

Historically browsed jewelweed populations exhibit greater tolerance to deer herbivory than historically protected populations

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Summary

1. Browsing by overabundant white-tailed deer (*Odocoileus virginianus*) has altered ecological relationships in forest communities across eastern North America. Recent but limited work suggests that deer browsing also selects for particular plant defensive traits.

2. We hypothesized that browsing by deer has imposed selection on defensive traits in an annual native wildflower, orange jewelweed (*Impatiens capensis*).

3. To test this hypothesis, we collected individuals from 26 natural populations across a 5000 km² area in New York State, USA. Half of these populations were historically protected from deer and half were exposed to heavy browsing. We planted individuals in common gardens subjected to natural deer browsing or no browsing.

4. Individuals from historically browsed populations exhibited significantly higher tolerance than those from historically protected populations. Herbivory by deer reduced lifetime fruit production by only 20% in historically browsed populations, as opposed to 57% in historically protected populations. Two mechanisms were correlated with this increased tolerance: increased number of flowering days and increased fruits per flowering node.

5. *Synthesis.* The increased tolerance of historically browsed populations suggests that these populations evolved increased tolerance or that historically protected populations lost tolerance over time. Variation in tolerance traits in native plant species may allow them to persist in the face of rapid ecological change.

Key-words: defence trait, eastern deciduous forest, New York-USA, *Odocoileus virginianus*, orange jewelweed, plant–herbivore interactions, understorey, white-tailed deer

Introduction

Over the past 80 years, white-tailed deer (*Odocoileus virginianus*) densities have exploded across eastern North America. In the Great Lakes region, current deer densities are approximately five times greater than they were prior to European settlement (Rooney & Waller 2003). The ecological impacts of this overabundance, especially on plant community composition, have been studied since the 1970s. Because deer forage selectively, they alter competitive relationships among plant species (for review, see Côté *et al.* 2004). In doing so, they alter ecosystem processes such as soil development and nutrient cycles (Hobbs 1996).

Recent work suggests that deer are also important agents of natural selection in these systems (Stinchcombe & Rausher 2001; McGraw & Furedi 2005; Parker *et al.* 2010). Plants

browsed by deer tend to be smaller, less likely to flower and less likely to survive than those protected from deer (Augustine & Frelich 1998; Knight 2004). In theory, such effects on individual plants should lead to divergence among populations in diverse traits, including defensive traits. Defensive traits are broadly categorized in terms of resistance, which reduces the preference or performance of herbivores, and tolerance, which allows plants to replace browsed tissue or reproduce after damage. However, little is known about whether herbivores rapidly select for predictable parallel changes in defensive traits across natural plant populations (Agrawal *et al.* 2012).

Two previous studies have sought evidence for the evolution of plant defensive traits in response to deer browsing. A feeding trial showed that Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) preferred western red cedar (*Thuja plicata*) seedlings from a site on an island historically lacking large mammalian herbivores to a mainland site where deer had been present for millennia (Vourec'h *et al.* 2001). In another experiment, sika deer

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(*Cervus nippon*) preferred nettles (*Urtica thunbergiana*) from a historically unbrowsed population over ones from a population subject to browsing for more than 1200 years in Japan (Kato, Ishida & Sato 2008). Although the results of these two experiments are intriguing, they are limited by lack of replication at the population level. Lennartsson, Tuomi & Nilsson (1997) found that individuals from five populations of field gentian (*Gentianella campestris*) that were historically grazed by cattle or mown exhibited overcompensation in response to simulated grazing (clipping), suggesting the evolution of tolerance to damage in these populations.

The evolution of tolerance could explain why some plant species that are palatable to white-tailed deer have persisted in areas of high deer density in eastern North America. Tolerance, the degree to which plant fitness is affected by herbivore damage relative to fitness in the undamaged state (Strauss & Agrawal 1999), can involve at least two mechanisms: pre-damage investment in resources (analogous to constitutive defences) and post-damage alteration in resource allocation (analogous to induced defences) (Hochwender *et al.* 2012). The best studied mechanisms of tolerance include enhanced leaf photosynthetic activity following herbivore damage, increased branching or tillering following damage and greater utilization of stored reserves following damage (Tiffin 2000; Núñez-Farfán, Fornoni & Valverde 2007).

In this study, we evaluated whether populations of a native annual plant, orange jewelweed (*Impatiens capensis* Meerb; Balsaminaceae), show evidence of divergence in their tolerance of deer herbivory. We collected individuals from 26 natural populations with contrasting browsing histories. We hypothesized that individuals from populations historically accessible to deer would better tolerate deer herbivory than individuals from populations historically protected from deer – a result that would constitute evidence for a response to past selection. We then evaluated pre- and post-damage mechanisms of tolerance.

Materials and methods

STUDY ORGANISM

Orange jewelweed, an annual herb of forested wetlands, is a preferred food plant of deer (Williams, Mosbacher & Moriarity 2000). This species has seeds that typically disperse <1.5 m from parent plants (Argyres & Schmitt 1991) and exhibits well-studied local adaptation in morphological and life-history traits among natural populations (Schmitt, Ehrhardt & Swartz 1985). It has a mixed mating system, producing two distinct types of flower: tiny, obligately self-pollinating cleistogamous flowers and showy, protandrous chasmogamous flowers (Gleason & Cronquist 1963). In addition to deer, invertebrates occasionally feed upon *I. capensis* in the eastern United States, including chrysomelid beetles, leaf miners, caterpillars, aphids, grasshoppers and katydids (Steets, Salla & Ashman 2006).

COLLECTION SITES

In 2012, we identified 15 'historically protected' and 15 'historically unprotected' *I. capensis* populations from four regions in New York State across a 5000-km² area (see Table S1 in Supporting Information).

'Historically protected' populations were located in sites inaccessible to deer because of physical barriers such as steep slopes (>70°), fences or dense urban development. 'Historically unprotected' populations were located in sites with no physical barriers preventing access by deer. Because deer are hyper-abundant in this region, we assumed that accessible sites have a history of moderate or intense browsing, whereas inaccessible sites have not.

Our unit of replication was the population, and we attempted to collect plants from as many populations as possible. We chose to infer the histories of contemporaneous populations because there are no long-term records of management, browsing damage or fine-scale deer densities for multiple populations in the eastern United States. Faced with similar experimental constraints, others have employed similar methods (e.g. Lennartsson, Tuomi & Nilsson 1997; Vourc'h *et al.* 2001; Kato, Ishida & Sato 2008), although with fewer populations. To corroborate our inferences, we surveyed sites for evidence of browsing in summer 2013. We observed no evidence of browse at any of the 'historically protected' sites. In 'historically unprotected' sites, between 20% and 100% of individuals had been browsed by deer (Table S1). In the final experiment, we excluded plants from two 'historically protected' sites that exhibited signs of disease and plants from the two 'historically unprotected' sites with <30% browsed.

From 6 to 20 May 2012, we collected 100 seedlings with 2 true leaves at random from each population. Once seedlings were collected, their roots were gently washed and they were planted in plug trays filled with potting soil (Espoma organic potting mix, Millville, NJ). Seedlings were held in partial sun in a screened enclosure in trays that were rotated every 3 days until the experiment began.

COMMON GARDEN

The experiment was conducted at the Cornell Mundy Wildflower Garden (42.75 N, 76.78 W), a forested floodplain in Ithaca, NY, within a deer enclosure area established in 2007. On 23 May 2012, we planted 10 seedlings from each population with 4–6 true leaves inside the deer enclosure ('fenced treatment') and 10 outside the deer enclosure ('unfenced treatment') in a balanced randomized design. The two treatments were 120 m apart. Seedlings were spaced at a low density, 15 cm apart (Huber *et al.* 2004) in grids covered in porous weed barrier (DeWitt Pro Premium weed fabric). A border row of non-experimental seedlings was established around each common garden to avoid edge effects. We replaced seedlings that died within the first week of the experiment.

Deer naturally browsed all but 16 plants in the unfenced site between 3 and 13 July 2012. The 16 unbrowsed plants were excluded from subsequent analyses (6.2%, 8 individuals each from historically unprotected and historically protected populations).

In order to ensure that growing conditions were similar in the fenced treatment site and the unfenced treatment site, we (i) compared growth rates before browsing and (ii) planted two fenced control blocks (of 30 and 10 plants, respectively) adjacent to the unfenced site. Both lines of evidence indicated that growing conditions were similar in both sites. Before deer browsing occurred, plants in each treatment had produced the same number of seeds (Table 1). On the day 40 census, mean height was slightly greater in the fenced site (mean ± 1SE = 24.1 ± 0.6 cm) than in the unfenced site (23.0 ± 0.7 cm), but the treatment*history interaction was not significant (Table 1). On the day 69 census, mean height of control plants in the unfenced site (40.8 ± 14.2 cm) was not significantly different from that of the fenced plants (38.6 ± 10.4) (Table 1). We therefore

Table 1. Three comparisons between growing conditions in the protected and unprotected common garden. Influence of treatment (fenced or unfenced), history (historically unprotected or historically protected), treatment*history, region, and population nested within history and region on (a) seed production pre-browsing, (b) height before browsing, and (c) height of protected and control plants on 30 July 2012. Bold *P*-values indicate $P < 0.05$

Response variable	Effect	Statistic	<i>P</i> -value
Seed production before browsing (25 June 2012)	Treatment	$\chi^2 = 0.15$	0.6979
	History	$\chi^2 = 0.13$	0.7205
	Treatment *History	$\chi^2 = 0.50$	0.4777
	Region	$\chi^2 = 0.16$	0.9969
	Pop [History, Region]	$\chi^2 = 461.09$	<0.0001
Height before browsing (18 June 2012)	Treatment	$F_{1,402.8} = 4.68$	0.0311
	History	$F_{1,21.1} = 0.01$	0.9120
	Treatment *History	$F_{1,402.8} = 0.15$	0.7024
	Region	$\chi^2 = 12.67$	0.0004
	Pop [History, Region]	$\chi^2 = 105.86$	<0.0001
Height 30 July 2012	Treatment	$F_{1,63.1} = 1.75$	0.1900
	History	$F_{1,6.1} = 0.04$	0.8557
	Treatment *History	$F_{1,63.6} = 3.68$	0.0596
	Region	$\chi^2 = 0.90$	0.1714
	Pop [History, Region]	$\chi^2 = 1.39$	0.1190

interpreted the presence or absence of browsing by deer to be the key explanatory variable in this experiment.

We assessed plants weekly for survival and damage from deer browsing and measured plant height on 24 May, 5 June, 18 June, 3 July, 30 July, 22 August and 19 September. We assessed plants weekly for: date, height and node of first self-pollinating flower; date of first self-pollinating fruit; date, height and node of first open-pollinating flower; and date of first open-pollinated fruit. To obtain total fruit counts, we counted intact and dehiscent self-pollinated fruits (pedicels persist on the stem) on 5 June, 25 June, 13 July, 22 August, 19 September, 26 September, 3 October and 10 October, and intact and dehiscent open-pollinated fruits on 9 September and 19 September. Total flowering days were calculated as the days from first self-pollinating flower until death.

For each individual, the last fruit count before death was considered lifetime fruit production. The number of fruits was used as an

estimate of the number of seeds. Seeds per self-pollinated fruit were estimated as the mean of a subsample of fruits ($N = 54$). Seeds per open-pollinated fruit were estimated as the mean of a subsample of fruits ($N = 19$). An individual's lifetime seed production, a proxy of fitness, was calculated as total self-pollinated fruits * mean seeds per self-pollinated fruit + total open-pollinated fruits * mean seeds per open-pollinated fruit (Steets, Salla & Ashman 2006). Population means were then calculated for lifetime seed production and all performance metrics. We used a ratio (lifetime seed production when unprotected divided by that when protected) to calculate tolerance, which was correlated with absolute difference ($R^2 = 0.81$, $F_{1,24} = 5.84$, $P < 0.0001$).

DATA ANALYSIS

Generalized linear mixed-effects models of measured traits (fitness, growth, phenology, mixed mating, architecture) were constructed in JMP Pro 11 (SAS Institute Inc., Cary, NC, USA) using restricted maximum likelihood (REML) estimation (Littell *et al.* 1996). Models of these traits included browsing history ('historically unprotected' or 'historically protected'), treatment ('fenced' or 'unfenced') and their interaction as fixed effects and geographical region and population nested within history and geographical region as random effects.

We first tested whether historically unprotected populations were more able to tolerate browsing than historically protected populations (a significant treatment*history interaction term) by modelling lifetime seed production. Because of overdispersion, we modelled count data (number of flowers, number of seeds) using a zero-inflated negative binomial distribution (O'Hara & Kotze 2010). Other variables were normally distributed. We then constructed models to test for effects of history on phenological traits (days to first flower, total flowering days) and architectural traits (height of lowest flower, number of flowering nodes, closed-pollinated seeds per flowering node). Again, we included the same fixed and random effects. To determine whether history affected mixed mating expression (likelihood of developing open-pollinating flowers), we constructed a logistic regression model with history, treatment, history*treatment, region, and population [history, region] as effects.

Mean population tolerance was calculated as the mean lifetime seed production of a population in an unprotected treatment divided by its lifetime seed production in the protected treatment. Finally, we constructed a GLM to evaluate the influence of history and three responses to browsing (ratio of browsed to unbrowsed traits for total flowering days, number of flowering nodes and seeds per flowering node) upon mean population tolerance. This GLM analysis also evaluated two-way interactions of the three browsing responses with

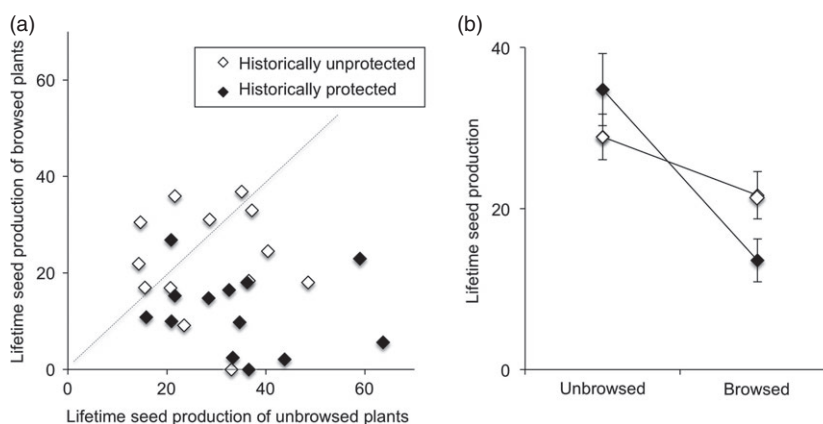


Fig. 1. (a) Lifetime seed production of 26 populations of *Impatiens capensis* in the fenced (unbrowsed) versus unfenced (browsed) treatment. The unity line depicts full compensation (fitness of a plant population in the browsed state equals fitness in unbrowsed state); overcompensation was observed in populations above the line. (b) Mean (± 1 SE) lifetime seed production as predicted by population history and treatment.

Table 2. Influence of treatment (fenced or unfenced), history (historically protected or historically unprotected), treatment*history, region, and population nested within history and region on lifetime seed production, measures of phenology, mixed mating system expression, and measures of architecture. Bold *P*-values indicate $P < 0.05$

Response variable	Effect	Statistic	<i>P</i> -value
Lifetime seed production	Treatment	$\chi^2 = 11.88$	0.0006
	History	$\chi^2 = 4.83$	0.0280
	Treatment * History	$\chi^2 = 4.71$	0.0301
	Region	$\chi^2 = 7.83$	0.0979
	Pop [History, Region]	$\chi^2 = 41.65$	0.0266
Days to first flower	Treatment	$F_{1,387.5} = 3.12$	0.0780
	History	$F_{1,21.17} = 1.96$	0.1759
	Treatment * History	$F_{1,387.8} = 0.54$	0.4647
	Region	$\chi^2 = 2.29$	0.1305
	Pop [History, Region]	$\chi^2 = 130.14$	<0.0001
Total flowering days	Treatment	$F_{1,381.9} = 21.67$	<0.0001
	History	$F_{1,21.2} = 0.98$	0.3323
	Treatment * History	$F_{1,382} = 13.41$	0.0003
	Region	$\chi^2 = 3.76$	0.05243
	Pop [History, Region]	$\chi^2 = 30.09$	<0.0001
Probability of producing open-pollinating flowers	Treatment	$\chi^2 = 80.10$	<0.0001
	History	$\chi^2 = 0.00$	0.9997
	Treatment * History	$\chi^2 = 0.00$	0.9997
Height of lowest flower	Treatment	$F_{1,368.6} = 85.01$	<0.0001
	History	$F_{1,22.04} = 3.16$	0.0892
	Treatment * History	$F_{1,368.6} = 1.28$	0.2594
	Region	$\chi^2 = 0.56$	0.4531
	Pop [History, Region]	$\chi^2 = 128.19$	<0.0001
Number of flowering nodes	Treatment	$F_{1,351.4} = 511.44$	<0.0001
	History	$F_{1,21.8} = 2.11$	0.1605
	Treatment * History	$F_{1,351.7} = 0.66$	0.4171
	Region	$\chi^2 = 0.36$	0.5485
	Pop [History, Region]	$\chi^2 = 44.95$	<0.0001
Seeds per flowering node	Treatment	$\chi^2 = 13.19$	0.0003
	History	$\chi^2 = 1.09$	0.2959
	Treatment * History	$\chi^2 = 0.77$	0.3792
	Region	$\chi^2 = 12.91$	0.0117
	Pop [History, Region]	$\chi^2 = 42.13$	0.0238

history. We did not include time to first flower or height of first flower in this analysis because plants commenced flowering before browsing was first observed.

Results

Historically unprotected populations were more tolerant of browsing than historically protected populations. Deer browsing reduced mean lifetime seed production by 57% in historically protected populations but only 20% in historically

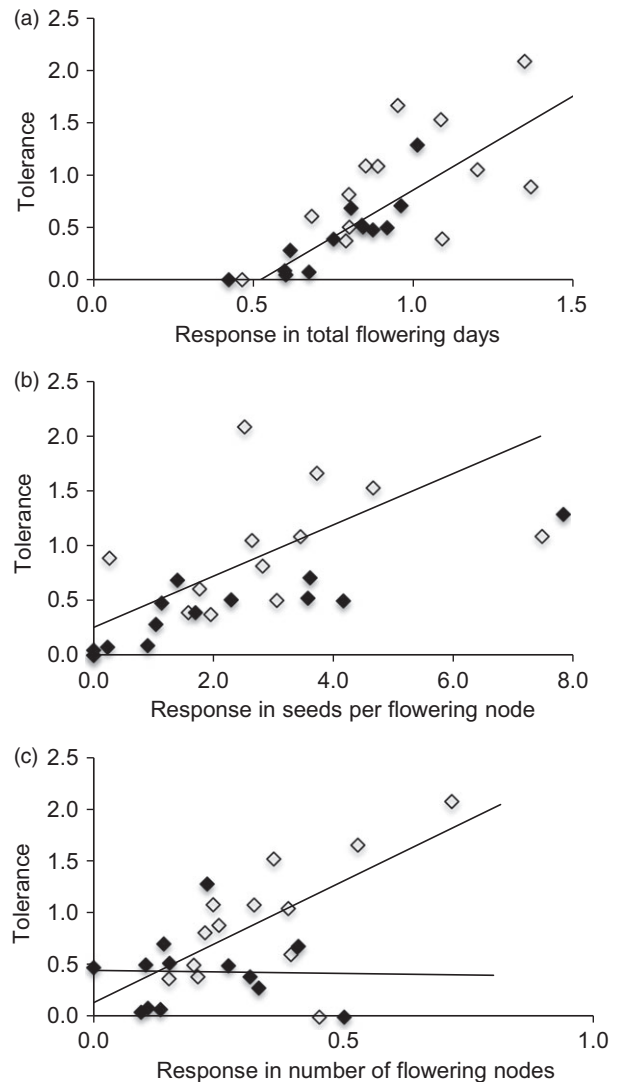


Fig. 2. Relationship between population mean tolerance and responses to browsing (ratio of browsed to unbrowsed traits for total flowering days, number of flowering nodes and seeds per flowering node). Filled symbols represent historically protected populations and unfilled symbols represent historically unprotected populations. One best-fit line is shown in panels a and b, where historically unprotected and historically protected populations had the same relationship, whereas two lines are shown for panel c where there was a significant interaction between browsing history and the extent to which response in number of flowering nodes predicted tolerance.

unprotected populations (Fig. 1b; treatment*history interaction in Table 2). Six of 13 historically unprotected populations produced more seeds when damaged than when protected, whereas only one of 13 historically protected populations showed such overcompensation (Fig. 1a) (Williams' corrected $G = 5.29$, $P = 0.0267$). Browsing decreased mean plant height by $6.8 \pm 0.8\%$ (range: 0–41.7%), and browsed plants did not produce open-pollinating flowers.

Historically unprotected and historically protected populations did not differ in days to first flower (Table 2), but other reproductive traits were impacted by plant browsing history and browsing itself. For example, browsing reduced

Table 3. Influence of history (historically unprotected or historically protected), responses to browsing (ratio of browsed to unbrowsed traits) and two-way interactions on tolerance of *Impatiens capensis* in terms of lifetime seed production. Bold *P*-values indicate $P < 0.05$

Response variable	Effect	t ratio	<i>P</i> -value
Tolerance	History	0.58	0.5661
	Response in total flowering days	3.77	0.0014
	Response in number of flowering nodes	4.80	0.0001
	Response in seeds per flowering node	4.42	0.0003
	History * Response in total flowering days	-0.22	0.8277
	History * Response in number of flowering nodes	2.85	0.0106
	History * Response in seeds per flowering node	1.66	0.1147

the total number of flowering days by 20% for historically protected populations (protected: 87.4 ± 26.6 , unprotected: 68.1 ± 30.4) but did not affect historically unprotected populations (protected: 81.5 ± 23.2 , unprotected: 79.8 ± 28.2) (Table 2). Contrary to our expectations, browsing history did not influence mixed mating system expression (the probability of producing one or more open-pollinating flowers (Table 2). When browsed, plants produced first flowers that were 29% closer to the ground regardless of browsing history (protected: 26.4 ± 1.9 cm, unprotected: 18.7 ± 1.9 cm) (Table 2). Both historically unprotected and protected populations also flowered at significantly fewer nodes when browsed (Table 2), but historically unprotected populations produced 160% more seeds per flowering node when damaged (14.3 ± 1.3) compared to when fenced (5.5 ± 1.3) (Table 2).

In testing for mechanisms of tolerance in seed production, we found all three responses (ratio of browsed to unbrowsed traits for total flowering days, number of flowering nodes and seeds per flowering node) were positive predictors of tolerance when included in a single model (Table 3). Populations that were more tolerant to browsing in terms of seed production achieved this by increased flowering days and seeds per flowering node when browsed compared to when protected (Fig. 2). The ratio of the number of flowering nodes when browsed compared to when protected was also positively correlated with tolerance, but only in historically unprotected populations (Fig. 2). These three specific plant responses influenced tolerance to herbivory independently, as they were not significantly correlated with each other ($n = 26$ for the three pairwise correlations, $P_s > 0.05$).

Discussion

Individuals from historically unprotected populations of *I. capensis* were nearly three times as tolerant (in the currency

of lifetime seed production) as those from historically protected populations. Herbivory also reduced mean number of flowering days for historically protected populations but not for historically unprotected populations. These results point towards two plausible historical scenarios: (i) heavily browsed *I. capensis* populations have recently evolved tolerance to browsing, or (ii) protected populations have lost the ability to tolerate browsing. Overall, the results of this study provide the first evidence that the overabundance of deer has led to the evolution of reproductive traits that allow for compensation following browsing.

Because response to browsing in flowering duration and number of seeds produced per flowering node were highly correlated with tolerance in plants from both histories, these could well be targets of natural selection in response to herbivory by white-tailed deer. Additionally, the ability of historically unprotected populations to produce more flowering nodes seems to be diverging from that of historically protected populations. The high degree of phenotypic variation among populations for all of these traits (when measured in a common environment) suggests that the traits are heritable. Together, our results suggest that historically unprotected *I. capensis* populations have evolved an increased ability to branch at secondary meristems when the apical meristem is damaged (Fig. S1), as has been demonstrated in other species subject to vertebrate or invertebrate herbivory (Rosenthal & Welter 1995; Lennartsson, Tuomi & Nilsson 1997; Juenger, Lennartsson & Tuomi 2000). Lennartsson, Tuomi & Nilsson (1997) found that some historically damaged (mowed or grazed) populations of field gentian exhibited higher tolerance than historically undamaged populations. Although there was pronounced variation in both their results and ours, together they show the power of replicated population studies, which can suggest evolutionary change as well as the potential mechanisms that plants employ to adapt to a changing environment.

In contrast to expectations from previous studies, historically unprotected populations did not produce a greater proportion of self-pollinating flowers than historically protected populations. Herbivory has been reported in other contexts to both increase and decrease selfing rates, reflecting selection for reproductive assurance or for increased genetic variation under stress, respectively (Campbell, Thaler & Kessler 2013). Across 10 natural populations of *I. capensis*, Steets & Ashman (2004) found that the proportion of self-pollinating flowers had a significant positive relationship with herbivory. In another experiment, Steets, Salla & Ashman (2006) demonstrated that insect herbivory in the field reduced the production of open-pollinating flowers by 59–70% and that of self-pollinating flowers by 16–23%. In our experiment, browsing decreased mean plant and browsed plants did not produce open-pollinating flowers. This may occur because only plants with adequate resources are capable of producing open-pollinating flowers (Waller 1984). If a height threshold must be reached for *I. capensis* to initiate open-pollinating flowers, then a lack of open-pollinating flower production in browsed plants

could also be a passive consequence of reduction in plant size (Schmitt, Eccleston & Ehrhardt 1987).

It is worth noting that our experiment utilized field-collected seedlings, not descendants from a common environment. Accordingly, we cannot definitively conclude whether differences among populations are due to genetic differentiation, maternal environmental effects or early plasticity. Indeed, we detected population and regional differences early in the life cycle (Table 1), and Steets & Ashman (2010) found that *I. capensis* maternal plants experiencing high rates of herbivory produced offspring that were larger in size. For these reasons, we restricted our analyses to comparisons of damaged and undamaged states within populations. The extent of our population replication across regions reduces the potential for a systematic bias in environmental conditions. Nevertheless, it is possible that an unmeasured environmental variable co-varied with browsing history. If this is the case, browsing history was nevertheless predictive of tolerance.

It should be noted that white-tailed deer are not the only herbivores of *I. capensis* in the study area. Although we observed negligible damage by other herbivores in the field and in the common garden experiment, many natural populations of *I. capensis* are subject to damage by insects, fungi and other natural enemies. In a classic study, Schemske (1984) found significant genetic differentiation between two populations of *Impatiens pallida*, a closely related species to *I. capensis*, that were differentially attacked by a host-specific beetle, *Rhabdopterus praetexus*. Recent work has questioned whether multispecies assemblages of herbivores select for 'pairwise' co-evolution (in which specific plant traits are paired with specific herbivores) or 'diffuse' co-evolution (in which defences against various enemies were positively genetically correlated) (Strauss, Sahli & Conner 2005). In a common garden experiment, for example, Stinchcombe & Rauscher (2001) found a negative genetic correlation between resistance to deer herbivory and resistance to generalist insect herbivory in ivyleaf morning glory (*Ipomoea hederacea*) that suggested diffuse co-evolution. Future experiments could test whether the exclusion of insect herbivores affects the expression of tolerance to deer herbivory in *I. capensis*.

Our results suggest a correlation between previous browsing and tolerance to deer herbivory in a common native wildflower. This relatively rapid divergence could be due to the fact that *I. capensis* is a strict annual with a limited seed bank. In the eastern United States and other forested regions where the removal of carnivores and habitat modifications have led to increases in herbivore abundance, the persistence of a plant species will depend on its ability to evolve defensive traits. The evolution of defensive traits in one species may also have indirect effects on community composition (Lennartsson, Tuomi & Nilsson 1997; Chase, Leibold & Simms 2000). The evolution of tolerance over short time scales (Agrawal *et al.* 2012) represents a previously unappreciated factor enhancing the ability of some native plants to persist in the face of rapid ecological changes.

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Data accessibility

Data set available from the Dryad repository (Martin, Agrawal, and Kraft 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Site characteristics, including location and browsing history, of the 26 *Impatiens capensis* populations

Figure S1. Individuals in unfenced treatment 20 days after browsing by deer from the (a) Central Park population (historically protected) and (b.) Pelham Bay population (historically unprotected). Note the differences in branching architecture.

SUPPORTING INFORMATION

Table S1 Site characteristics, including location and browsing history, of the 26 *Impatiens capensis* populations

Site	Region	History	Lat	Long	Description	Proportion browsed in field 2013	Area (m ²)	Density (plants/m ²)	Canopy cover (%)
Allaben	CAT	Unprotected	42.11	-74.35	Forested flat valley	72	105	88.5	75
Bear	CAT	Unprotected	42.03	-74.27	Forested gentle slope	34	160	97.0	65
Jewett	CAT	Unprotected	42.28	-74.3	Forested flat valley	64	55	59.5	45
Beaver	CAT	Protected	42.29	-74.3	Forested gorge	0	40	20.0	40
Waterfall	CAT	Protected	42.15	-74.52	Forested steep slope	0	75	37.5	50
Coon	COR	Unprotected	42.29	-77.04	Forested intermittent creek	34	200	117.0	75
Hornby	COR	Unprotected	42.28	-77.02	Partially forested swamp	30	70	50.0	50
Shady Grove	COR	Unprotected	42.2	-77.04	Forested near road	30	150	90.0	60
Battery	COR	Protected	42.29	-77.04	Forested steep slope	0	40	20.0	60
Kerrick	COR	Protected	42.23	-76.99	Forested steep slope	0	110	55.0	70
Kettle	COR	Protected	42.33	-77.18	Forested steep slope	0	40	20.0	40
Ellis Hollow	ITH	Unprotected	42.43	-76.39	Suburban forest near road	52	75	63.5	50
Lake	ITH	Unprotected	42.54	-76.59	Partially forested swamp	84	150	117.0	40
Mundy	ITH	Unprotected	42.45	-76.47	Forested swamp	92	240	166.0	50
Ponds	ITH	Unprotected	42.45	-76.36	Forested swamp	80	50	65.0	60
Treman	ITH	Unprotected	42.4	-76.59	Forested swamp near road	68	100	84.0	75
Ithaca Falls	ITH	Protected	42.45	-76.49	Partially forested gorge	0	60	30.0	60
Ringwood	ITH	Protected	42.44	-76.37	Forested steep slope	0	40	20.0	60
Slope	ITH	Protected	42.4	-76.59	Forested steep slope	0	75	37.5	60
Spencer	ITH	Protected	42.42	-76.51	Forested gorge	0	60	30.0	50
Taughannock	ITH	Protected	42.55	-76.6	Partially forested gorge	0	165	82.5	50
Pelham Bay	NYC	Unprotected	40.86	-73.8	Urban forested swamp	96	95	95.5	50
Staten Island	NYC	Unprotected	40.58	-74.13	Urban forested swamp	100	45	72.5	60
Central Park	NYC	Protected	40.77	-73.97	Urban pond shore	0	55	27.5	60
Inwood	NYC	Protected	40.87	-73.93	Urban forest	0	110	55.0	60
Van Cortlandt	NYC	Protected	40.89	-73.89	Urban forest edge	0	350	175.0	30

Fig S1 Individuals in unfenced treatment 20 days after browsing by deer from the (a.) Central Park population (historically protected) and (b.) Pelham Bay population (historically unprotected). Note the differences in branching architecture.

