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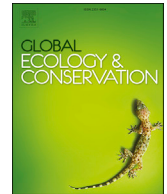
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Original Research Article

Demographic hallmarks of an overbrowsed population state in American ginseng

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ABSTRACT

Effects of high deer herbivory in North America on populations of favored plant browse species have been well-documented, however since less palatable plants now dominate the understory, we asked whether these species could be vulnerable as well, and if so, what symptoms might signal that this was occurring? Using American ginseng (*Panax quinquefolius* L.) as our representative less palatable understory plant, we compared two sub-populations within a single natural population that were differentially exposed to browse; one isolated from deer by growing atop a large, flat-topped boulder, and a browse-exposed subpopulation in the surrounding low-lying area. We tested the hypothesis that deer effects would be manifested in all parts of the life history; through reduced growth, survival and reproduction. In turn, we hypothesized that browse would reduce population growth rates, and that differences in stage structure of the population would be produced. Taking advantage of a 20 year record of formal demographic censusing, we showed that browse effects were manifested primarily in reduced size-specific growth, while size-specific fertility and survival were relatively unaffected by exposure to browse. Demographically, these differences in growth were sufficient to drive population size reductions of 4.5%/y in the off rock subpopulation while the on rock plants slowly increased in number. High browse off the rock resulted in high proportions of plants in a stunted juvenile state in the off rock population relative to the on rock plants. A high proportion of juveniles is therefore a clear symptom of an understory subjected to chronic overbrowsing, providing land managers a rapid way to assess whether deer could be impacting understory biodiversity. The sharp demographic contrasts we observed between browsed and unbrowsed subpopulations also implies that promotion of refugia within managed lands will likely become increasingly important management tools for biodiversity preservation as long as unchecked deer populations persist.

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1. Introduction

"Since then I have lived to see state after state extirpate its wolves. I have watched the face of many a newly wolfless mountain, and seen the south-facing slopes wrinkle with a maze of new deer trails. I have seen every edible bush and seedling browsed, first to anemic desuetude, and then to death."

—Aldo Leopold, from 'Thinking Like a Mountain', Sand County Almanac, 1949

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Since publication of Leopold's iconic Sand County Almanac, numerous studies have demonstrated the cascading effects of predator removal and predator re-introduction in a diverse array of biological communities (Pace et al., 1999). While many of the classic cases of trophic cascades were described in aquatic systems (Paine, 1966), profound impacts of top predator abundance have been demonstrated repeatedly in terrestrial communities as well (Schmitz et al., 2000; Terborgh et al., 2001; Rooney and Waller, 2003; Beschta and Ripple, 2009). In systems where herbivore abundance strongly affects vegetation, the loss of keystone predators can be particularly impactful (Côté et al., 2004). Overabundant herbivores can then shape the vegetation over time by profoundly altering recruitment patterns of overstory trees and reducing both abundance and diversity of the understory (Waller and Alverson, 1997; Russell et al., 2001; Côté et al., 2004; Habeck and Schultz, 2015).

In the eastern deciduous forest of the U. S., two top predators have been functionally extinct for more than a century. Eastern cougars (*Puma concolor*) were officially declared extinct in 2011, but this reflected a condition that had existed for approximately 8 decades (U. S. Fish and Wildlife Service, 2011), and they were uncommon to rare for several decades prior to that. The other top predator in eastern forests, the gray wolf (*Canis lupus*), had a similar history of being functionally extinct in most of its former eastern range by 1900 (Carson et al., 2014). Hunting by humans also kept white-tailed deer populations (*Odocoileus virgianus*) low, along with their predators. Over the past several decades, management by state wildlife agencies on behalf of human hunters successfully resurrected large deer herds, ultimately resulting in densities that have far exceeded those found in pre-settlement forests in most regions (Waller and Alverson, 1997; Russell et al., 2001; Côté et al., 2004; Habeck and Schultz, 2015). The subsequent widespread overbrowsing of understory tree seedlings, shrubs, and herbaceous understory plants is well-documented (Rooney and Waller, 2003; Côté et al., 2004). Indeed, it has been argued that the absence of keystone predators along with mismanagement of their populations resulted in white-tailed deer being recognized as keystone species in its own right (Waller and Alverson, 1997) due to their broad-ranging impacts on the entire ecosystem.

Frequently, ecologists have been concerned that common understory plant species may be gradually going extinct due to overbrowsing (Carson et al., 2014). Particular attention has been paid to browsing of seedlings and saplings of commercially valuable tree species that appear to be favored foods of deer (Côté et al., 2004; Bradshaw and Waller, 2016). However, since overstory trees persist for decades to centuries, future overstory species composition, not outright extinction, has been the primary immediate concern with trees. Somewhat less attention has been paid to effects of overbrowsing on forest understory herbaceous plants, probably because many have little direct economic value. In addition, due to the longevity of most understory herbs and the existence of perennating structures underground, the long-term effects of herbivory are difficult to observe over short time spans. Yet it would be valuable to identify populations in this stage of 'anemic desuetude' as a precursor to extinction in order to enable conservation action prior to critical endangerment.

Among understory species that have been studied with respect to deer herbivory, *Trillium*, a showy and palatable understory wildflower species, has provided an excellent model species (Anderson, 1994; Augustine and Frelich, 1998; Rooney and Gross, 2003; Jenkins et al., 2007; Knight et al., 2009; Kalisz et al., 2014). Anderson (1994) showed that mean height of Trillium plants was a strong indicator of deer browse intensity. Beauvais et al. (2017) even showed that reduced plant sizes in deer-browsed sites were reflected in the record of herbarium specimens. Rooney and Gross (2003) demonstrated population declines of 3.5% per year, even with relatively low browse rates. Jenkins et al. (2007) demonstrated the effect of herbivory in truncating the age-structure of natural populations in Great Smokey Mountain National Park, TN, U.S.A. Using matrix models for 12 Pennsylvania populations, Knight et al. (2009) demonstrated that a browse rate of only 15% was sufficient to threaten Trillium's long-term persistence.

Several approaches have been employed to evaluate deer browse effects, each with its own advantages and disadvantages. Some studies have compared dynamics of different populations that naturally experience contrasting browse rates (e.g., Knight et al., 2009); this has the advantage of examining realistic rates in the current environment, but may not include populations at 'natural' pre-settlement rates, or browse rates that would be 'desirable' from a conservation standpoint. In addition, the reasons for the differences in browse rates (e.g., proximity to edge habitat) may be correlated with other factors (e.g., light) that also influence plant population dynamics. Others have modeled deer browse effects by removing or including browsed plants from the data set in the calculation of vital rates (e.g., Rooney and Gross, 2003; McGraw and Furedi, 2005); this allows for easy manipulation of browse rates and allows a nice dissection of affected model parameters, though it assumes browse effects on an individual are confined to a particular year. Others have taken an experimental approach, fencing areas to remove deer and observing the response over time (e.g., Augustine and Frelich, 1998; Heckel et al., 2010; Kalisz et al., 2014; Sabo et al., 2017; Wilbur et al., 2017). Exclusion experiments permit a rigorous, spatially controlled test of browse effects and result in an entire community response; therefore they are well-suited to examining rates of recovery following release from high browsing rates. However, unless such experiments are very long-term, allowing re-colonization by a full complement of understory plants, this approach primarily captures the initial recovery period, rather than a continuous condition of low browse rates. Finally, a few studies have used naturally-occurring refugia within populations exposed to browsing (Rooney, 1997; Carson et al., 2005); if the refugia have been in existence for a long time, then plant demography in the refugium presumably reflects performance, including the whole-community effects such as increased competition, that may counter some positive effects of no browsing. However, in extreme refugia, browse rates may be zero, which could be unrealistically low relative to a desirable, or generally achievable, rate.

In long-term demographic studies of the widespread medicinal plant, American ginseng, early work focused on human harvest, but deer browsing occurs at much higher rates than harvest (Furedi, 2004; McGraw and Furedi, 2005). Unlike Trillium, ginseng is not a 'preferred' food plant for deer, an idea supported by detailed analyses of interactions between deer

and plants observed with wildlife cameras (Hruska et al., 2014), and the fact that deer will often only partially browse the leaves on a given plant that is within easy reach. However, deer will consume the aboveground stalk, leaves, flowers and fruits occasionally, especially as other understory plants become scarce. Though browsing rates varied among populations and years, most populations censused did experience significant loss of reproductive adult plants by the end of each growing season (Furedi, 2004). These losses catalyzed reduced population growth rates both through lost reproduction and reduced plant size (Furedi, 2004; Farrington et al., 2008). Using the data removal approach described above, McGraw and Furedi (2005) showed that virtually all ginseng populations have low population viability at current rates of deer browse, but would be viable with significant reductions in browse. Experimental studies confirmed that in addition to consuming leaf material, deer were ginseng seed predators, and not dispersers (Furedi and McGraw, 2004). Defoliation, especially early in the season, was shown to decrease plant size and reproductive output in ginseng (Furedi, 2004, Farrington et al., 2008). A decrease in stature of plants in herbarium specimens was also shown over the past two centuries, consistent with hypotheses about effects of both human harvest and deer browse (McGraw, 2001).

Virtually all ginseng populations studied have experienced significant browse; therefore it is not known what characteristics a ginseng population would have in a forest with a rich, dense understory that has not been strongly impacted by deer. However, in one population we censused for 20 seasons, we were fortunate to discover a subset of plants growing on top of an isolated, flat-topped, 2.5−4 m high 'boulder' that has not experienced deer browsing in its history. This 'control' group allowed us to examine effects of chronic overbrowsing in order to characterize the nature of 'anemic desuetude' in the rest of the population in a demographic sense. Therefore, in this study, we (1) examined growth, survival, and reproduction in the two groups of plants, (2) projected relative population growth rates, (3) performed a life table response analysis, dissecting the cause of differential population growth rates, and (4) tested whether size structure differences on and off the rock could yield a static signature of browse intensity across many populations. Based on prior studies of browse effects, we expected that the browse-exposed population off the perched rock would experience reduced performance in all three measures, relative to the on rock (protected) subgroup, and that this would in turn reduce population growth rate in equal measure. We further hypothesized that demographically Aldo Leopold's 'anemic desuetude' would be evident in population-level performance over time, and this would be in turn manifested at a given point in time by large differences in the size structures resulting from those demographic contrasts. We expected that the life table response analysis would show deer effects on population growth by mechanisms related to both growth and reproduction.

2. Methods

2.1. Perched forest communities

Coopers Rock State Forest is a 5158 ha forest in northern West Virginia, U. S. A. The primary feature of the forest is the 400 m deep canyon cut by the Cheat River. The upper margins of the canyon and other stream-dissected areas of the forest are rimmed by weather-resistant Pottsville sandstone. As streams or rivers cut away less-resistant layers beneath, large blocks of Pottsville sandstone break away to form intact blocks of rock isolated by large cracks that eventually erode to isolate the forest community on top of them. Such blocks are found wherever this erosion pattern exposes the edge of the resistant sandstones, and they range in size from a few square meters to >1000 m^2 and 1−40 m high.

On one such sandstone block (ca. 12 m × 26 m), the continuous 2.5−4 m high vertical wall on all sides was sufficient to prevent white-tailed deer from browsing the vegetation, resulting in sharply contrasting forest floor vegetation (Fig. 1). Except near the rock edges, soil depth was similar to the surrounding off-rock areas, and supported tree growth. While the overstory was not different from the surrounding vegetation, the herbaceous vegetative cover was continuous on the rock, and the understory flora was far taller and more diverse than the surrounding off-rock community. Vegetative cover in the off-rock community varied between 0 and ~10%.

Fig. 1. Images showing (A) off-rock vs. (B) on-rock understory communities where ginseng plants were located.

During our early surveys of Population 27 in the off-rock surroundings, we discovered three clusters of ginseng plants on top of the rock. They were formally censused (procedure described below) along with the surrounding population since 1998.

2.2. Formal censusing protocol

Beginning in 1998, two formal censuses were performed annually through summer, 2017. Since ginseng is harvested, plants were marked cryptically with subterranean aluminum nails engraved with unique identifying numbers. In spring (between May 25 and June 15) each year, all marked plants were visited and scored for presence, number of leaves, height of stalk, length of longest leaflet on each leaf, width of longest leaflet on each leaf, reproductive status (forming buds or not), as well as evidence of harvest, browse, insect damage and fungal disease. In late summer (July 25 – August 15), plants were revisited, berries and seeds were counted, and damage status was re-assessed. Leaf area for each plant was estimated by multiple regression using maximum leaflet lengths and widths, then summing across all leaves on the plant (Souther and McGraw, 2011a).

2.3. Browse rates

Two independent estimates of annual deer browsing rates were made. First, monitoring every 3 wk by Furedi (2004) showed that vegetative stalks persisted for 3–4 weeks after browsing. Therefore, in the two censuses occurring in all other years, we estimated that we effectively sampled browsing for 6 weeks of the ca. 15 wk growing season. Hence, the number of observed browsed stalks was multiplied by 2.5 as one estimate of browse rate. This first estimate may have underestimated browse rates because some browsed stalks may have been missed in each census (they are harder to visually detect than plants with leaves). A second estimate of browse rate was done by adding the total number of 'missing' plants in the population that were known to be alive because they emerged in a later year. This rate probably overestimated browse because it assumed that missing plants were entirely due to deer, however other factors could have caused them to be missing in any given year (e.g., rodent, rabbit, ground hog browsing), though these other causes were likely to be infrequent. Both measures were used to estimate an average browse rate for ginseng in the focus population, but also to provide a comparison with 30 populations censused in the same way across 7 states (Indiana, Kentucky, Maryland, New York, Pennsylvania, Virginia, and West Virginia; McGraw et al., 2017). All of these populations were censused annually from 2004 to 2016.

2.4. Growth, survival, and reproduction

To estimate growth rate, we used a non-destructive approach by examining the relative growth rate of leaf area (RGR-LA) for any plant that persisted for at least 5 years in the population (McGraw and Garbutt, 1990). The slope of ln (leaf area) vs. year was used as the estimate of RGR-LA. RGR-LA for plants on and off the rock was compared with a *t*-test.

Survival was assessed annually for all plants on and off the rock. Since survival is known to be size-dependent and to vary among years, both leaf area and year were included in the logistic model, as well as location on or off the rock with 'survived/died' as the dependent variable.

Total reproductive output via seeds was broken into two components; (a) produced seeds or did not produce seeds, and (b) for seed-producing plants, the number of seeds produced. The former was scored at the fall census based upon the presence of forming berries and was a nominal dependent variable. The latter was scored by counting bulges in each forming berry and summing for each plant. Berries contain 1, 2, and infrequently, 3 seeds so accurate counts were readily obtained. Natural log of seed number was analyzed with a general linear model having plant size and year as independent variables, along with location on or off the rock. All one-leaf plants were excluded from both of these analyses as ginseng is not able to produce seeds at that life history stage.

2.5. Net population change: 2005–2015

To plot observed change in subpopulation numbers on and off the rock, N was incremented as follows;

$$N_{t+1} = N_t + new\ seedlings - deaths,$$

The census interval was from spring census (t) to the following spring census (t+1). Since new seedlings germinated in May and were counted at the spring census, this number accounted for any seedling losses prior to the census. Deaths were counted as plants that were alive at census t, but were missing at the second census and were not seen for at least two growing seasons later. Because occasional early browsing or other damage to the meristem may prevent a plant from being observed aboveground at the spring census in a given year, we waited two growing seasons to pronounce the individual as 'dead'. Hence the observed population change concluded in 2015 (using the 2016 and 2017 censuses to confirm death).

In the course of censusing, we added new (previously undiscovered, non-seedling) plants to the census as they were found. These new plants were not used in calculating net population change until the following year. The relative changes on and off the rock were illustrated by starting with a theoretical cohort of 100 in both locations, and multiplying by the observed N_{t+1}/N_t at each location for every year between 2005 and 2015.

2.6. Projection matrix model and LTRE

We chose to use the traditional discrete-class matrix structure (Caswell, 2001) rather than an integral projection model for this analysis because unlike some plants that have more continuous size variation, ginseng does exhibit discrete 'behaviors' in the early life history stages (seeds, seedling 1-leaf, and juvenile 2-leaf). In addition, sample sizes were limited in the adult classes, in part due to effects of herbivory (Furedi, 2004). The 1-leaf plants, distinctive because none produced flowers or berries, were split into new seedlings and >1 y old seedlings. New seedlings had lower survival and growth than older 1-leaf plants as the former are in the early phases of establishing a tap root, and are more vulnerable to mid-season drought and other stresses. Juvenile plants having two leaves are distinct from 1-leaf plants because most of them do produce flowers, and therefore can act as males in the population. However, production of the large seeds and fleshy fruit is rare to infrequent in this intermediate stage. The juvenile 2-leaf plants were split into equal size small (<50 cm^2 leaf area) and large (>50 cm^2) classes. Adults (3-leaf and 4-leaf plants) were partitioned into three size classes based on log-linear divisions based on leaf area (small adults, <100 cm^2; medium adults, 100 cm^2 < leaf area<250 cm^2; large adults, >250 cm^2); this partitioning accounts for the significantly greater seed production in larger adults than in smaller adults. Using leaf area to distinguish classes of 2-leaf and larger plants allowed for growth, stasis, or shrinkage between years; the latter was particularly important for the resulting model in determining accurate population growth rates and explaining population growth rate differences (Salguero-Gomez and Casper, 2010).

Due to innate dormancy that is released only after two winters, all individuals pass through a seed stage in the soil. Although ginseng seeds have been shown to persist in the soil at some sites for up to 4 years, in Population 27, two sequential on-site seed cage studies showed persistence for only 2 years at this site. Therefore two seed stage classes were included in the matrix model; 9 month old and 21 month old seeds (age when censused in late spring). The seed cage study allowed us to calculate initial 9 month survival, survival within the seed bank from 9 to 21 months, and germination from the 9 month old and 21 month old seed pools. Size-specific fertilities (mean number of 9 month old seeds per adult of each size class the previous year) were determined as the product of seed number, 9 month survival observed in the seed cage study and a loss rate specific to on rock vs. off rock environments. This loss rate was included because seed cages protected dispersed seeds to an unknown degree. To calculate the loss rate we determined the ratio of observed new seedlings to the expected new seedling number based upon seed production and 9 month survival. The transition probability from 9 to 21 month old seeds was determined directly as the mean of the two seed cage studies (Souther and McGraw, 2011b). Germination rates (transition from seed to 1-leaf new seedlings) were also determined from the seed cage study. The results of the age-, stage- and size-based class partitioning of the life history was a 9 × 9 transition probability matrix model.

Transition matrices were determined for each pair of years from 2005 to 2014 (ten total matrices) for the off rock subpopulation. The sample size ranged from 355 to 428, resulting in a well-parameterized model. In years prior to 2005, a small amount of harvest occurred and therefore in order to focus on deer browse effects in isolation, we did not include those years in this study. Transition matrices from 2015 onward could not be estimated because of the unknown mortality status of missing plants.

The deer-isolated 'on rock' subpopulation numbered between 7 and 30 plants in the 20 census years. This number of observations was insufficient to construct a separate population projection matrix for each year. To construct a matrix for comparison to the off rock subpopulation, we pooled the transition observations across pairs of years to construct a single matrix. While the observations were therefore not entirely independent as some individuals were repeatedly sampled, these observations were made across ten widely varying growing seasons and provided a good composite measure of demographic response to the on rock environment.

Life table response experiments were then performed to allow the dissection of differences in λ between two matrices into components due to each transition probability (Caswell, 2000). We compared the finite rates of increase for the 10 year mean matrix for the off rock subpopulation with the composite matrix of the on rock subpopulation. The contribution to the difference in lambda in the on rock vs. off rock subpopulations was partitioned into components due to change in matrix elements and sensitivity of λ to those elements;

$$\Delta\lambda = \sum \Delta a_{ij}\left(\frac{d\lambda}{da_{ij}}\right),$$

where $d\lambda/da_{ij}$ is the sensitivity and Δa_{ij} is the difference in a_{ij} between the two matrices.

2.7. Size structure and browse rate

To examine how a static population measure could indicate a state of long-term overbrowsing, we examined the stable size distribution differences between the on rock composite matrix and off rock mean matrix of Population 27. Next, in order to test the fidelity of our proposed indicators beyond Population 27, we examined the association between several possible size structure indicators (proportion of 1-leaf seedlings, proportion of 2-leaf juveniles, proportion of adults, and ratio of non-juveniles to juveniles) and our two browse estimates in 30 natural populations over a wide area by correlation analysis.

All asymptotic population statistics were determined using MATLAB (v. R2015b, The Mathworks, Inc.).

3. Results

3.1. Browse rates

The overall browse rate for Population 27 (the focus population of this study) was slightly above the 30-population median by either measure; ranking 12th (out of 30) by one measure and 14th (out of 30) by the other (Fig. 2). Population 27 is therefore near the middle of the set of natural populations we studied across seven eastern U.S. states. The focus population's annual browse rate estimate was 20−25% by the two measures used in this study. No plants on the rock were browsed in any of the 20 census years (1998−2017).

3.2. Individual plant performance

Mean relative growth rate of plants that persisted at least 5 years on the rock was higher than the same measure for the surrounding population (Fig. 3A). Plants on the rock had an RGR significantly greater than 0 (one-sample t-test, t = 4.1514, p = 0.0013), indicating an increase in mean plant leaf area. Indeed, after a decade, mean leaf area of plants on the rock nearly tripled. However, mean RGR-LA for plants in the browse-exposed population was negative, showing a declining leaf area (one sample t-test; t = −1.6749, p = 0.0473). This corresponded to a 10% decline in mean leaf area over a decade in the browse-exposed portion of the population.

Survival of individual plants to the following year was size-dependent, as expected (Leaf Area Effect, Likelihood Ratio Chi-square = 94.5375, p < 0.0001). There was no statistical support for a survival difference between locations (Location Effect L-R Chi-square = 1.2868, p = 0.2566). However, the effect of size on survival depended on location (Location x Leaf Area Effect, L-R Chi-square = 4.3360, p = 0.0373). Inspection of the logistic regressions of survival on size at the two locations showed that survival was lower at small sizes on the rock, but this pattern was reversed above a size threshold of ca. 37 cm^2 (Fig. 3B).

No evidence was found to support a main effect of location on components of reproduction (on vs. off the rock; p > 0.10). The chance that a plant would produce seeds increased only as a function of size (L-R Chi-square = 180.5527, p < 0.0001). In addition, the effect of size on whether a plant was reproductive did not depend on the location (p > 0.10). With separate logistic regressions, on rock and off rock plants showed similar patterns of sharply increasing reproductive probabilities with plant size (Fig. 3C). For plants that successfully produced berries, mean number of seeds was a function only of plant leaf area ($F_{Leaf\ area}$ = 84.8808, p < 0.0001) and not location ($F_{Location}$ = 0.0168, p = 0.8970), but there was a trend suggesting a dependency of the size effect on location ($F_{Leaf\ Area\ x\ Location}$ = 3.3220, p = 0.0688). Predicted seed numbers tended to be greater for small reproductive plants on the rock than for those off the rock, but this pattern was reversed for large plants (Fig. 3D).

3.3. Net population change

The bulk of the population (91% as of 2017) was located off the rock, and this part of the population declined steadily in numbers from 2005 to 2015 at a rate equivalent to 4.5%/y (Fig. 4). By contrast, the small subpopulation on the rock grew haltingly with episodic recruitment, with a net increase of 50% after one decade. This continued for the following two
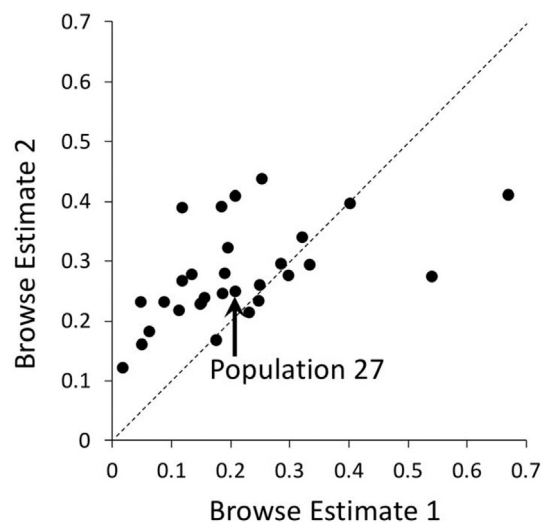

Fig. 2. Browse estimates using two approaches plotted for 30 natural populations of ginseng. Browse estimate 1 was based on direct observation of browsed stalks. Browse estimate 2 was based on missing plants at each census. The browse rate estimates for the focus population for the present study (Population 27) are identified for comparison.
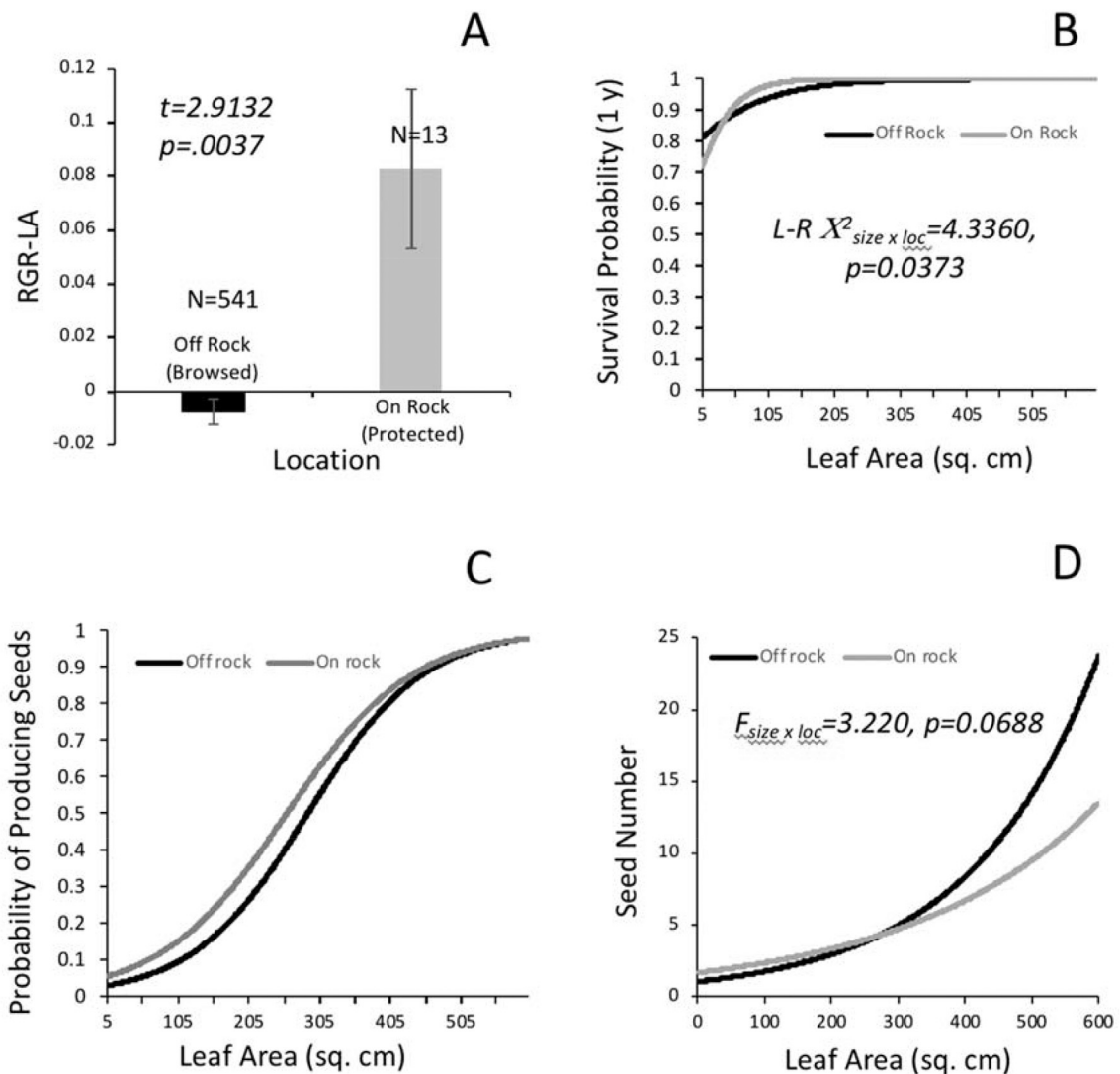
Fig. 3. Comparison of performance measures on and off the perched rock boulder feature, including (A) relative growth rate for plants that survived 5 years or more (means ± 1 s e.; two sample t-test), (B) probability of surviving for 1 year as a function of leaf area (logistic regression), (C) probability of producing berries as a function of leaf area (logistic regression) for plants with more than one leaf, and (D) seed numbers predicted by log linear regression on leaf area for plants that produced seeds.

summers, by which time the number of plants had nearly tripled in number due to a second large pulse of new seedlings (data not shown).

3.4. Matrix model results and LTRE

Based on the mean population projection matrix for the off rock subpopulation, that group of plants was predicted to shrink in numbers at a rate of 4.51% per year when at the stable stage distribution (Fig. 5A). This was almost precisely the same as the observed annual rate of decline from 2005 to 2015. Meanwhile, the on rock subpopulation was predicted to increase at a rate of 3.73% per year (Fig. 5A). This rate would translate to a 44% rate of increase over a decade, again not very different from the observed rate from 2005 to 2015, though clearly the on rock plants were not in a stable stage distribution.

Remarkably, the LTRE clearly showed that all six of the top positive contributors to the difference in λ between on rock and off rock subpopulations were due to contrasts in matrix parameters describing growth to larger classes (Fig. 5B). Growth into the largest and second largest adult classes were most important, followed by growth into the small adult class. Size-specific fertility parameter differences on and off the rock were not important contributors to Δλ, all having absolute values < 0.002 (data not shown).
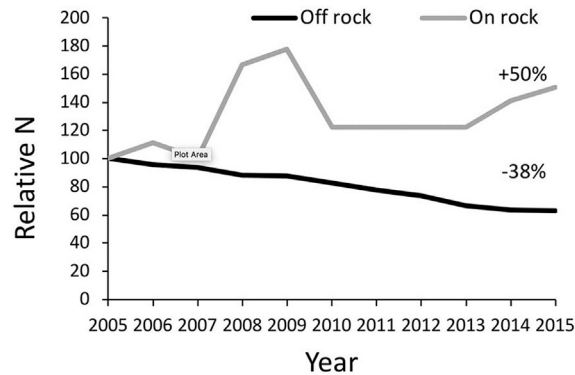
Fig. 4. Relative population sizes of ginseng on and off the perched rock boulder feature determined over 10 years of monitoring in Population 27.
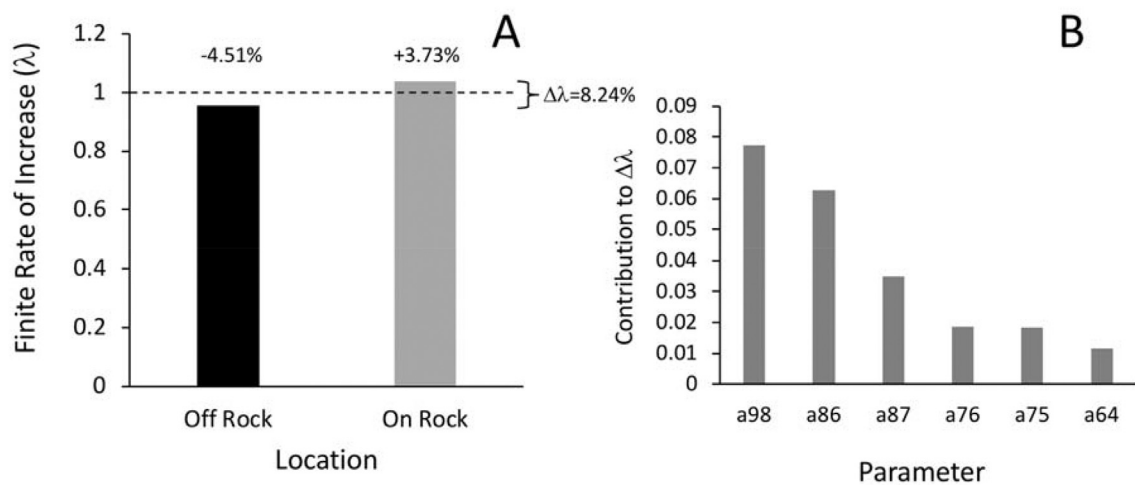

Fig. 5. (A) Finite rates of increase for on rock vs. off rock subpopulations, and (B) LTRE results for the six most important stage transitions accounting for the larger population finite rate of increase on the rock. All a_{ij} are transitions from stage j to stage i, and therefore in this case are all showing growth transitions among classes.

3.5. Size structure and browse rates

The stable stage distribution of the composite matrix for the on rock subpopulation and the mean matrix for the off rock subpopulations in Population 27 showed distinct differences in almost all stages (Fig. 6). The on rock subpopulation had more seeds in the soil, more new seedlings and more medium and large adults, as a proportion of the total in the stable stage distribution, while the off the rock subpopulation was enhanced in the older seedling and juvenile categories.

By placing Population 27 in the broader context of 30 natural populations, we were able to examine which of the size structure indices showed a correlation to the browse indices. Indeed, almost all of the size structure indices showed some correlation to browse. For example, the larger the number of browsed stems observed with eaten stalks (browse estimate 1), the fewer 1-leaf plants were found in the population ($r = -0.6222, p = 0.0002$). The strongest association was the positive correlation shown between the second browse estimate and the proportion of the population in the 2-leaf plant classes (Fig. 7). Across the 30 populations, the proportion of juveniles ranged widely, from 17 to 58% of the whole population. At the upper end, these proportions corresponded with browse estimates of more than 40%. Compared with the other 29 populations, Population 27 was near the middle of the scatterplot (Fig. 7), again suggesting it was not atypical.

4. Discussion

Interpreting individual- and population-level contrasts between on rock and off rock subpopulations as a browse effect makes the assumption that absence or presence of deer was the only difference between the two environments. *Sensu stricto*, this is clearly not the case. One obvious difference is soil depth on the rock, which could in turn affect water and nutrient availability. In August 2017, we measured soil depth in the vicinity of ginseng plants on the rock and found an O horizon
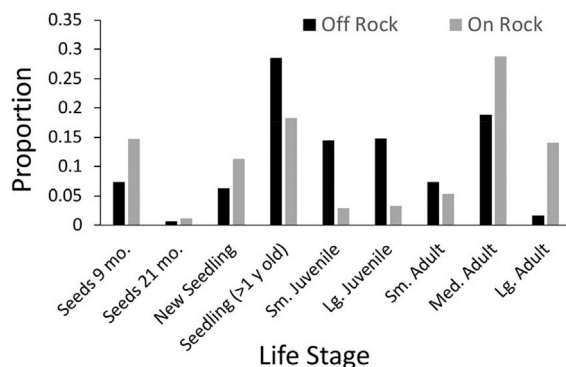
Fig. 6. Stable stage distributions of On rock and Off rock subpopulations in Population 27. These distributions were determined by finding the right eigenvalue of the composite on rock matrix and the mean off rock matrix.

varying between 5 and 35 cm deep, with almost no other soil horizons above the perched rock surface. From prior experience digging ginseng roots, we find most rooting does occur within this depth range, however fine roots accessing deeper water supplies are found in larger plants at sites with deeper soils. The prediction of greater drought stress on the rock was reinforced by notations on our annual August census sheets of wilting or early senescence in 5 of 20 census years. Relatively undeveloped soil would likely reduce ginseng growth on the rock relative to an unbrowsed condition off the rock, thus underestimating the negative 'effect of browse' relative to what we observed; our 'browse effect' interpretation is likely conservative.

Another abiotic contrast of the on rock and off rock microsites could be overstory canopy coverage. In other work, ginseng responded positively to smaller canopy openings (Wagner and McGraw, 2013; Chandler and McGraw, 2015, 2017). However, the rock surface was small, and large trees adjacent to it were overhanging the rock subpopulation. In addition, multiple trees up to 15 cm in diameter were growing on the rock surface itself, such that the tree canopy difference was minimal. Intense shading from herbaceous competitors, likely an indirect deer browse effect, would have more than compensated for any reduction in tree canopy experienced by ginseng plants on the rock (see Fig. 1), again making the abiotic environment more favorable for the off rock subpopulation with respect to light. We therefore conclude that browse difference between on rock and off rock subpopulations would have been even greater if the lower quality microenvironment on the rock had not tempered the contrast. Comisky et al. (2005) demonstrated that low rocks in the Alleghany National Forest that were exposed to browse closely resembled the off rock vegetation, while high browse-protected rocks acted as refugia, with higher species diversity and much higher reproductive output from herbaceous plants found there. This affirms our interpretation that the overwhelming observed difference between the high rock and the surrounding vegetation was due to deer browse.

Over 30 wide-ranging populations, two browse estimates revealed a wide range of browse rates (1.5%–67% for one measure; 12%–44% for the other) for ginseng populations without obvious deer refugia (McGraw et al., 2017). No precise measure is available because populations would have to be visited at least 6 times during the season to assess actual browse rates and such a high human visitation rate could itself alter browse probability. Therefore, some uncertainty in natural browse rates is inevitable. The two estimates were similar, and near the median, for Population 27 (20–25% each season); we conclude that this population is representative of deer impacts in the middle range of those experienced by natural populations. The presence of a 'control' group of plants in unbrowsed vegetation atop a rock therefore presented a unique opportunity to examine 'average' effects of browsing on this species. There was only one such 'control' group within one of the 30 populations, however the fact that it was typical of other populations with respect to deer browse suggests that our findings are more broadly relevant.

Contradicting our original hypothesis, browse effects on survival, growth, and reproductive were not spread evenly across size-dependent measures on individual plants. Instead, the primary effect of exposure to browse was to reduce the size-dependent growth rate (RGR-LA) of individuals in the browse-exposed region of the population to a mean that was negative; plants off the rock were actually shrinking in mean leaf area. This pattern of shrinkage following browse has been observed for other understory species, such as Trillium (Knight et al., 2009). We interpret this slow decline in mean size of plants as a primary signal of Aldo Leopold's 'anemic desuetude' (Leopold, 1949) at the plant level for this forest floor herb. Because smaller plant size results in higher mortality and lower reproductive output, browse has consequences for these components of plant performance as well at the population level, but there were only subtle differences between off rock and on rock plants in terms of their size-dependent survival and reproduction.

Physiologically, the effect of browsing on growth is explained by the fact that it curtails energy storage in the tap root for re-growth the following growing season. Ginseng, like most understory perennials, exhibits deterministic growth within a growing season, and the top does not re-grow once browsed. Therefore, a shortened growing season effectively reduces energy storage in the form of non-structural carbohydrates in the root. Smaller 'adult' plant sizes have been identified in other deer-browsed understory species as well, including reduced height and leaf area in Trillium (Anderson, 1994, Beauvais et al.,
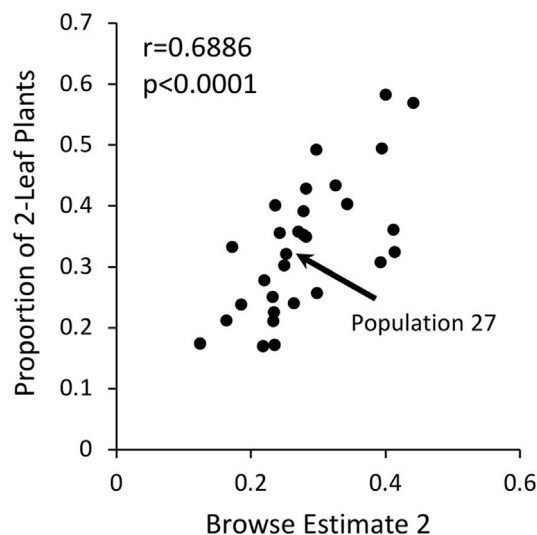
Fig. 7. Correlation of browse estimate 2 with proportion of juveniles in the population across 30 natural populations of ginseng.

2017), and reduced leaf size in Maianthemum (Rooney, 1997). Off the rock, deer may also have had nonconsumptive, indirect effects as well. In *Arisaema triphyllum*, for example, Heckel et al. (2010) found that deer activity increases soil compaction and decreases leaf litter depth, contributing to declines in *A. triphyllum* size and seed rain, and resulting in shifts toward male-dominated populations, even though this species was rarely consumed by deer. Sabo et al. (2017) further suggested that the direct effect of deer browse were compounded by deer-mediated environmental alterations, including soil compaction.

The contrasting performance of individual plants was reflected in demographic projections that forecasted long-term increases in the rock subpopulation, and by contrast, declines in the off rock subpopulation. Indeed, although the browse-protected subpopulation showed episodic recruitment and stochastic fluctuations typical of low N populations, the net change over a decade nevertheless closely reflected the long-term positive trajectory predicted by the composite projection matrix model for those plants. The decline seen off the rock, based on larger numbers, was steadier over time, and again reflected the projections closely. The modeling projections assumed non-connectivity between on-rock and off-rock sub-populations, which strictly speaking is not the case. However, the model projections closely mirrored observed changes, so if, for example, seed production from the boulder subpopulation was altering population change off the rock, its effect was undetectable. The LTRE showed that greater rates of growth to larger size classes (reflecting higher RGR) was the primary reason for higher growth rate in the browse-protected group of plants on the rock within Population 27; reinforcing the primacy of growth effects at the population level. The contrasting demographic parameters resulted in altered stable stage distributions, which, in turn, reflected the state of 'anemic desuetude' in the population. The high proportion of 'juvenile' 2-leaf plants in ginseng may be the best indicator that deer have been chronically overbrowsing a population. By contrast, a large proportion of new seedlings (reflecting a larger seed pool) and a large proportion of large fecund adults is likely an indicator that a population is not being overbrowsed.

A juvenile-heavy stage-distribution was also found to be a consequence of harvest by humans (Mooney and McGraw, 2009). However, when humans harvest plants, unlike deer, the roots are destroyed − the skewed structure in that case is a consequence of removing larger individuals from the population, not due to stunting. This suggests a way to distinguish anemic desuetude produced by deer and the skewed distribution produced by human harvesters: In the case of deer, a large proportion of 2-leaf 'juvenile' plants are likely to be old 'stunted' individuals, while in human harvested populations, juveniles will largely be young, growing, and in the process of transitioning from seedling to adult. In ginseng, ages can be determined by counting annual bud scars on the rhizome (Lewis and Zenger, 1982). Indeed, in the complete published data set for 30 populations of ginseng (McGraw et al., 2017), although only a small proportion of older plants were aged using the bud scar approach, 36% of the observations of plants more than 30 years old were 2-leaf 'juvenile' plants, and one of these was more than 50 years old. This pattern is not readily explained by human harvest effects but is consistent with deer browse effects.

Refugia such as large rock or boulder tops that are out of reach of deer could be important sources of recolonization of surrounding communities if browse rates were reduced through improved habitat management in the future (Carson et al., 2005). Within Population 27, the single rock top subpopulation of ginseng has become more significant over the 20 year census period. At the beginning of our censusing efforts (1998), the boulder top subpopulation comprised 3% of the plants and 2% of the seeds produced in the larger population. By 2017, the boulder subpopulation accounted for 9% of the plants and 37% of the seeds produced by the overall population. Given the subpopulation trajectories we showed, this trend is likely to continue. Indeed, certain other rock top species we noted (e.g., *Sanguinaria canadensis*, *Asarum canadense*, *Actaea racemosa*, *Urtica dioica*, *Polygonatum odoratum* and *Thalyctrum* sp.) were rare or absent altogether in the off rock community, suggesting

that more palatable species were farther along on this trajectory. Ultimately, of course, density-dependence within ginseng will likely limit the boulder top subpopulation. Assuming no density-dependence to this point, backward projection suggests this group of plants originated ca. 9 decades ago.

In practical terms, most forest communities are unlikely to contain many rock refugia to act as biodiversity preservation hotspots. Certain other microsites (e.g., slash left by logging operations or very steep slopes; Grisez, 1960, Rooney, 1997) may be somewhat protected from overbrowsing by deer, which could provide partial refugia. Land managers could also create refugia by fencing areas and allowing them to recover, however this strategy requires significant initial investment and maintenance to be effective in the long term. Moreover, recovery could be quite slow due to the 'ghost of herbivory past' (Carson et al., 2005); a general problem with the exclusion approach to conservation. The obvious more permanent remedy is to manage deer populations with the health of the ecosystem and biodiversity preservation as the primary goal (deCalesta and Stout, 1997; Rooney, 2001; Côté et al., 2004; Latham et al., 2005). When human hunting is inadequate for achieving this goal, reintroduction of top predators should be seriously considered (McShea, 2012). The success of such reintroduction efforts in certain regions of the world provides examples that could readily be followed, even in areas close to human-dominated habitats (Creel et al., 2005; Beschta and Ripple 2009, 2010). Recovery of vegetation from overbrowsing would likely be fastest for species such as ginseng that are secondary food sources for deer and therefore have persisted through decades of overbrowsing, albeit in a state of 'anemic desuetude'. Recovery will also be more rapid for communities that do have natural refugia as a source of recolonization.

Beyond their immediate importance for plant conservation, refugia from overbrowsing may be important for whole-community preservation. For example, pollinator guilds associated with rich understory vegetation (Motten, 1986) could be preserved within refugia. Ginseng seeds represent a food source for thrushes and other birds (Elza et al., 2016). Indeed, the origin of the on rock subpopulation was very likely seed dispersal by wood thrushes as they have been observed annually at that site. The degree to which isolated refugia can have cascading conservation effects has not been thoroughly investigated. As overbrowsing by deer remains unaddressed in much of the range of white-tailed deer in the eastern U. S., the role of refugia in preservation of biodiversity at all levels will likely continue to increase.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.gecco.2018.e00435.

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