al. 1984). The dominant habitat association at ABS is the scrubby flatwoods, a xeromorphic shrub habitat characterized by low-growing shrubs (1–2 m) interspersed with slash pine, *Pinus elliottii* (Abrahamson 1984; Myers 1990). This is an ancient ecosystem, as witnessed by the high incidence of endemic flora and fauna present, characterized by recurrent fire (Abrahamson 1984; Menges and Hawkes 1998). This ecosystem is currently a significant focus of conservation concern due to relentless development pressure throughout Florida, where less than 40% of pre-settlement scrub habitat remains, mostly in isolated fragments (ESM Fig. S1; Abrahamson 1984; Myers 1990). The resulting competition for space between humans and the natural environment has resulted in a dire need for conservation management plans to protect the remaining scrub habitat from further species loss and habitat degradation. Ideally, such management plans would be based upon a firm ecological understanding of the dynamics of these complex ecosystems.

The scrubby flatwoods habitat is dominated by three oak species (*Quercus geminata*, *Q. inopina*, and *Q. chapmanii*), which collectively make up 85–90% of the aboveground biomass (Schmalzer and Hinkle 1996; Seiler et al. 2009). The dominance of these species makes them a natural choice as focal host-plant species in this study since insect herbivores upon them would likely comprise the bulk of the herbivore assemblage in this habitat type. Co-occurring oak species within Florida (including the scrubby flatwoods) have been shown to be phylogenetically overdispersed (Cavender-Bares et al. 2004), with a combination of conserved and convergent traits that allow for species coexistence and survival in this habitat which is characterized by high-intensity fires at moderate frequencies (5–20 years; Menges and Hawkes 1998). *Q. inopina* belongs to the red oak clade and is the dominant plant species within this habitat association (ESM Fig. S2i). It is a relatively short-statured plant (1–1.5 m; ESM Fig. S3a, d) with relatively heavier leaves than *Q. geminata* and *Q. chapmanii* (ESM Fig. S2c). *Q. geminata* belongs to the live oak clade and generally has the same size stature as *Q. inopina* but with more branches (ESM Fig. S3a–d) bearing many small and thick leaves (ESM Fig. S2a–g). *Q. chapmanii* belongs to the white oak clade and is the tallest of these three oak species (ESM Fig. S3a, d). Leaves of *Q. chapmanii* are typically thinner than those of the

other two oak species and contain higher amounts of tannin (ESM Fig. S2b, h). Other species of shrubs (e.g., *Vaccinium* sp., *Sabal* sp., and *Lyonia* sp.) do co-occur in the scrubby flatwoods but in considerably lower numbers. Prescribed fires are conducted routinely at ABS as a restoration and management tool.

Plot establishment

In May 2005, 15 plots (30 × 30 m) were established in the scrubby flatwoods habitat along a chronosequence of TSF using fire history data provided by ABS (available at http://www.archbold-station.org/abs/index.htm; ESM Fig. S1). Five TSF intervals (1, 4, 6, 11, and 19 years since last fire) were selected to span the natural range of fire return intervals in the scrubby flatwoods (Myers 1990; Menges and Hawkes 1998), and three plots were established within each of the five TSF intervals. Plots were established in 15 different burn units, providing statistical independence among plots. We attempted to select sites with a similar fire size and intensity as these factors could also influence the recolonization and within-patch population dynamics of insect herbivores (Sousa 1984; Knight and Holt 2005).

Within each plot, 15 individuals of each oak species (*Q. geminata*, *Q. inopina*, and *Q. chapmanii*) were randomly selected and marked for subsequent insect and plant sampling on three different sampling dates (July, September, and November). On each plant, ten newly flushed leaves were randomly selected and marked at the petiole with indelible ink. New leaves were easily distinguishable from older leaves as they were softer and lighter green in color, and marked leaves were approximately 1 month in age. A total of 675 individual plants were marked (five individuals × three sampling dates × three species × 15 plots). We chose not to sample the same-plant individuals across sampling dates because the removal of leaves for physical and chemical analyses, and insect sampling (see below) were destructive methods and may have influenced future census results with repeated sampling of the same individual plant.

Characterization of plant architecture and leaf quality

Small-scale factors, such as plant architecture and leaf quality, may influence host-plant selection behavior and insect herbivore community structure (Feeny and Bostock 1968; Strong et al. 1984). Because these small-scale factors may vary across the growing season, individual plants were sampled in July, September, and November 2005 (hereafter referred to as the "sampling session"). During each sampling session, five marked plants of each oak species were randomly selected per plot. Plant height, diameter at base, the number of branches from the main stem, and the number of leaves were measured to characterize plant shape and size (hereafter collectively referred to as "plant architecture"). Ten marked leaves were removed from each of these plants, and the physical and chemical characteristics of the leaves were measured (hereafter collectively referred to as "leaf quality"). Physical traits included leaf toughness [measured as the force required to penetrate a leaf surface using a 2-mm diameter rod (force gauge series FB; Imada, Northbrook, IL)], leaf area and average width and length [measured using a leaf area meter (model 3000, LI-COR, Lincoln, NB)], leaf thickness, leaf mass, and specific leaf mass (Table 1).

Leaf chemistry was also characterized on collected oak leaves. Tannin concentrations were determined using the radial diffusion method described by Hagerman (1987), which involves extracting tannins from dried leaves using methanol and placing extracted tannins into wells in agar plates infused with bovine serum albumin. As the tannin extracts diffuse across the plates, the tannins bind to proteins, and circular precipitates form around the wells. The amount of tannin was correlated with the area of the precipitate. We established a standard curve with known quantities of tannin acid and used this curve to determine quantities of tannin in leaf samples.

Characterization of local habitat and landscape heterogeneity

Larger scale factors, such as local and surrounding habitat structure, can also influence host-plant selection behavior through variations in host-plant apparency and movement into and within the local habitat (Feeny 1976; Holt 1993). In order to characterize these larger scale factors, we sampled habitat structure within plots in September 2005 using the point-intercept method. Four equally spaced 30-m transects were established within each plot, and a 0.5-cm diameter rod was vertically placed at 2-m intervals along the entire length of these transects. The identity of all plant species touching this rod and height of interception were recorded; these data were used to calculate plant density per plot (total abundance of plants per plot), average and coefficient of variation in vegetation height, vegetation overlap (number of plant interceptions per location), plant species richness, openness (number of locations without plant interception), and host-plant abundance. These measures are collectively referred to as "habitat structure".

The surrounding habitat may also influence herbivore communities since the surrounding landscape may serve as a source habitat for cross-system flows of herbivores, predators, and nutrients (Holt 1993; Polis et al. 1997; Rand et al. 2006). In order to characterize landscape structure, detailed vegetation maps provided by ABS

Table 1 Measured variables used in the principal component analyses to describe the leaf quality, plant architecture, habitat structure, and landscape heterogeneity of *Quercus inopina*, *Q. geminata*, and *Q. chapmanii* individuals

SEM variables (PCA axis 1)	Measured variables used in PCA	Contributions to SEM variables		
		Q. inopina	*Q. geminata*	*Q. chapmanii*
Leaf quality	Leaf area	−0.924	−0.723	−0.923[a]
	Average width	−0.214	−0.371	−0.227
	Thickness	−0.988[a]	−0.341	0.990
	Leaf mass	−0.299	−0.576	−0.291
	Toughness	0.197	0.368	0.995
	Length	−0.107	−0.740	−0.108
	Amount of tannin	0.993	−0.334	0.123
	Specific leaf mass	−0.104	0.959[a]	0.118
	% variation explained by PCA axis 1	85.76	71.28	82.7
Plant architecture	Number of leaves	−0.995	0.298	0.996
	Number of branches	−0.996	0.103	0.997
	Plant diameter at base	−0.993	−0.949	−0.990
	Plant height	0.998[a]	0.996[a]	0.998[a]
	% variation explained by PCA axis 1	93.14	81.57	91.5
Habitat structure	Vegetation overlap	0.898	0.478	0.899
	Plant density	0.930[a]	0.898[a]	0.930[a]
	Openness	−0.322	−0.318	−0.321
	Plant height	0.162	0.155	0.160
	Variation in plant height (cv)	0.473	0.507	0.491
	Oak abundance	0.402	0.254	0.239
	Plant richness	−0.131	−0.118	−0.122
	% variation explained by PCA axis 1	76.12	78.63	78.65
Landscape heterogeneity	Habitat richness	−0.201	−0.215	−0.203
	Total edge	−0.226	−0.229	−0.225
	Diversity index of habitat types	−0.105	−0.216	−0.215
	Number of patches	−0.952[a]	−0.948[a]	−0.952[a]
	Mean shape index	−0.105	−0.109	−0.104
	% variation explained by PCA axis 1	93.39	93.99	93.19

PCA Principal component analysis, *SEM* structural equation modeling, *cv* coefficient of variation

[a] Variables with the greatest contributions to SEM predictor variable (PCA axis 1)

were used in ArcView 3.3 (ESRI 1999). Sectors, referred to as "buffers", of fixed radii ranging from 50 to 200 m in size were centered at 25-m increments on each plot and used to establish the habitat composition of surrounding areas. For each buffer size-class, landscape indices typically used to describe aspects of landscape complexity were measured (Riitters et al. 1995). These included habitat richness (the number of different subhabitat types, see "Study site"), the number of habitat patches, the diversity of habitat types, the total amount of habitat edge, and the mean shape index of the focal habitat. Buffers of 100-m radius were used in the SEM analyses described below because they exhibited the greatest variance in landscape heterogeneity between the different TSF intervals.

Arthropod sampling and identification

Arthropods were sampled in July, September, and November 2005, 1 week following plant sampling, on marked plants (those surveyed 1 week earlier) using a 15-inch-diameter sweep net and making 20 sweeps across the entire plant. The arthropod abundance and richness data consisted of the combined set of 20 sweeps per plant. Arthropods were collected on sunny days (between 10 a.m. and 2 p.m.) on all sampling dates and therefore excluded nocturnal feeding insects and exclusively internal feeding insects (e.g., gallmakers). Arthropod herbivores (hereafter referred to as "insect" herbivores) were identified to the species level and verified by comparison with specimens at the Florida State Arthropod Collection at the Division of Plant Industry

(Gainesville, FL) and the ABS Arthropod Collection (Lake Placid, FL).

Data analysis

Data reduction

A total of 24 predictor variables were measured to describe host-plant, local, and surrounding habitat characteristics. In order to reduce the number of variables to manageable levels for the regression and SEM analyses described below, principal component analyses (PCA) were performed using the R 2.12 software program for each oak species separately (R Development Core Team 2010). PCA reduced the original 24 measured variables to four variables that retained most of the original variation. PCA loadings for the measured variables are compiled in Table 1. In order to collapse herbivore community composition into one response variable, we performed non-metric multidimensional scaling (NMDS) on the herbivore community data. NMDS determined similarity in community composition of herbivore species on different observational units (i.e., host-plant individuals) and was performed for each oak species separately. NMDS analyses were performed in R 2.12 using the vegan package (Oksanen et al. 2010).

Regression analyses

For each oak species, we examined the effect of TSF, sampling session, and their interaction on herbivore abundance, species richness, and community composition by performing separate linear and quadratic regressions. Individual herbivore responses were averaged within plots to yield one average herbivore abundance, richness, and community composition for each burn unit per sampling session. We found that all quadratic terms were not significant and therefore excluded the nonsignificant terms from the final models. Similarly, to examine the effects of TSF on leaf quality, plant architecture, and habitat structure, we performed linear and quadratic regressions for each oak species. Individual plant responses were averaged within plots to yield one average plant or habitat response for each burn unit. All regression analyses were performed in R 2.12 (R Development Core Team 2010).

SEM analyses

Structural equation modeling was performed to better understand how fire influenced herbivore assemblages and whether these effects were direct or indirectly mediated through fire-induced changes in plants. SEM compares observational data to causal hypotheses/models and distinguishes relationships as being direct or indirect (Shipley 2000; Grace 2006). Relationships indicated by one-way arrows imply causation, whereas double-headed arrows indicate unanalyzed patterns of correlation. Standardized path coefficients (standardized partial regression coefficients) indicate the strength of relationships, and R^2 terms were assigned to each response variable to indicate the amount of variation explained by the predictor variables.

Using the scores from the first PCA axes, we proposed a full causal model based on preliminary data collected in 2004 (T. Kim unpublished data; Fig. 1a). PCA scores were inherently centered, thereby removing correlations between the predictor variables. TSF was suspected to have direct effects on leaf quality, plant architecture, and habitat structure, which, along with landscape heterogeneity, may have affected insect herbivore abundance, richness, and community composition. TSF may have also had direct effects on herbivore community structure through direct mortality, forced migration out of the focal habitat, and delayed recolonization back into the focal habitat following fire, depending on the severity and intensity of the fire. Because insect herbivore species vary in their phenology, the time of sampling in the growing season may have also influenced the species of insect herbivores collected, and was therefore added into the model as "sampling session". Preliminary data showed that within-season variation in leaf quality was significant; therefore, arrows connecting sampling session and leaf quality were added to tease apart indirect effects of sampling session on herbivore community structure. However, there was little within-season variation in plant and habitat structure, so arrows connecting sampling session with plant architecture and habitat structure, respectively, were omitted from the analyses. Finally, we suspected that the relationships between TSF and leaf quality, plant architecture, and habitat structure would be non-linear. Therefore, we compared SEM results of models with and without quadratic TSF terms. Linear and quadratic TSF terms were correlated; therefore, double-headed arrows were added between these terms in the structural equation models.

Alternative structural equation models were generated by modifying the full causal model using a backward stepwise elimination process in which non-significant relationships were removed from the full model (starting with the least significant relationship) until all relationships within the model were significant (Chou and Bentler 2002; Grace 2006). χ^2 goodness-of-fit tests were performed to assess the fit of the structural equation models with data collected in 2005. Proposed models with P values >0.05 indicated good fits (Shipley 2000; Grace 2006). Other goodness-of-fit measures were used to confirm model fits, such as the Comparative Fit Index (CFI) and Root Mean Square Error of Approximation (RMSEA). Akaike's Information Criterion values were compared across all models in order to select the most appropriate structural equation model. All SEM analyses were
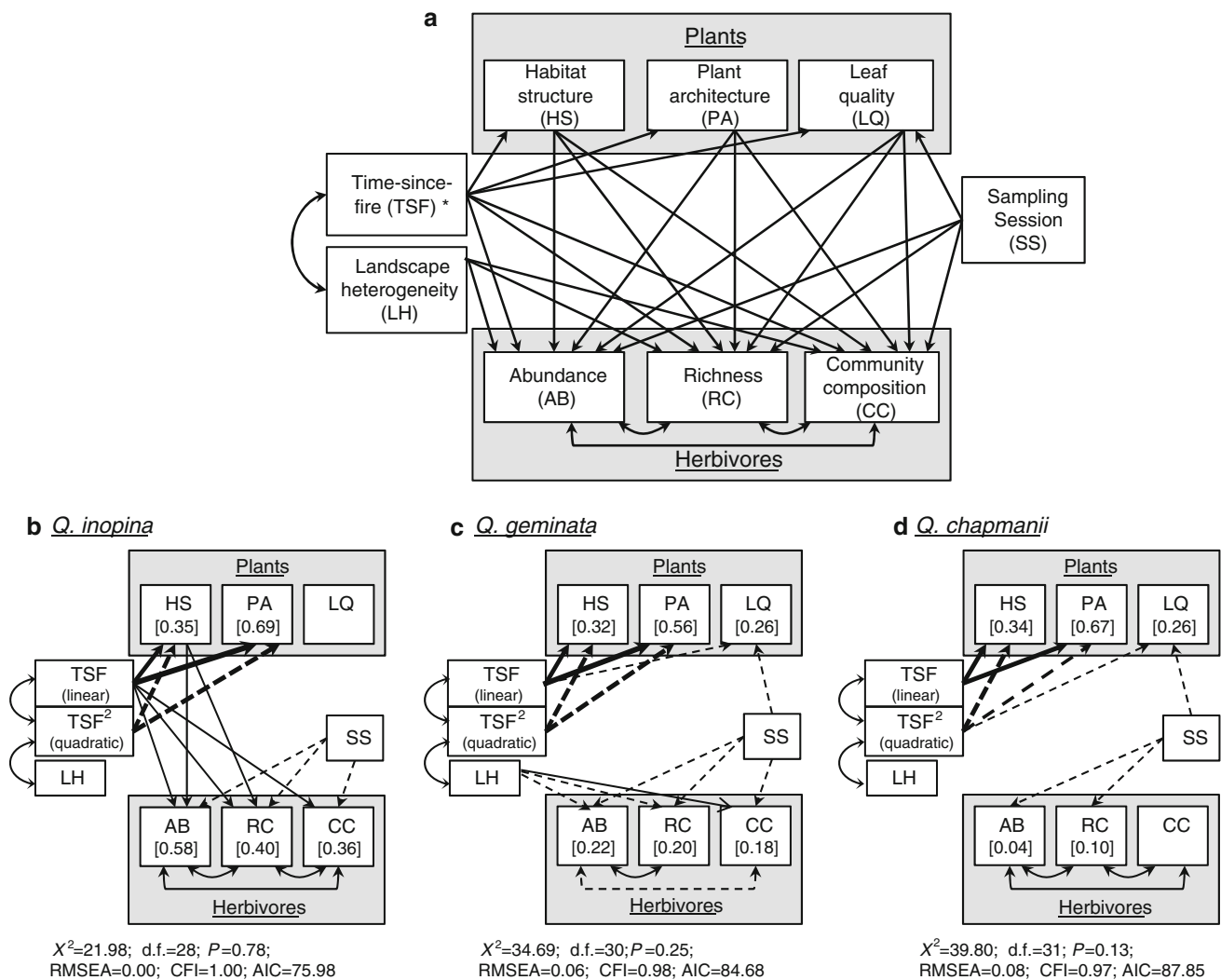
Fig. 1 Structural equation models investigating the direct and indirect effects of fire on herbivore abundance, richness, and community composition. *Double-headed arrows* indicate correlations; *single-headed arrows* indicate causal relationships. **a** Our proposed full causal model, **b–d** final structural equation model results for *Quercus inopina*, *Q. geminata*, and *Q. chapmanii* herbivore assemblages, respectively. *Solid arrows* Significant ($P < 0.05$) indicate positive relationships; *dashed arrows* indicate significant negative relationships. *Thickness of arrows* indicates the strength of interaction [refer to ESM Tables S1 and S3 for numerical values of the standardized path coefficients (*single-headed arrows*) and correlation coefficients (*double-headed arrows*), respectively]. *Numbers in square brackets* indicate the amount of variation by the predictor variables (R^2 values). *Asterisk* indicates that both linear and quadratic TSF terms as well as their correlation are included. *RMSEA* Root Mean Square Error of Approximation, *CFI* Comparative Fit Index, *AIC* Akaike's Information Criterion

performed in MPlus (Muthen and Muthen 2004). Because of the hierarchical nature of the datasets (individual plants nested within plots), the clustering function was used in MPlus which adjusts standard errors to accommodate non-independencies in the dataset (Muthen and Satorra 1995).

Results

PCA results: characterizing plant quality, habitat structure, and landscape heterogeneity

The first axis of each PCA explained most of the variation in the corresponding dataset (range 71.3–93.9%; Table 1).

Leaf area, specific leaf mass, and leaf thickness explained most the variation in leaf quality traits for *Q. inopina* (85.8%), *Q. geminata* (71.3%), and *Q. chapmanii* (82.7%) leaves, respectively. Plant height contributed most to the first PCA axis of plant architecture for all three oaks (average 88.7%). The total plant density per plot explained most of the variation in habitat structure traits (average 77.8%). Finally, landscape heterogeneity was largely characterized by the number of habitat patches within a 100-m buffer around the centroid of the plot (average 93.5%). Loadings and relative contributions of each measured variable of the first PCA axis are shown in Table 1.

Regression analyses: the effects of fire and sampling session on herbivore community structure

There was considerable overlap in the total abundance and richness of herbivore species found on the three oak species during the entire growing season (Table 2). Two-spotted spider mites (*Tetranychus urticae*) and Sminthurid springtails (*Dicyrotoma atra*) were the numerically dominant species on the oaks, accounting for 51, 69, and 67% of the total herbivore abundance for *Q. inopina*, *Q. geminata*, and *Q. chapmanii*, respectively. However, the composition of the herbivore species on each oak species did vary (ESM Fig. S4), and also varied with TSF and sampling session (Fig. 3). Specifically, TSF had positive effects on the abundance and richness of herbivores species on *Q. inopina*, where late-successional stands harbored more individuals and a larger number of herbivore species (linear regression: abundance $F_{1,39} = 10.05$, $P = 0.0020$; richness $F_{1,39} = 6.44$, $P = 0.015$), but it did not affect the abundance and richness of herbivores on *Q. geminata* and *Q. chapmanii* (all $P > 0.10$; Fig. 2a–f). Also, sampling session had significant negative effects on herbivore abundance and richness: there was a lower abundance and a lower number of species when plants were sampled later in the growing season compared to sampling earlier in the season, and these negative effects were consistent across each oak assemblage (linear regression: all $P < 0.05$, Fig. 2a–f). Sampling session also influenced the composition of herbivore communities found on *Q. inopina and Q. chapmanii*, but not *Q. geminata* (linear regression: *Q. inopina* $F_{2,39} = 15.17$, $P < 0.0001$; *Q. chapmanii* $F_{2,39} = 3.74$, $P = 0.03$; Fig. 2g–i). Finally, there was a significant interaction between TSF and sampling session for *Q. inopina* herbivores (linear regression: $F_{2,39} = 5.31$, $P = 0.009$) such that the composition of herbivore species varied little across the growing season within recently burned stands compared to the long unburned stands (Fig. 2g). Conversely, the composition of herbivores found on *Q. geminata* varied more throughout the growing season in recently burned stands compared to long unburned stands (Fig. 2h).

Regression analyses: the effects of fire on leaf quality, plant architecture, and habitat structure

We found significant non-linear effects of TSF on habitat structure (quadratic regression: $F_{8,36} = 2.215$, $P = 0.05$, $R^2_{adj} = 0.1844$). As habitats recover following fire, plants quickly occupy available space to form dense stands at mid-successional stages (6–10 years post-fire). In this system, die-backs occur following peak density stages which lower plant density and increase habitat openness in later successional stages (Fig. 3a). Similarly, a significant

non-linear relationship between plant architecture and TSF was observed where average plant height increased with succession followed by a decrease in average plant height due to self-thinning of stems (quadratic regression: $F_{8,36} = 8.917$, $P < 0.001$, $R^2_{adj} = 0.5955$; Fig. 3b). These effects were consistent among the oak species studied. Finally, TSF had a significant non-linear relationship with *Q. inopina* leaves where early- and late-successional plants had on average thinner leaves than mid-successional plants; however, TSF did not affect *Q. geminata* or *Q. chapmanii* leaves (quadratic regression: $F_{8,36} = 2.716$, $P = 0.01$, $R^2_{adj} = 0.242$; Fig. 3c).

SEM: direct and indirect effects of fire on herbivore community structure

Since we found significant non-linear terms in the regression analyses above, we compared structural equation models with and without quadratic TSF terms. Models without quadratic TSF terms had poor fits ($\chi^2_{Q.chap} = 19.61$, $df = 10$, $P = 0.033$; $\chi^2_{Q. ino} = 20.6$, $df = 10$, $P = 0.02$; $\chi^2_{Q.gem} = 25.7.6$, $df = 10$, $P = 0.04$); therefore we only describe results from SEM analyses that include the quadratic TSF term.

SEM: herbivores on Q. inopina

Although soft-bodied mites and collembolans made up 51% of the total number of herbivore species found on *Q. inopina*, there were more beetles and hemipterans (suborder Auchenorrhyncha) on *Q. inopina* than on the other two oak species (Table 2). For this herbivore assemblage, the effects of fire were largely indirect, mediated through fire-induced changes in habitat structure (Fig. 1b). Specifically, host plants within dense stands of vegetation (i.e., mid-successional stands) housed a higher abundance of herbivores than plants in less dense stands at early- and late-successional stages. Similarly, densely vegetated mid-successional stands had higher species richness than less dense stands.

Fire effects were also direct, having positive effects on the abundance, richness, and community composition of herbivores on *Q. inopina*, matching results from the regression analyses reported above. As succession proceeded, herbivore abundance and species richness increased, and changes in herbivore community composition were observed, irrespective of changes in leaf quality, plant architecture, and habitat structure. Finally, within-season variation in herbivore community structure was observed where herbivore abundance and richness decreased throughout the growing season, and changes in community composition were observed. Results from the regression analyses complement the SEM results by highlighting a significant interaction between sampling session

Table 2 Herbivorous arthropod species collected on *Q. chapmanii*, *Q. inopina*, and *Q. chapmanii* in 2005

Arthropod species	Order: Family	Feeding/habitat	*Quercus inopina* (n)	*Quercus geminata* (n)	*Quercus chapmanii* (n)
Smithurus sp.	Acari: Sminthuridae	LC	314	229	414
Tetranychus urticae	Acari: Tetranychidae	SF	125	187	190
Homoeolabus analis	Coleoptera: Attelabidae	LC, POS	0	0	1
Brachys areosus	Coleoptera: Buprestidae	LM, LC, POS	3	0	1
Metachroma anaemicum	Coleoptera: Chrysomelidae	LC	17	8	3
Neochlamisus insularis	Coleoptera: Chrysomelidae	LC, POS	17	6	3
Notolomus basilis	Coleoptera: Curculionidae	PF	6	5	5
Pachybrachis conformis	Coleoptera: Chrysomelidae	LC	0	2	3
Unknown larvae	Coleoptera: Chrysomelidae	LC	7	3	8
Anchastus asper	Coleoptera: Elateridae	LC	1	5	0
Epicauta heterodera	Coleoptera: Meloidae	LC	1	0	0
Microcentrus perditus	Hemiptera: Aetalionidae	SF, POS	0	0	1
Balcutha sp.	Hemiptera: Cicadellidae	SF	1	0	0
Deltocephalus obtectus	Hemiptera: Cicadellidae	SF	1	0	0
Erythroneura comes	Hemiptera: Cicadellidae	SF	54	29	36
Eutettix nitens	Hemiptera: Cicadellidae	SF, POS	12	12	3
Excultanus excultus	Hemiptera: Cicadellidae	SF	0	0	1
Gyponana fastige	Hemiptera: Cicadellidae	SF	5	5	13
Jikradia melanota	Hemiptera: Cicadellidae	SF	110	56	93
Polana quadrinotata	Hemiptera: Cicadellidae	SF	2	0	2
Cedusa sp.	Hemiptera: Derbidae	SF, POS	2	1	10
Flatoidinus punctatus	Hemiptera: Flatidae	SF	2	2	4
Hysteropterum fuscomaculosum	Hemiptera: Issidae	SF	148	102	67
Idioderma virescens	Hemiptera: Membracidae	SF	0	1	2
Dendrocoris fruticicola	Hemiptera: Pentatomidae	SF, POS	8	5	3
Pelitropis rotulata	Hemiptera: Tropiduchidae	SF	0	1	3
Aptenopedes hubbelli	Orthoptera: Acrididae	LC	8	7	17
Aptenopedes nigropicta	Orthoptera: Acrididae	LC	7	10	9
Aptenopedes sphenarioides	Orthoptera: Acrididae	LC	2	0	1
Chortophaga australiur	Orthoptera: Acrididae	LC	1	0	0
Melanoplus forcipatus	Orthoptera: Acrididae	LC, POHS	2	1	0
Orocharis luteolira	Orthoptera: Podoscirtidae	LC	13	8	6
Odontoxiphidium apterum	Orthoptera: Tettigoniidae	LC	1	3	3
Manomera sp.	Phasmida: Diapheromeridae	LC	1	0	0
Total abundance			856	599	902
Total richness			28	24	27

Arthropods consisted of a mixture of leaf chewers (LC), pollen feeders (PF), sap feeders (SF), and leaf miners (LM). Arthropods were considered as primarily oak specialists (POS) or primarily oak habitat specialists (POHS)

and TSF on herbivore community composition. In particular, across-session differences in community composition were greater in long-unburned habitats versus recently burned habitats (irrespective of changes in the plant community), indicating that herbivore communities were more similar in composition throughout the growing season in early-successional stands compared to herbivore communities in late-successional stands. Furthermore, herbivore communities in late-successional stands become more similar to those early-successional stands later in the growing season.

SEM: herbivores on Q. geminata

The herbivore community found on *Q. geminata* was both less abundant and less speciose than those found on
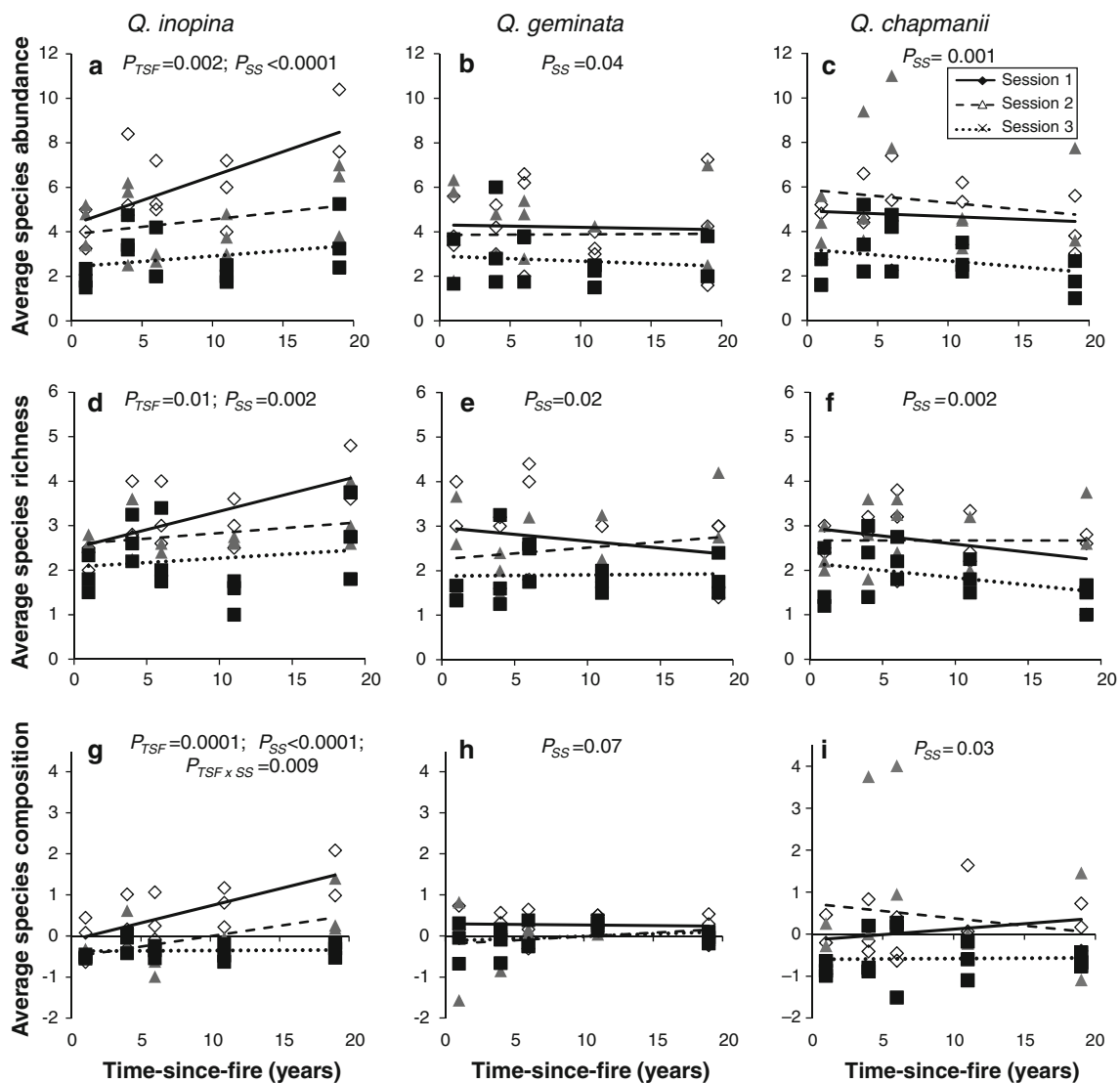
Fig. 2 Relationships between time-since-fire (*TSF*) and sampling session (*SS*) on herbivore abundance (**a–c**), richness (**d–f**), and community composition [non-metric multidimensional scaling (NMDS); **g–i** for herbivore assemblages on *Q. inopina*, *Q. geminata*, and *Q. chapmanii*. *Lines* best fit linear regressions, *points* average values at each site

Q. chapmanii and *Q. inopina* (Table 2). Although fire had strong non-linear effects on habitat structure, plant architecture, and leaf quality, these effects did not influence the herbivore communities on *Q. geminata* (Fig. 1c). Instead, landscape heterogeneity had direct negative effects on the abundance and richness of *Q. geminata* herbivores where plots embedded in "patchy" landscapes (i.e., landscapes with a high number of distinct habitat patches; Table 1) harbored more individuals and herbivore species than less patchy landscapes. Herbivore community composition also varied with landscape heterogeneity. Landscape heterogeneity was highly correlated with TSF, suggesting another possible indirect effect of fire on herbivore community structure (see "Discussion"). Finally, as with herbivores found on *Q. inopina*, sampling session also directly

influenced *Q. geminata* herbivore communities where herbivore abundance and richness decreased, and community composition changed throughout the growing season.

Herbivores on *Q. chapmanii*

Here also, fire had direct, non-linear effects on habitat structure, plant architecture, and leaf quality, but these effects did not further influence herbivore community structure on *Q. chapmanii* which harbored more spider-mites and collembolans than both *Q. geminata* and *Q. in-opina* (Table 2). Because of the lack of a fire effect for these taxa, fire had no effect on the *Q. chapmanii* herbivore assemblages (Fig. 1d, ESM Table S1c). Instead, herbivore
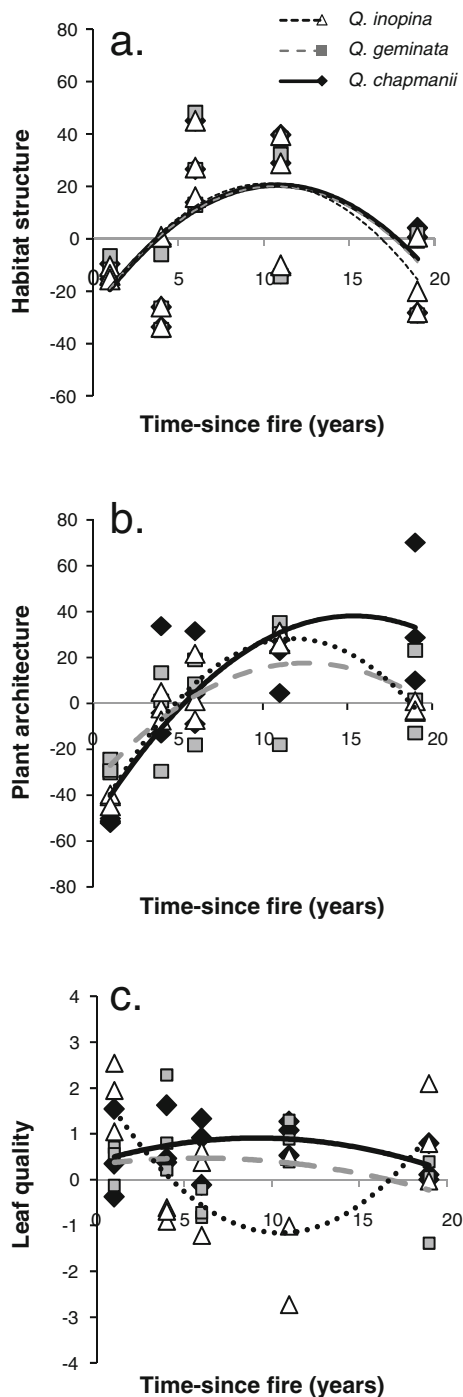
Fig. 3 Relationships between time-since-fire and habitat structure
(**a**), plant architecture (**b**), and leaf quality (**c**) of *Q. chapmanii*,
Q. geminata, and *Q. inopina*. *Lines* Best-fit quadratic regressions,
points average values from each site

community structure was directly affected by sampling
session in that herbivore abundance and richness decreased
throughout the growing season, with no changes in
community composition. However, since R^2 values for
herbivore abundance and richness on *Q. chapmanii* were
low ($R^2 = 0.04$ and $R^2 = 0.10$, respectively), other

unmeasured variables could have been important in struc-
turing these communities (see "Discussion").

Discussion

In fire-maintained habitats, fire can have important effects
on consumers by affecting in situ survival, recolonization,
and within-patch population dynamics. These effects can
be direct, through mortality and forced migration out of a
habitat, or indirect, being mediated by shifts in habitat
structure and resource availability (Sousa 1984; Swengel
2001). Previous studies investigating fire effects on insect
herbivore communities have often (1) assumed fire effects
to be only indirect, (2) focused on a single aspect of the
vegetation structure at one spatial scale, ignoring possible
interactions with other factors at multiple spatial scales, or
(3) focused on comparing results from burned versus
unburned plots, ignoring possible non-linear effects of TSF
on herbivore communities. To the best of our knowledge,
this is the first comprehensive study to address each of
these components for multiple herbivore assemblages (but
see Vogel et al. 2010, discussed below).

The indirect effects of fire on herbivore communities

In all three SEM analyses, we observed a strong direct
effect of fire on multiple factors known to influence host-
plant selection behavior (Strong et al. 1984; Swengel 2001;
Fig. 1). Specifically, TSF had a non-linear relationship
with habitat structure, plant architecture, and leaf quality,
where plant density, plant height, and leaf thickness,
respectively, initially increased following fire, but later
decreased at late-successional stages. Self-thinning is
common in many forest and shrub ecosystems (including
the Florida scrub) as a response to high competition
(Mohler et al. 1978; Johnson 1982; Givens et al. 1984).
Since we did not find much evidence of mammalian her-
bivory by rabbits or deer in the scrubby flatwoods (par-
ticularly on the oak ramets), we feel confident in proposing
that low plant densities in long unburned stands may have
been due to self-thinning processes—and not to mamma-
lian herbivory. Moreover, since the resulting plants sur-
veyed in long unburned stands were a combination of those
that survived the thinning process and new resprouts, non-
linear TSF patterns in plant height and leaf quality are
reasonable outcomes.

Although fire influenced the vegetation structure for the
three oak species in similar ways, only herbivores on
Q. inopina were affected by fire-induced changes in habitat
structure. As plant density increased following fire, the
richness and abundance of herbivore species increased as
well. Similarly, as plant densities dropped following die-

backs, so too did herbivore species richness and abundance. The positive relationship between herbivore species richness and abundance with plant density may have be linked with increased spatial heterogeneity and food availability within dense plots or to an increased probability of finding host-plants in dense stands (Feeny 1976; Strong et al. 1984). Population regulation of herbivores by bottom–up forces has been observed across many fire-maintained or arid systems (Siemann 1998; Marques et al. 2000; Wenninger and Inouye 2008) and could explain why more herbivores were found in denser plots than in sparse plots in our study. Additionally, denser plots may have allowed colonizing herbivores to better detect host-plants within a broader matrix of non-host-plant species or habitats (Root 1973; Hamback and Englund 2005). Positive relationships between host-plant density (or area) and herbivore density have been observed within a wide variety of insect species, including beetles and *Auchenorrhynchan hoppers* (Matter 1997; Cronin 2003; Grilli 2010; Sahlin and Schroeder 2010), and insect movement studies suggest that these relationships are due to the increased ability of insect herbivores to detect host-plants during dispersal (Hamback and Englund 2005). This could be the case with *Q. inopina* herbivores, where dense plots allowed for better host-plant detection; however, once in the focal patch, increased food availability within dense stands may have allowed for increased population growth and species co-existence.

The direct effects of fire on herbivore communities

Quercus inopina herbivores were the only herbivores to show a direct response to TSF. As succession progressed, herbivore richness and abundance increased, and community composition changed, irrespective of changes that occurred to habitat structure. Herbivores within late-successional stands may have had more time to accumulate within sites and a greater opportunity to colonize focal habitats, especially in the case of weak dispersers. Brown et al. (1992) found similar patterns of time-since-disturbance in leafhoppers in grassland habitats, where late-successional sites harbored more and different leafhopper species than early-successional sites, irrespective of successional changes in aboveground biomass. These authors linked their results to tradeoffs in dispersal and competitive abilities among leafhopper species, such that generalists and strong dispersers dominated early-successional sites and were displaced by specialists and weaker dispersers later in succession. Tradeoffs in dispersal and competitive ability may explain the similar patterns of community composition observed with TSF in our *Q. inopina* system. For example, *Erythroneura comes* (a generalist leafhopper species with strong dispersal abilities) was found in higher number in recently burned plots, whereas weak dispersing specialist beetles, such as *Neochlamisus insularis*, were found only in later successional stands.

Landscape context affects herbivore communities

For *Q. geminata* herbivores, landscape heterogeneity had a strong effect on herbivore assembly, such that plots embedded in more heterogeneous (i.e., patchy) landscapes supported a higher abundance and richness of insect herbivore species. This classic positive relationship between habitat heterogeneity and species diversity is commonly observed for arthropod communities (Dennis et al. 1998; Di Giulio et al. 2001; Hendrickx et al. 2007). In our study, patches of different habitat types surrounding the focal habitat may have served as source habitats for different herbivore species to colonize the focal stands following fire. This possibility suggests that herbivores found on *Q. geminata* may be more influenced by landscape context than by host-plant selection behavior due to potential spillover from a surrounding heterogenous environment. Furthermore, since fire frequency and intensity have been demonstrated to influence landscape heterogeneity in the Florida scrub (Menges and Hawkes 1998), fire-mediated changes to the landscape can also be considered another indirect pathway of fire, albeit one operating at a much larger spatial scale than those considered above.

Passively dispersed species not affected by measured traits

Quercus chapmanii herbivores were mostly spider-mites (*Tetranychus urticae*) and springtails (*Dicyrotoma atra*). Intriguingly, these taxa were not affected by any of the measured variables or by TSF. This absence of effect makes sense in terms of the basic natural history of these taxa. Mites and springtails are ubiquitous and passive aerial dispersers; consequently, their movement into the habitat and host-plant selection may not have been driven by host-plant quality or plant abundance, but rather by unmeasured variables, such as wind direction and speed (Englund and Hamback 2007; Moser et al. 2009). Although many herbivores found on *Q. inopina* and *Q. geminata* are aerial dispersers and are presumably affected by some degree by wind direction and speed, spider-mites and springtails are much weaker in their ability to navigate within the air column and to determine where to settle due to their lack of wings (Schowalter 2006). As winged insects settle within a habitat, they can easily navigate to preferred host plants should they land on less desirable plants. On the other hand, since spider-mites and collembolans have limited short-distance dispersal abilities following settlement, recruitment onto host plants may simply be a function of where they land, rather than host-plant preference or

selection (Krainacker and Carey 1990; Hamback and Englund 2005). We suggest that the importance of spatial heterogeneity in physical flux processes at a local spatial scale may be an underappreciated factor contributing to the local spatial heterogeneity in the abundance and richness of herbivore communities.

Within-season variation with herbivore community assembly

There was overlap in the total abundance and richness of herbivore species on all three oaks. As a result, common factors were observed to influence all three herbivore assemblages. In particular, both regression and SEM results indicated that sampling session unsurprisingly negatively influenced herbivore community structure in that plants sampled later in the growing season (September and November) harbored fewer individuals and number of species than did plants sampled at the height of the growing season in July (Andrewartha and Birch 1954). In the case of *Q. inopina* herbivores, the linear regression results showed that the strength of the sampling session varied with TSF, where late-successional stands had a greater change in community composition across the growing season than early-successional stands (Fig. 2). The reverse pattern was found for *Q. geminata* herbivores. Surprisingly, the SEM results for *Q. inopina* and *Q. geminata* showed that the total effects of fire (ESM Table S2) were similar in strength (or stronger) to the seasonal effects, indicating that processes occurring at longer time scales (e.g., succession) can play equally important roles as short-term processes (e.g., seasonality) in structuring insect herbivore communities.

Conclusions

Using a combination of linear regression analyses and structural equation modeling, we were able to give a comprehensive view of how different factors (at varying spatial scales) can influence the assembly of insect herbivore communities in the Florida scrub. In our study, we found different factors (including fire) to be significant in structuring the three herbivore assemblages, despite large overlap in community structure. We suggest that factors affecting recolonization (e.g., dispersal ability and proximity of source habitat) and within-patch population dynamics (e.g., resource availability) are important to the organization of these herbivore assemblages, but in ways that differ among host-plant species and among herbivore taxa. In one herbivore assemblage (*Q. chapmanii*), we found that no measured factor influenced community organization, since the majority of herbivore species

belonging to this assemblage are passive dispersers and can easily disperse and colonize different habitats. In another herbivore assemblage (*Q. geminata*), community organization was influenced by landscape heterogeneity, as surrounding patches may have served as important source habitats for colonizing herbivores. Finally, in the last herbivore assemblage found on the dominant oak species (*Q. inopina*), we suggest that resource availability, host-plant detectability, and time-since-disturbance are all important factors for recolonization by allowing time for weak dispersers to reach their focal habitat and increase in population size. In all three cases, a better understanding of the dispersal mechanisms and searching behaviors of the target herbivore species could help to improve our understanding of the importance of fire effects on community organization.

We did not find plant quality to influence herbivore assemblages despite the findings of previous studies that have suggested plant quality as an important factor in insect herbivore community organization (Strong et al. 1984; Denno et al. 1995). One possibility is that we overlooked important leaf quality traits. However, since a total of eight leaf traits known from prior work to influence herbivore preference (both physical and chemical properties) were measured, we feel reasonably confident that we have adequately characterized leaf quality. Another alternative hypothesis is that leaf quality may in fact not be important for these herbivores. In most cases, the herbivores species sampled were found on all three oak species (e.g., suggesting a generalist feeding strategy), although in many cases there was bias towards one oak species, suggesting some level of preference (Table 2). Oaks are known to house a large suite of specialist internal feeders (e.g., gall-makers and leaf miners) which could respond more strongly to changes in leaf quality (Egan and Ott 2007; Cornelissen and Stiling 2008). A study focusing on fire effects for such internal-feeding herbivores could reveal significant leaf quality effects.

In this study, we found fire effects to be both direct and indirect, mediated by local habitat structure, and we found fire effects to be non-linear, changing in strength and direction throughout succession. In a similar study, Vogel et al. (2010) examined the effects of prescribed fires on butterfly assemblages in a tall prairie habitat by decomposing fire effects as direct or indirectly mediated through changes in vegetation and floral resources. As in our study, these authors also found non-linear fire effects on vegetation characteristics, but the changes in vegetation structure (mostly bare ground cover) in that study only influenced habitat specialists. Fire effects in their system were largely direct for habitat generalist species. Our study differs from and complements that of Vogel et al. (2010) in that we incorporated environmental heterogeneity at multiple

spatial scales into our SEM analyses. We found large-scale features, such as habitat structure and landscape heterogeneity, to be important in structuring herbivore assemblages, which in turn were influenced by fire. In Vogel et al. (2010), the percentage of bare ground in the focal habitat (a form of habitat structure) was also significant in influencing specialist butterflies; however, this variable accounted for only 5–21% of the variation in their datasets. A possible feature important to the organization of butterfly communities discussed in that paper is landscape context; however, the authors did not explicitly measure the importance of landscape-level traits. Our study incorporated landscape metrics into the structural equation models and found that the number of habitat patches surrounding the focal habitat is an important feature structuring *Q. geminata* herbivores. Similar SEM frameworks focusing on both local and landscape features can be used to examine fire effects on arthropods as part of conservation efforts to protect rare and endangered insect species (Kwilosz and Knutson 1999; Mollenbeck et al. 2009) or to control outbreaks of pests, such as bark beetles and grasshoppers (Santoro et al. 2001; Vermeire et al. 2004). An understanding of whether fire effects are direct or indirect, non-linear or linear, and how they might vary with different herbivore assemblages or species can reveal whether fire effects are indeed simple or complex, and such knowledge can help land managers to select appropriate features of fire regimes, such as fire frequency, size, and intensity, so as to maintain biodiversity.

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