PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Plant–animal interactions in suburban environments: implications for floral evolution

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Abstract Plant interactions with mutualists and antagonists vary remarkably across space, and have played key roles in the ecology and evolution of flowering plants. One dominant form of spatial variation is human modification of the landscape, including urbanization and suburbanization. Our goal was to assess how suburbanization affected plant–animal interactions in *Gelsemium sempervirens* in the southeastern United States, including interactions with mutualists (pollination) and antagonists (nectar robbing and florivory). Based on differences in plant–animal interactions measured in multiple replicate sites, we then developed predictions for how these differences would affect patterns of natural selection, and we explored the patterns using measurements of floral and defensive traits in the field and in a common garden. We found that *Gelsemium* growing in suburban sites experienced more robbing and florivory as well as more heterospecific but not conspecific pollen transfer. Floral traits, particularly corolla length and width, influenced the susceptibility of plants to particular interactors. Observational data of floral traits measured in the field and in a common garden provided some supporting but also some conflicting evidence for the hypothesis that floral traits evolved in response to differences in species interactions in suburban vs. wild sites. However, the degree to which plants can respond to any one interactor may be constrained by correlations among floral morphological traits. Taken together, consideration of the broader geographic context in which organisms interact, in both suburban and wild areas, is fundamental to our understanding of the forces that shape contemporary plant–animal interactions and selection pressures in native species.

Keywords Suburbanization · Floral evolution · Florivory · Nectar robbing · *Gelsemium sempervirens*

Introduction

Plant–animal interactions have played a central role in the evolution and diversification of flowering plants (e.g., Farrell and Mitter 1998). Because plants interact simultaneously with both mutualists, such as pollinators, as well as antagonists, such as herbivores, florivores, and nectar robbers, understanding the effects of species interactions on the evolution of plant phenotypes requires an understanding of community context (e.g., Strauss and Armbruster 1997). There is widespread recognition that plant–animal interactions and subsequent patterns of natural selection can vary spatially (e.g., Thompson and Cunningham 2002). One dominant form of spatial variation that can have dramatic effects on the abundance of species and their interactions is human modification of the landscape (Niemelä 2011). The goal of this study was to assess how one common form of human-induced landscape change, urbanization, affected plant–animal interactions, and to develop and test predictions about patterns of floral evolution.

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Human activities have drastically altered Earth's ecosystems. Chief among these changes is the alteration of habitats and the conversion of forests, pastures, and rangelands into residential, commercial and industrial sites (McKinney 2002). The ecological consequences of land-use change associated with urban development ("urbanization" hereafter) have received considerable attention (Niemelä 2011). Compared to more wild lands, urban areas often experience lower native species diversity and higher remaining species density (Marzluff 2001), and community shifts towards species that are human commensals or that can take advantage of altered environments (McKinney and Lockwood 1999; Hansen et al. 2005). Studies have found that changes in the abundance, composition, or behaviors of mutualists and antagonists of plants in urban sites (e.g., Cane et al. 2006; Fenoglio et al. 2009; Raupp et al. 2010) can lead to altered plant–animal interactions. For example, canopy trees receive significantly greater levels of invertebrate leaf herbivory when growing in urban sites in Sydney, Australia compared to forest interiors (Christie and Hochuli 2005), and urbanization can alter the relative importance of top-down vs. bottom-up drivers of food webs (Raupp et al. 2010).

Although less well studied, the effects of urbanization on plant–animal interactions may also extend to the floral interface. For example, flowers interact with consumers such as nectar robbers and florivores (McCall and Irwin 2006; Irwin et al. 2010) as well as mutualist pollinators. Nectar-robbing carpenter bees (*Xylocopa* spp.) often rely on wooden houses for nest sites (Gerling et al. 1989). Increased nest sites in urban areas could increase carpenter bee abundance and robbing of plants in urban sites. Moreover, the abundance and composition of mutualist bee pollinators are sensitive to the type and magnitude of human disturbance (Winfree et al. 2009), and changes in bee abundance, composition, or behavior could lead to changes in plant–pollinator interactions and pollen flow. Given the importance of flowers for plant fitness, assessing how urbanization alters flower interactions with both antagonists and mutualists warrants further investigation.

Because urbanization can alter plant–animal interactions that are important selective agents on floral attractive and defensive traits (Adler 2008), urbanization also has the potential to alter patterns of natural selection and evolution. However, in comparison to the ecological consequences of urbanization, the evolutionary implications of urbanization are less well understood (but see Majerus 1998). Striking examples have shown that direct human actions, such as overharvesting, hunting, and pest/disease management, can alter the pattern and rate of evolutionary change in targeted species (e.g., Palumbi 2001). However, the degree to which urbanization alters the direction and strength of natural selection on native species not harvested

or hunted by humans remains largely unexplored (Shochat et al. 2006; Cheptou et al. 2008). Studies have revealed that human-induced evolutionary change can occur on contemporary timescales and over small spatial scales (Stockwell et al. 2003; Cheptou et al. 2008). However, in general we lack a clear mechanistic understanding of how urbanization affects natural selection and evolution for native species in persistent urban populations (but see Badyaev et al. 2008; Rodewald et al. 2011).

Here we investigated how urbanization affected plant–animal interactions, including interactions with antagonists (nectar robbers and florivores) and mutualists (pollinators). Finding consistent differences in plant–animal interactions across multiple replicate sites, we then developed predictions for how these differences would affect patterns of floral evolution, and explored patterns of floral attractive and defensive traits in the field and in a common garden to determine whether observed traits corresponded to predicted patterns. This study does not measure phenotypic selection in the field; instead, we explore patterns and develop predictions that can be tested in future research. We studied the native vine *Gelsemium sempervirens* (Loganiaceae; hereafter "*Gelsemium*") in the southeastern United States. We focused on *Gelsemium* growing in suburban sites, a dominant land-use type imposed by urban expansion, compared to those in "wild" sites that were either unmanaged or managed for the utilization of natural resources. Specifically, we asked the following three questions and tested the following predictions:

How does suburbanization affect the frequency and intensity of plant–animal interactions?

We predicted that the frequency or intensity of *Gelsemium* interactions with antagonists (robbers and florivores) and mutualists (pollinators) would be higher in suburban compared to wild sites. Suburban sites in residential neighborhoods may harbor more insects if they also have more nesting materials, such as for wood-nesting bees (e.g., wooden houses), and/or more abundant or diverse food resources [e.g., in garden plantings (Hope et al. 2003; Jha and Kremen 2013)] for robbers, florivores, and pollinators. This prediction assumes that nesting and food resources affect bee and other insect abundance (e.g., Potts et al. 2003, 2005), that habitat modification has not been too severe in suburban areas, and that increased abundance of antagonists and mutualists would result in increased frequency or intensity of plant–insect interactions. Alternatively, if floral resources are higher in suburban sites, they may lure insects away from *Gelsemium*, resulting in decreased floral damage (Irwin et al. 2001) and increased competition for pollinators (Hennig and Ghazoul 2011). How these complex species interactions

unfold in suburban compared to wild sites has rarely been explored.

To what degree does suburbanization affect the traits that antagonists and mutualists use to discriminate among plants?

Given well-known effects of conditionality and community context in affecting species interactions (Bronstein 1994), we predicted that the plant community in which *Gelsemium* was embedded (suburban or wild) would affect the relationship between floral and defensive traits and species interactions.

Finding differences in plant–animal interactions in suburban vs. wild sites, we then asked:

How do floral attractive and/or defensive traits differ for plants growing in suburban and wild sites in the field and in a common garden?

Using *Gelsemium* in a common garden allowed us to assess the degree to which potential differences in traits observed in the field were due to genetic differences or simply plastic responses to the environment. We predicted that floral traits in suburban vs. wild sites would correspond to observed differences in plant–insect interactions across site types, suggesting an evolutionary response to selection in suburban vs. wild sites.

Materials and methods

Study system

Focal species

We studied the perennial vine *Gelsemium sempervirens* (Loganiaceae) and its pollinators, nectar robbers, and florivores. *Gelsemium* is native to the southeastern USA and grows naturally in forested patches of both suburban and wild areas. Plants bloom from March to April, producing up to several hundred yellow, tubular flowers. Each flower has five petal lobes; individual flowers bloom for 3–5 days and produce nectar that is attractive to floral visitors (Irwin and Adler 2006). *Gelsemium* is self-incompatible and distylous. Each plant has either long styles and short anthers (pin plants) or short styles and long anthers (thrum plants) that are mutually incompatible. The pollen grains of thrum and pin flowers overlap in size (Ornduff 1979), but thrum flowers are generally larger than pin flowers, with both thrum and pin flowers producing similar amounts and concentrations of nectar (Leege and Wolfe 2002). *Gelsemium* reproduces by seed and is typically not clonal in field sites.

Fruits are dehiscent capsules that mature in the fall. Seeds produced in the fall can germinate the subsequent spring. *Gelsemium* is considered a fast-growing vine, and thus, although *Gelsemium* is perennial, it reproduces and grows over a time period that is relevant to measure patterns of natural selection and evolutionary response to species interactions as a function of suburbanization.

The dominant animals interacting with *Gelsemium* flowers are generalist pollinators, nectar robbers, and florivores. Leaf herbivory is rare. In the southeastern USA, *Gelsemium* is pollinated most frequently by bees, including *Bombus bimaculatus*, *Apis mellifera*, *Osmia lignaria*, and *Habropoda laboriosa* (Adler and Irwin 2005). In wild-growing plants, pollen supplementation can increase fruit set (Adler and Irwin 2012), suggesting the importance of pollinator attraction to plant fitness. *Gelsemium* flowers are nectar robbed by *Xylocopa virginica* (carpenter bees, Xylocopidae) that make slits near the corolla base to take nectar. Robbing rates range from 0 to 100 % of flowers per plant (Irwin and Adler 2006). Robbing can reduce estimates of male plant reproduction (R. E. Irwin and L. S. Adler, unpublished data), a result likely driven by changes in pollinator behavior. *Gelsemium* flowers are also damaged by florivores (Leege and Wolfe 2002), larvae of a univoltine generalist (*Amphipyra pyramidoides*, Noctuidae). Florivores not only eat petal tissue, which can make flowers less attractive to pollinators in some plant species (McCall and Irwin 2006), but also stigmas and anthers.

While floral morphological traits, such as flower number and size, likely affect pollinator, nectar robber, and florivore attraction to plants, chemical traits may also affect these plant–insect interactions. Gelsemine, the principal indole-related alkaloid in *Gelsemium*, has been isolated from leaves, flowers, and nectar (Adler and Irwin 2005). Gelsemine deters floral visitors, including pollinators and nectar robbers (Adler and Irwin 2005), and is toxic to mammals (Kingsbury 1964).

Study sites

Our study sites were in forested patches in Wake, Durham, and Chatham Counties, North Carolina, USA. The Raleigh-Durham-Cary metropolitan area in Wake and Durham Counties has undergone rapid urban growth, increasing its land area by two-thirds in the 1990s alone (US-EPA 2006). The availability of land and state-supported infrastructure have, as in many parts of the southeastern US, led to a mosaic of housing sprawl and woodlands (Wear and Greis 2004). Persistent, undeveloped forest patches remain in both newer and older housing developments (suburban sites) as planned urban green space or as undevelopable land. Suburban sites were defined as persistent forest fragments within single-family residential communities.

Suburban sites were typically within a metropolitan area, which was defined as that containing human-built structures (>2.5 buildings ha^{-1}), human surface-cover types (>20 %), and a resident human population reaching relatively high densities in some cases [approximately 186 people per square kilometer based on the US Census Bureau (Pickett et al. 2001)]. Suburban sites were in close juxtaposition with forested patches that were unmanaged or managed for their natural resources (wild sites). Within both suburban and wild sites, we used wild-growing *Gelsemium* in persistent forested habitat.

We conducted measurements in three paired suburban-wild sites in 2005, six paired sites in 2007, and one paired site for the creation of the common garden. We selected paired suburban and wild sites addressing three spatial scales: between pairs, within pairs, and within sites. At the broadest scale, we ensured that paired sites were distinct by choosing pairs >5 km apart. Within each pair, suburban sites were typically <5 km from wild sites to minimize variation due to factors other than degree of suburbanization. At the individual-site scale, we minimized effects of adjacent developments in wild sites by using whenever possible 10+ acre forested patches, and we ensured that paired suburban and wild sites had similar *Gelsemium* density. For suburban sites, we selected forest surrounded by residential land within a 300-m radius because some bee pollinators spend >96 % of their foraging effort within 300 m of focal foraging sites (Elliott 2009), although some bees can fly further (Greenleaf et al. 2007). We chose sites with a range of housing ages, values, and styles, although most were in middle- and upper-middle class neighborhoods. Ages of the housing developments ranged from 10 to >30 years old (in 2007), with average sales prices of \$161,673–\$429,500 USD (Wake and Durham County tax assessors). Because we only worked in three to six site pairs and we limited our sites to middle- and upper-middle income neighborhoods, we included site-pair as a fixed and not a random factor in statistical analyses described below (Bolker et al. 2009).

Field and common garden methods

How does suburbanization affect the frequency and intensity of plant–animal interactions?

We estimated robbing, florivory, and pollination to plants in the suburban and wild site pairs at peak bloom (early April). In each site, we haphazardly chose 15 plants in 2005 and 17–25 plants in 2007, with approximately equal representation of pin and thrum morphs. We measured robbing by counting the number of flowers per plant with nectar-robber holes and the number of holes per flower. To measure florivory, we counted the number of flowers damaged by florivores. On each plant, we also counted the number of flowers open to calculate the proportion of flowers with robbing or florivory. To test the hypothesis that suburbanization increased the likelihood of robbing and florivory, we used one-tailed paired *t*-tests with the percent of plants in each site that experienced robbing or florivory as response variables in each year. To test whether suburbanization affected the intensity of robbing and florivory to *Gelsemium*, we used an ANOVA [type III sum of squares (SS)] with site type, block (pair), and year as factors and proportion of flowers with robbing or florivory as response variables (both arcsine-square root transformed). We did not include floral morph in this analysis because morph had no effect on robbing ($F < 2.84$, $P > 0.10$) or florivory ($F < 2.06$, $P > 0.15$) in either year.

We estimated pollination in 2007 only using stigma pollen loads of emasculated flowers. For *Gelsemium*, higher pollinator visitation is associated with increased pollen deposition to pin and thrum flowers ($r = 0.32$, $n = 57$, $P = 0.015$). At peak bloom on up to three flowers per plant, we emasculated elongated buds. Once corollas started senescing, we collected the stigmas and stained them in basic fuchsin dye (Kearns and Inouye 1993). We counted both conspecific and heterospecific pollen deposition under a compound microscope. For each plant, we calculated mean conspecific (square-root transformed) and heterospecific pollen (log $x + 1$ transformed) receipt per stigma per day as well as the proportion of heterospecific pollen (arcsine square-root transformed) received per stigma per day. We used ANOVAs (type III SS) with site type, block (pair), and floral morph as factors to test how suburbanization affected conspecific and heterospecific pollen receipt and the proportion of heterospecific pollen receipt.

To what degree does suburbanization affect the traits that antagonists and mutualists use to discriminate among plants?

We examined the associations among floral and defensive traits and levels of robbing, florivory, and pollination plants received in suburban and wild sites. We measured floral and defensive traits on the same plants used to census plant–insect interactions in 2005 and 2007. For floral traits, we measured the number of flowers open (floral display size) when we censused interactions, corolla and petal length and width (to the nearest 0.01 mm using digital calipers), and floral morph (pin or thrum). We measured corolla and petal length and width on three flowers per plant and calculated the mean value per trait per plant.

As a defensive trait, we measured leaf gelsemine. On each plant, we collected up to 20 leaf pairs. Leaf alkaloids are positively correlated with flower alkaloids within field plants (Irwin and Adler 2006), so sampling leaves allowed us to estimate floral gelsemine without destroying floral

displays. Leaf gelsemine concentrations are positively correlated within plants across the season, justifying the use of one time point to represent season-long estimates (Irwin and Adler 2006). Leaves were dried and stored at room temperature. We extracted alkaloids from powdered leaves, sonicating the material in 0.5 N HCl. We adjusted the pH of the homogenate to 12 using 6 N NaOH. Alkaloids were extracted by solid phase extraction using Extrelut columns (EM Science, Gibbstown, NJ) and dichloromethane as an eluent. We then evaporated the dichloromethane, dissolved the alkaloids in 0.5 mL methanol, and analyzed the samples using an HP 5890 series II gas chromatograph (Hewlett Packard, Palo Alto, CA) with autosampler and Peak Simple software [column and conditions as in Irwin and Adler (2006)]. We used commercial gelsemine as a standard for quantification (Indofine Chemical, Hillsborough, NJ).

To test whether suburbanization affected the traits that insects used to discriminate among *Gelsemium*, we used an analysis of covariance (ANCOVA) (type III SS) with site type, block (pair), floral morph (pin or thrum), and year as factors, floral display size, corolla and petal length and width, and leaf gelsemine as covariates, and proportion of flowers with robbing or florivory as response variables (both arcsine-square root transformed). All variance inflation factors were less than nine, suggesting that multicollinearity did not strongly affect the results. Non-significant interactions between site type and traits were removed from the final model. A significant effect of traits would suggest that those traits alter the intensity of robbing or florivory. A significant interaction between traits and site type would suggest that suburbanization alters the traits that robbers and florivores used to discriminate among *Gelsemium* individuals. For 2007 only, we used a similar ANCOVA to test whether site type altered conspecific and heterospecific pollen receipt per stigma per day (square-root and $\log(x + 1)$ transformed, respectively) and the traits important for pollen receipt.

How do floral and/or defensive traits vary among plants growing in suburban and wild sites in the field and in a common garden?

For field measurements we used data on floral and defensive traits measured on plants in suburban and wild sites in 2005 and 2007 (described above). We used a multivariate ANOVA (MANOVA) with site type, block (pair), floral morph, and year as factors and floral display size (log transformed), corolla and petal length and width, and leaf gelsemine (square-root transformed) as response variables. A significant MANOVA was followed by univariate ANOVAs for each trait. We also examined the degree to which traits were phenotypically correlated using Pearson's correlations both across sites and morphs as well as within sites and morphs and by year. Correlations among traits could constrain the degree to which plants can respond to any one species interaction if interactors are selecting on different traits in opposite directions (Strauss and Irwin 2004). To assess significance of the pairwise correlations, we followed guidelines of Gotelli and Ellison (2004) and reported unadjusted significance values because the sequential Bonferroni correction can inflate the type II error rate. Finally, if species interactions act as important selective agents on floral traits, we would expect that evolutionary response to selection would result in greater trait differences in older vs. younger neighborhoods. Thus, for the data collected in 2007 (the year in which we measured six suburban sites), we used regression to analyze the relationship between neighborhood age and floral attractive and defensive traits. Neighborhood age was not associated with socioeconomic status in our dataset, as indicated by the average value of the parcels surrounding each site ($r = -0.52$, $n = 6$, $P = 0.29$).

For the common garden we chose one suburban-wild site pair studied in 2005 and 2007 from which to create plants for the common garden. Because we created the common garden from one site pair, if we find differences in floral traits between the two sites, we can simply say that the two sites differed and we can compare those differences to predictions generated from plants measured in the field (see above). However, to more definitively ascribe differences due to suburbanization, we would need to create a common garden using more site pairs, which was beyond the scope of this study but can be done in future research.

We randomly chose eight plants (hereafter referred to as "genotypes") from each site, and collected cuttings in summer 2009. The eight plants per site were a mix of pin and thrum morphs. We propagated the cuttings in the greenhouse and then made a second series of cuttings from the propagated plants to minimize carryover of environmental differences and maternal effects. When we made the second series of cuttings, we made replicate cuttings per genotype so that we could estimate genotypic effects of site on floral traits. In total, we had 25 plants from the suburban site (two to seven replicates for each of the eight genotypes) and 38 plants from the wild site (two to seven replicates for each of the eight genotypes); sample sizes differed slightly between sites because some replicate cuttings failed to take root. Plants were maintained in the greenhouse in a common environment, and we measured floral traits upon flowering in spring 2013. We did not measure leaf gelsemine because results from the field measurements suggested no differences in leaf gelsemine between suburban and wild sites (see "Results"). We measured corolla and petal length and width on up to three flowers per plant, and then calculated the mean value per trait per plant.

To test the prediction that differences in floral traits between suburban and wild sites from plants measured in the field matched floral trait differences when plants were grown in the greenhouse, we used one-tailed and/or two-tailed t-tests on phenotypic and genotypic means. The predicted direction of effect for each floral trait was based on the trait expression in the field in suburban vs. wild sites observed in 2005 and 2007; we used one-tailed t-tests for corolla length and width because suburban plants had larger measurements for these traits in field plants, and two-tailed t-tests for petal length and width because these traits did not differ between suburban and wild sites (see "Results"). It is important to note that the plants measured in 2005 and 2007 in the field were not permanently marked and thus not necessarily the same plants as those collected for cuttings for the common garden in 2009; thus, the plants in the common garden represent an independent sample to compare to the 2005 and 2007 floral measurements. We did not include floral morph in analyses because we found no effect of floral morph on any floral trait measured in the greenhouse ($F_{1,71} < 0.56$, $P > 0.46$ in all cases). To assess whether floral traits differed among genotypes, we used a MANOVA with genotype as a factor and the floral traits as response variables. A significant MANOVA was followed by univariate ANOVAs for each trait. Finally, we measured phenotypic (based on plant means) and genotypic (based on genotypic means) correlations among floral traits both within and across sites to assess the degree to which traits

could independently evolve in response to different species interactions.

Results

How does suburbanization affect the frequency and intensity of plant–animal interactions?

Suburbanization was associated with differences in the frequency and intensity of *Gelsemium* interactions with antagonists and mutualists. Plants in suburban sites were at least 40 % more likely to receive florivory than plants in wild sites in both 2005 (paired t-test, $t_2 = 3.05$, $P = 0.05$; Fig. 1a) and 2007 ($t_5 = 2.35$, $P = 0.03$; Fig. 1b). Moreover, plants in suburban sites were at least 18 % more likely to receive robbing than plants in wild sites, but the difference was only statistically significant in 2005 ($t_2 = 3.27$, $P = 0.04$; Fig. 1c) and not 2007 ($t_5 = 0.62$, $P = 0.28$; Fig. 1d). Florivory and robbing intensities were also higher in suburban vs. wild sites. Across 2005 and 2007, the percent of flowers per plant with florivory and with robbing were both 42 % higher in suburban compared to wild sites (florivory $F_{1,315} = 6.07$, $P = 0.01$; robbing $F_{1,315} = 9.11$, $P = 0.003$). Interactions also varied across years for the percent of flowers with florivory ($F_{1,315} = 15.59$, $P < 0.0001$) and the percent of flowers with robbing ($F_{1,315} = 19.77$, $P < 0.0001$). There was no significant site type by year

Fig. 1 Mean (±1 SE) percent of plants with florivory in **a** 2005 and **b** 2007 and the mean percent of plants with robbing in **c** 2005 and **d** 2007 in suburban and wild sites. *Asterisks* above bars indicate statistically significant differences at $P \leq 0.05$
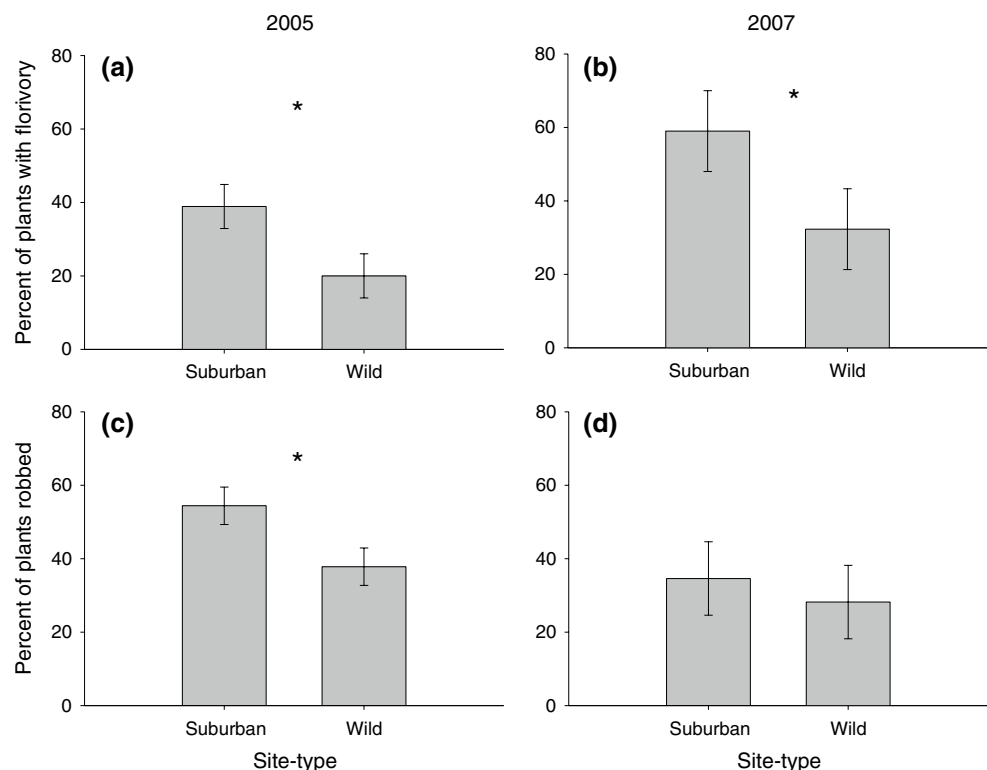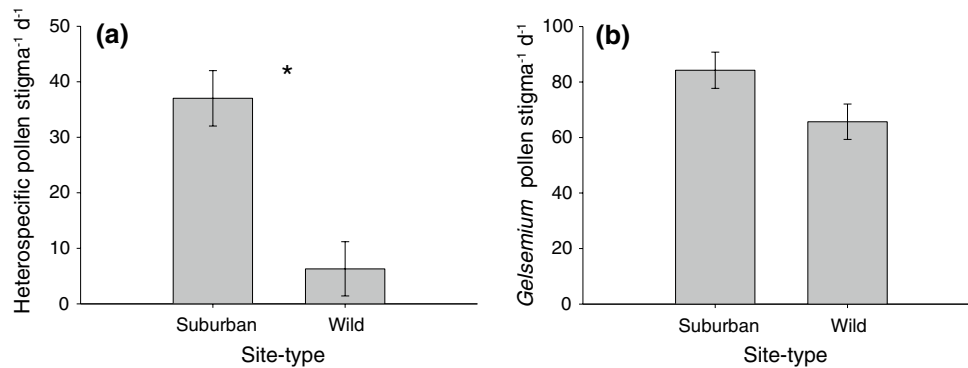
Fig. 2 Mean number of pollen grains received (± 1 SE) per stigma per day, separated by **a** heterospecific pollen and **b** conspecific pollen, for plants growing in suburban and wild sites. Note the different scales on the *y*-axes. *Asterisks* above bars indicate statistically significant differences at $P \leq 0.05$

interaction for percent of flowers with florivory or robbing ($F_{1,315} < 2.11$, $P > 0.15$), indicating that the effects of suburbanization on interactions were consistent across years. Suburbanization also affected pollination. Plants in suburban sites received six times more heterospecific pollen per stigma per day than plants in wild sites ($F_{1,165} = 26.31$, $P < 0.0001$; Fig. 2a). In addition, the proportion of heterospecific pollen received per stigma per day was two times higher in suburban compared to wild sites (mean proportion of heterospecific pollen received per day ± 1 SE, suburban $= 0.201 \pm 0.020$ vs. wild $= 0.109 \pm 0.020$; $F_{1,165} = 14.82$, $P = 0.0002$). Plants in suburban sites also received 20 % more conspecific pollen deposition than plants in wild sites, but this difference was not statistically significant ($F_{1,165} = 1.55$, $P = 0.22$; Fig. 2b). Finally, the only effect of floral morph on pollen receipt was that of heterospecific pollen received per day, with pin flowers receiving 16 % more heterospecific pollen than thrum flowers ($F_{1,165} = 5.13$, $P = 0.02$). Taken together, these results suggest that floral interactions with both antagonists and mutualists are higher in suburban compared to wild sites.

To what degree does suburbanization affect the traits that antagonists and mutualists use to discriminate among plants?

We found no evidence that site type altered how antagonists and mutualists responded to *Gelsemium* floral or defensive traits. There were no significant interactions between site type and any floral or defensive trait that we measured for any species interaction (florivory, robbing, heterospecific or conspecific pollen deposition; $P > 0.05$ in all cases). However, some floral traits affected the intensity of species interactions across suburban and wild sites (patterns were consistent both within and across site types, data not shown). In particular, plants with narrower corolla tubes ($F_{1,315} = 4.12$, $P = 0.04$) and a larger

floral display (average number of flowers produced per day; $F_{1,315} = 3.75$, $P = 0.054$) received more florivory, and plants with longer corolla tubes ($F_{1,315} = 5.80$, $P = 0.02$) and narrower petal lobes ($F_{1,315} = 5.34$, $P = 0.02$) received more robbing. No floral traits affected *Gelsemium* pollen deposition ($P > 0.05$ in all cases). However, plants with narrower corollas received more heterospecific pollen deposition ($F_{1,315} = 4.05$, $P = 0.046$). We found no evidence that leaf gelsemine affected the intensity of florivory, robbing, or pollen deposition in this study ($P > 0.05$ in all cases).

Because florivores and robbers can reduce estimates of female and male plant fitness (McCall and Irwin 2006; Irwin et al. 2010), these results lead to a number of predictions. For example, we predict positive selection for plants with wider, shorter corollas, narrower petal lobes, and smaller floral display size in suburban compared to wild sites due to increased plant interactions with florivores and robbers. If heterospecific pollen deposition reduces female fitness, then pollinators could also contribute to selection for wider corollas in suburban compared to wild sites.

How do floral and/or defensive traits vary among plants growing in suburban and wild sites in the field and in the common garden?

Field measurements

We found significant differences in floral traits in wild-growing *Gelsemium* in suburban vs. wild sites (MANOVA, $\lambda = 0.09$, $F_{6,316} = 4.65$, $P < 0.0001$). Plants in suburban sites had flowers with wider corollas than plants in wild sites ($F_{1,324} = 3.97$, $P = 0.05$), as would be predicted if there has been evolutionary response to selection for wider corollas to reduce florivory and heterospecific pollen deposition. However, plants in suburban sites also had flowers with longer corolla tubes ($F_{1,328} = 3.78$, $P = 0.05$), which was opposite to our prediction of evolutionary response

Table 1 Pearson product moment correlations among floral morphological traits, floral display size, and leaf gelsemine across sites, site types (suburban and wild), and floral morphs of *Gelsemium sempervirens*

	Corolla length	Corolla width	Petal length	Petal width	Floral display size	Leaf gelsemine
Corolla length	–	0.46***	0.38***	0.60***	0.11 NS	0.25*
Corolla width	0.49***	–	0.51***	0.47***	−0.05 NS	0.25*
Petal length	0.30***	0.50***	–	0.52***	−0.14 NS	0.38***
Petal width	0.50***	0.66***	0.61***	–	−0.03 NS	0.41***
Floral display size	0.09 NS	0.04 NS	−0.09 NS	−0.17**	–	0.07 NS
Leaf gelsemine	0.03 NS	−0.01 NS	−0.08 NS	−0.06 NS	0.27*	–

Correlations measured in 2005 are *above the diagonal* and in 2007 *below the diagonal*. Sample sizes are $n = 90$ plants in 2005 and $n = 240$–247 plants in 2007

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.0003$, NS non-significant

to selection for shorter corollas to reduce nectar robbing. In addition, we found no significant differences between suburban and wild sites in petal lobe width ($F_{1,328} = 2.72$, $P = 0.10$) or floral display size ($F_{1,332} = 1.10$, $P = 0.30$), even though we predicted that these traits should be under selection by florivores and robbers. We found that floral traits differed between pin and thrum flowers (MANOVA, $\lambda = 0.27$, $F_{6,316} = 14.08$, $P < 0.0001$), with thrum flowers having longer, wider corollas and longer petals than pin flowers ($F > 4.14$, $P < 0.04$). Floral morphs did not vary significantly in leaf gelsemine ($F_{1,328} = 2.77$, $P = 0.10$).

Floral morphological characters (corolla and petal length and width) were significantly positively phenotypically correlated both within suburban and wild sites and floral morphs (data not shown) as well as across all plants (Table 1). However, correlations among floral morphology, floral display size, and leaf gelsemine were more variable. Many of these correlations varied from non-significant to significant, and they ranged from negative to positive associations (Table 1).

When we focused solely on suburban sites and examined the relationship between neighborhood age and floral traits, we found a positive relationship between neighborhood age and corolla length ($\beta \pm 1$ SE = 0.075 ± 0.027), such that plants growing in older neighborhoods had longer corolla tubes ($r^2 = 0.657$; $F_{1,4} = 7.66$, $P = 0.05$). We found a similar but weaker positive relationship between neighborhood age and corolla width ($\beta \pm 1$ SE = 0.063 ± 0.028), with older developments having a non-significant trend toward wider corollas ($r^2 = 0.556$; $F_{1,4} = 5.00$, $P = 0.089$). Finally, we found no relationship between neighborhood age and petal length ($F_{1,4} = 0.44$, $P = 0.54$) or petal width ($F_{1,4} = 1.12$, $P = 0.35$).

Common garden

Plants grown in the greenhouse from a single suburban-wild site pair differed in floral traits. Analyzing phenotypes, we found that on average, *Gelsemium* collected from cuttings from the suburban site had larger flowers than those from the wild site, with longer corolla tubes (one-tailed $t_{71} = 1.62$, $P = 0.055$), non-significantly wider corolla tubes (one-tailed $t_{71} = 1.41$, $P = 0.08$), longer petal lobes (two-tailed $t_{71} = 1.97$, $P = 0.053$), and wider petal lobes (two-tailed $t_{71} = 2.26$, $P = 0.027$; Fig. 3a–d). We found similar results when analyzing genotypic means; flowers were generally larger in plants from suburban sites. However, the analyses were only marginally significant for corolla length (one-tailed $t_{14} = 1.73$, $P = 0.053$) but not for corolla width (one-tailed $t_{14} = 1.03$, $P = 0.16$), petal length (two-tailed $t_{14} = 1.42$, $P = 0.23$), or petal width (two-tailed, $t_{14} = 1.52$, $P = 0.15$). Based on a power analysis of the genotypic means of floral morphological traits, to find statistical significance, we would have needed 60 genotypes for corolla width, 33 genotypes for petal length, and 29 genotypes for petal width. All floral traits had significant genetic variation (MANOVA, $\lambda = 0.12$, $F_{60,213} = 2.54$, $P < 0.0001$), including corolla length ($F_{15,57} = 2.45$, $P = 0.008$), corolla width ($F_{15,57} = 3.63$, $P = 0.0002$), petal length ($F_{15,57} = 2.71$, $P = 0.004$) and petal width ($F_{15,57} = 4.18$, $P < 0.0001$). Finally, floral traits were phenotypically and genotypically correlated (Table 2).

Discussion

A central goal of ecological and evolutionary research is to understand the factors driving variation in the abundance and diversity of organisms, their interactions, and subsequent implications for natural selection and floral evolution. Most of this research has focused on natural habitats, but one of the fastest growing habitats is land impacted by human development (Economic Research Service 2005). Here we found that suburbanization resulted in effects on plant–animal interactions at the floral interface. *Gelsemium* growing in suburban sites received more nectar robbing and florivory as well as more heterospecific pollen transfer.

Fig. 3 *Gelsemium sempervirens* grown from cuttings from a suburban site had larger corollas (**a**, **b**) and petals (**c**, **d**) than plants from a wild site when grown in a common greenhouse environment. *Bars* are means (±1 SE), and note the different scales on the *y*-axes. *Asterisks* above bars indicate differences at $P \leq 0.055$
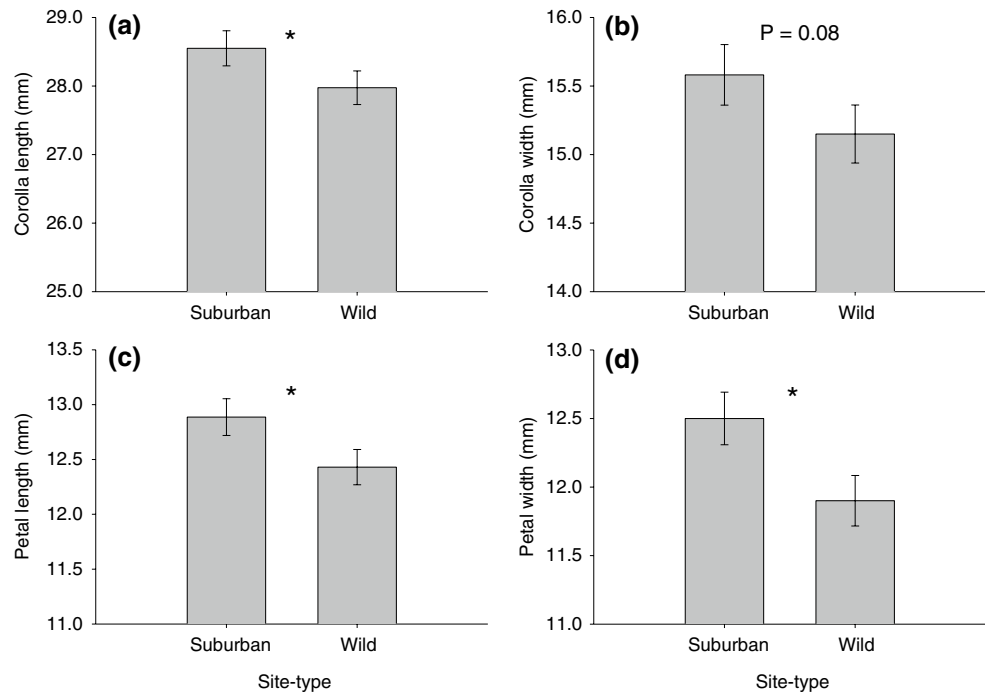

Table 2 Pearson product moment correlations among floral morphological traits of *G. sempervirens* across one suburban-wild site pair from plants grown in a common greenhouse environment

	Corolla length	Corolla width	Petal length	Petal width
Corolla length	–	0.60	0.50	0.57
Corolla width	0.67	–	0.73	0.70
Petal length	0.46 [NS]	0.75	–	0.69
Petal width	0.54	0.78	0.82	–

Correlations *above the diagonal* are based on phenotypic means and *below the diagonal* on genotypic means. Sample sizes are $n = 73$ plants for the phenotypic correlations and $n = 16$ genotypes for the genotypic correlations

All phenotypic correlations were statistically significant at $P \leq 0.0001$ and genotypic correlations at $P < 0.03$ unless indicated by [NS]

Floral morphological traits of *Gelsemium* influenced the susceptibility of plants to particular interactors. Observational data of floral traits measured in the field as well as floral traits measured in a common garden provided some supporting evidence as well as some conflicting evidence suggesting that floral traits may be evolving in response to differences in species interactions in suburban vs. wild sites. However, the degree to which plants can respond to any one interactor may be constrained by correlations among floral morphological traits. We discuss these findings and present avenues for future research.

The higher frequency and intensity of interactions with florivores and robbers in suburban compared to wild sites

is consistent with results for webs of species interactions in some other systems. For example, urbanization can affect trophic dynamics, with top-down consumptive interactions controlling arthropod populations more strongly than bottom-up effects in some urban settings (Faeth et al. 2005; but see Bang et al. 2012). Moreover, both the frequency of damage and leaf area removal by folivores of *Solanum lycocarpum* was higher in sites with greater urbanization in Minas Gerais, Brazil (Cuevas-Reyes et al. 2013). We are currently exploring variation in suburban sites to understand the mechanisms driving our results. The effect of suburbanization on floral interactions could be due to biotic factors, such as bottom-up variation in floral resource abundance and diversity (Potts et al. 2003) that may lure more floral consumers into suburban areas, or top-down variation in natural enemies of plant associates (reviewed in Raupp et al. 2010). Abiotic factors could also affect floral interactions. For example, heat island effects in suburban sites could increase insect growth, fecundity, and activity, which could lead to altered flower–insect interactions (Meineke et al. 2013). We are also exploring mechanisms associated with land policy and management, such as parcel size influencing the amount of forest cover and nesting habitat for robbing carpenter bees and other insects, as well as social drivers, such as socioeconomic factors, since floral resources or plant diversity may be higher in suburban areas with higher family incomes (Hope et al. 2003).

In addition to increased nectar robbing and florivory, *Gelsemium* flowers in suburban sites received significantly more heterospecific pollen than flowers in wild sites. In a

separate study, we found that bee abundance was significantly higher in some of the same suburban vs. wild sites that we studied here, but that sites did not differ in bee species richness or composition (Carper 2013), which matches some prior studies showing that urban and suburban areas can support abundant bee communities (e.g., Winfree et al. 2007; but see McIntyre and Hostetler 2001). Increased pollinator abundance may increase pollen deposition, but the costs vs. benefits of that pollen deposition (i.e., heterospecific vs. conspecific pollen) for plant fitness remain unknown. Increased heterospecific pollen deposition in suburban sites could clog *Gelsemium* stigmas or be allelopathic, reducing plant fitness. For example, in *Limnanthes douglasii rosea* (Limnanthaceae), plants that received heterospecific pollen first from field neighbors exhibited greater than a 50 % reduction in per flower fertility (Runquist 2012). The source of the heterospecific pollen received by *Gelsemium* in our study is unknown, but we hypothesize that it stems from suburban garden plantings when pollinators switch between foraging in suburban gardens and wild *Gelsemium* in suburban forests. While the importance of heterospecific pollen transfer between native and invasive species has been studied (Morales and Traveset 2008), further research is needed to determine how common heterospecific pollen transfer is between horticultural and native wild plants in suburban areas and its implications for wild plant fitness.

We found evidence that floral morphological traits influenced plant interactions with robbers and florivores as well as the amount of heterospecific pollen received. Other studies have also found that plant and floral traits influence susceptibility to robbing and/or florivory (reviewed in Irwin et al. 2004; McCall and Irwin 2006). Surprisingly, however, we found no evidence that leaf gelsemine affected the intensity of florivory, robbing, or pollen deposition in this study. This result was contrary to a previous study in which we found that plants with higher levels of leaf gelsemine were associated with lower levels of pollen deposition in some sites (Irwin and Adler 2006) as well as other studies that have documented the importance of plant chemistry for floral interactions (e.g., Adler and Irwin 2005; Kessler et al. 2008).

Given that suburban sites were associated with higher levels of robbing, florivory, and heterospecific pollen deposition than wild sites, and that plant susceptibility to species interactions is linked to floral morphological traits, our results have implications for patterns of natural selection and floral evolution. For example, because flowers with narrower corolla tubes are more susceptible to florivory and heterospecific pollen transfer, and these species interactions may reduce plant fitness in this and other systems (e.g., Runquist 2012; Carper 2013), we predicted that we would find evidence of evolutionary response to selection for

wider corollas in suburban relative to wild sites. Our predictions were partially upheld in both field measurements of floral traits as well as a common garden experiment. Wild-growing plants in suburban sites had wider corolla tubes, and when we grew plants from suburban and wild sites in a common garden in the greenhouse over two series of cuttings to remove maternal environmental effects, we found that plants from one suburban site pair had marginally wider corolla tubes and larger flowers overall. These results are suggestive of evolutionary response to selection driven by plant–animal interactions. We are not aware of studies that have shown different patterns of natural selection on plant traits via plant–animal interactions as a function of suburbanization, but studies are accumulating, both for vertebrates (e.g., Badyaev et al. 2008; Halfwerk et al. 2011; Rodewald et al. 2011) and invertebrates (reviewed in Kotze et al. 2011), documenting evolution in urban and suburban environments and the selective agents involved.

It is important to note that we cannot rule out that a number of factors other than phenotypic selection via plant–insect interactions could be driving differences in floral traits between suburban and wild sites that we observed, and thus, our data interpretations come with a number of caveats. First, the differences we observed in floral traits could be driven by other selective agents besides insect interactors, or by differences in abiotic conditions in suburban vs. wild sites. Our common garden experiment does provide suggestive evidence of evolutionary response to some selective agent, but we only measured traits in one site pair and on only eight genotypes per site pair. A larger common garden with more site pairs and more genotypes per site pair will provide further insight. Second, *Gelsemium* can be long-lived, and although the majority of neighborhoods we studied are likely older than the plants (neighborhood age range, 10 to >30 years old), we do not know the number of plant generations that have occurred post-neighborhood development nor how any potential patterns of selection have changed as neighborhoods have aged. However, the positive relationship between neighborhood age and floral size suggests that selection has had a longer time to operate in older neighborhoods; this hypothesis warrants further investigation. Third, *Gelsemium* are also grown as horticultural species in the south-eastern US. Although we did not observe horticultural *Gelsemium* growing in nearby suburban gardens for the site pairs we studied, we cannot rule out that the differences in floral traits we observed are also a result of gene flow with, or seed dispersal from, horticultural plants in suburban sites. Finally, genetic correlations among traits may also be important in the differences in traits we observed. In particular, floral morphological characters were positively phenotypically and genotypically correlated. These correlations may constrain the degree to which *Gelsemium* in

suburban and wild sites can respond to any one interactor and may prevent the evolution of optimal trait expression, especially if different plant–animal interactions select for larger vs. smaller floral morphological traits (i.e., florivory and heterospecific pollen selecting for wider corollas but nectar robbing selecting for shorter corollas). Only through further experimental investigation can we tease apart the importance of selection vs. other factors affecting trait evolution in suburban and wild sites.

Human-dominated landscapes are some of the fastest growing habitat types on earth, providing opportunities to examine the impacts of spatial variation on the ecology and evolution of native species. To fully evaluate the mechanisms and degree to which suburbanization alters trait selection via changes in species interactions, we not only need to document changes in patterns of species interactions due to suburbanization, but we also need to (1) measure phenotypic and genotypic selection, (2) isolate mechanisms responsible for potential changes in selection using experimental studies, and (3) identify human social drivers associated with variation in selective agents and patterns of phenotypic selection. By using multiple approaches, studies of natural selection in suburban and urban environments will move beyond documenting patterns due to urbanization to identify and understand underlying mechanisms, which facilitates the generalization of results. We propose the following directions for future research that could be applied in suburban and/or urban habitats.

Direction 1: compare phenotypic and genotypic selection on traits in suburban and wild sites

Community context can have powerful effects on trait evolution (Thompson and Cunningham 2002). To understand natural selection on traits requires measuring the direction and intensity of trait–fitness relationships across multiple replicated suburban and wild sites, as well as the degree to which potential ecological selective agents covary with suburbanization. This approach can be used on wild-growing plants, although a more powerful approach would be to use known genotypes in replicate common gardens in suburban and wild sites.

Direction 2: experimentally identify important selective agents

Manipulations are necessary to determine whether documented differences between site types in putative selective agents differentially affect host fitness, whether suburbanization affects the reproductive outcome of species interactions, and if manipulating selective agents alters trait–fitness relationships in suburban and wild sites. Moreover, even if suburbanization does not affect trait selection, by manipulating important ecological factors these experiments could also highlight potential effects of species interactions or other environmental factors that differ between suburban and wild sites on host fitness and potentially population dynamics.

Direction 3: identify human social factors associated with suburbanization driving variation in selective agents and patterns of phenotypic selection

In order to make predictions about when and how suburbanization will alter patterns of selection, elucidating underlying mechanisms is essential. This requires observational and experimental studies to determine the factors associated with suburbanization that cause the documented changes in selective agents and trait selection. Not only do we need to understand mechanisms associated with land-use change and management, but also underlying social factors and processes (Warren et al. 2010). Making the connection between ecological and evolutionary patterns and underlying social factors and processes will increase our capacity to engage in conservation and land-use planning that supports native species.

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