

# Demographic stimulation of the obligate understorey herb, *Panax quinquefolius* L., in response to natural forest canopy disturbances

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## Summary

**1.** Natural and anthropogenic forest canopy disturbances significantly alter forest dynamics and lead to multi-dimensional shifts in the forest understorey. An understorey plant's ability to exploit alterations to the light environment caused by canopy disturbance leads to changes in population dynamics. The purpose of this work was to determine if population growth of a species adapted to low light increases in response to additional light inputs caused by canopy disturbance, or alternatively, declines due to long-term selection under low light conditions.

**2.** To address this question, we quantified the demographic response of an understorey herb to three contrasting forest canopy disturbances (ice storms, tent caterpillar defoliation and lightning strikes) that encompass a broad range of disturbance severity. We used a model shade-adapted understorey species, *Panax quinquefolius*, to parameterize stage-based matrix models. Asymptotic growth rates, stochastic growth rates and simulations of transient dynamics were used to quantify the population-level response to canopy disturbance. Life table response experiments were used to partition the underlying controls over differences in population growth rates.

**3.** Population growth rates at all three disturbed sites increased in the transition period immediately after the canopy disturbance relative to the transition period prior to disturbance. Stochastic population models revealed that growth rates increased significantly in simulations that included disturbance matrices relative to those simulations that excluded disturbance. Additionally, transient models indicated that population size ( $n$ ) was larger for all three populations when the respective disturbance matrix was included in the model.

**4. Synthesis.** Obligate shade species are most likely to be pre-adapted to take advantage of canopy gaps and light influx to a degree, and this pre-adaptation may be due to long-term selection under dynamic old growth forest canopies. We propose a model whereby population performance is represented by a parabolic curve where performance is maximized under intermediate levels of canopy disturbance. This study provides new evidence to aid our understanding of the population-level response of understorey herbs to disturbances whose frequency and intensity are predicted to increase as global climates continue to shift.

**Key-words:** canopy gap, climate change, defoliation, forest disturbance, ice storm, lightning, *Panax quinquefolius* L., plant population and community dynamics, stochastic population growth, transient population dynamics

## Introduction

Forest disturbances occur as a result of both natural and anthropogenic influences, and range from discrete disturbance events to chronic disturbances that occur over longer time-scales (White & Pickett 1985). Disturbance influences the

structure and function of individual plants, populations and forest communities, and can differentially affect the various strata within forested systems (White 1979; Roberts & Gilliam 2003). Canopy disturbances are recurring sources of heterogeneity that lead to multi-dimensional shifts in forest understorey dynamics (Valverde & Silvertown 1998).

A suite of understorey environmental characteristics are altered by canopy disturbance, including light availability,

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temperature, humidity, surface soil moisture, nutrient availability and evapotranspiration (Liechty *et al.* 1992; Roberts & Gilliam 2003; Roberts 2004; Muscolo *et al.* 2014). Natural canopy disturbance regimes of mid-latitude mixed mesophytic forests most commonly involve the defoliation, limb loss and death of single trees or small clumps of neighbouring trees by ice storms, insect defoliation, lightning strikes and wind-throw (Taylor 1971; Sousa 1984; Roberts & Gilliam 2003; Muscolo *et al.* 2014).

Light is the primary resource that limits photosynthesis, growth and seedling establishment in relatively undisturbed forest understories (Chazdon & Pearcy 1991; Beckage *et al.* 2000; Neufeld & Young 2003; Whigham 2004; Wagner & McGraw 2013). Sunflecks play a critical role in the development and success of understory herbs by contributing up to 85% of the total photosynthetic photon flux density (PPFD) and up to 60% of some understory plants' daily photosynthesis and net carbon gain (Chazdon 1988; Chazdon & Pearcy 1991; Kursar & Coley 1993; Wagner & McGraw 2013). Wagner & McGraw (2013) found that microsites with higher sunfleck activity triggered an increase in light saturated photosynthetic rates as well as an increase in individual growth rates in *Panax quinquefolius* L. (American ginseng). However, this positive response is not ubiquitous. *Elatostema repens*, a tropical understory herb, experienced photoinhibition and a reduction in carbon gain when exposed to irradiance greater than  $700 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Le Gouallec, Cornic & Blanc 1990). Intense and long-lasting canopy disturbances could lead to high leaf temperature, increased water loss and eventual photoinhibition in obligate understory herbs that do not possess physical avoidance mechanisms and physiological adaptations to high light (Chazdon & Pearcy 1991; Oláh & Masarovičová 1997; Fournier *et al.* 2004; Roberts & Gilliam 2014). While many studies have documented a range of physiological responses to sunflecks, fewer have examined the longer term consequences for plant growth, survival, reproduction and ultimately population dynamics.

Population growth rate ( $\lambda$ ) is an integrated measure of plant survival, growth and fertility that has been used to quantify spatiotemporal variations in population dynamics as well as the ways in which population dynamics vary among changing environmental conditions (Caswell 1989; Horvitz & Schemske 1995; Valverde & Silvertown 1998). Horvitz & Schemske (1995) investigated how the population dynamics of a neotropical understory herb, *Calathea ovandensis* differed through space and time. In this study, Horvitz & Schemske (1995) determined that there was significant spatiotemporal variation in *C. ovandensis* demography, but that variations were not attributable to one single factor. Rather, variations were the result of differences in abiotic and biotic characteristics of each study plot, as well as environmental differences that varied with time in all plots (Horvitz & Schemske 1995). Valverde & Silvertown (1998) analysed the demographic response of the perennial woodland herb, *Primula vulgaris*, to varying levels of canopy openness to better understand the effect that forest regeneration and canopy closure had on populations of this understory species. Valverde

& Silvertown (1998) determined that canopy openness formed a positive relationship with population growth rate ( $\lambda$ ) whereby  $\lambda$  was generally higher in populations that experienced a brighter environment and lower in populations that were shaded. Valverde & Silvertown (1998) concluded that population growth of this understory herb slows as forest canopies close during forest regeneration, and further concluded that populations dynamics are altered as a result of natural canopy changes.

Guides for the commercial cultivation of *P. quinquefolius* often suggest that individual growth is greatest under light regimes near 25% of total available light (Vaughan, Chamberlain & Munsell 2011; Persons 2014). Additionally, Proctor & Palmer (2016) determined that the dry root weight of *P. quinquefolius* seedlings grown in a greenhouse was optimized under c. 35% of total available light, though the authors emphasize that optimal light environment is determined by both plant response to light and to location-specific environmental issues. Nevertheless, the demographic response of natural populations of *P. quinquefolius* to periodic increases in light caused by natural canopy disturbances is unknown. In 2013, Wagner and McGraw proposed that since the survival, growth and reproduction of *P. quinquefolius* are largely size dependent, the changes in growth brought about by light variability in sunflecks could predict the fate of *P. quinquefolius* subpopulations. However, their work did not scale up responses to the population-level, nor did their work consider the effects of canopy disturbance on *P. quinquefolius* demography (Wagner & McGraw 2013). This study builds upon these findings and assesses how population growth rates of an obligate understory plant, *P. quinquefolius*, vary in response to quantities and durations of light that exceed even those found in sunflecks. The 'slow' life-history traits that characterize *P. quinquefolius* are typical of many perennial understory herbs (Charron & Gagnon 1991; McGraw *et al.* 2013), making *P. quinquefolius* a good model species for understanding canopy disturbance effects generally.

The overarching goal of this research was to determine if a species found primarily in low light understory environments benefits demographically from additional inputs of light from canopy disturbances, or alternatively, due to long-term selection under low light conditions, such disturbances bring about a population decline. Secondly, we wanted to know if the demographic response was consistent across different canopy disturbance types, regardless of severity, duration and effects beyond light enhancement. To address these goals, we analysed the demographic consequences of three contrasting canopy disturbances observed over the history of studying 30 natural *P. quinquefolius* populations over a period of up to 18 years from a sample of 461 population-years of data.

## Materials and methods

### STUDY SPECIES

*Panax quinquefolius* is a long-lived, non-clonal obligate understory herb found throughout much of the eastern United States and in

southern portions of Canada (Whigham 2004; McGraw *et al.* 2013). *Panax quinquefolius* emerges from winter dormancy and begins elongation and leaf expansion in late April or early May, prior to complete closure of the tree canopy (Lewis & Zenger 1982; Hackney & McGraw 2001). Long pre-reproductive periods are common in *P. quinquefolius*, and flowering in reproductive individuals occurs in June and July, followed by fruit production and ripening from July to September (Carpenter & Cottam 1982; Charron & Gagnon 1991; McGraw *et al.* 2013). Similar to other forest herbs, *P. quinquefolius* produces relatively few large seeds (Bierzuchudek 1982; McGraw *et al.* 2013). Dispersal of fruit via gravity and frugivorous birds (Lewis & Zenger 1982; Hruska, Souther & McGraw 2014) takes place in August and September and is followed by plant senescence, as is common in many understorey herbs (Bierzuchudek 1982; McGraw *et al.* 2013). Like many forest herbs, *P. quinquefolius* seeds require a stratification period following dispersal, after which seeds can remain dormant in the seed bank (Bierzuchudek 1982; Whigham 2004). The stratification period for *P. quinquefolius* is typically 21 months, but germination after 33 or 45 months is also possible (McGraw *et al.* 2013). Newly emerged *P. quinquefolius* seedlings consist of a one-leaf plant with three leaflets. In the years that follow, individuals produce additional leaves with varying numbers of leaflets (Lewis & Zenger 1982; Anderson *et al.* 1993). Fruit production can occur in plants that have two leaves, but is more common in plants at the three- to four-leaf stage (Furedi 2004). Like most forest understorey herbs, *P. quinquefolius* seedlings have higher rates of mortality than more mature adult plants (Bierzuchudek 1982; Charron & Gagnon 1991; Whigham 2004; McGraw *et al.* 2013).

A previous study of the response of natural populations to spatial variation in forest floor sunflecks suggested that *P. quinquefolius* is pre-adapted to the light regimes of old growth forests (Wagner & McGraw 2013). Old growth forests are characterized by an overstorey with well-developed canopy layers as well as temporally and spatially heterogeneous gap formations and closures (Knohl *et al.* 2003; Spies *et al.* 2006; Manabe *et al.* 2009; Wagner & McGraw 2013). A separate study that focused on the response of *P. quinquefolius* to timber harvest found that initial *P. quinquefolius* survival decreased following tree removal, while the growth rate of surviving individuals increased (Chandler & McGraw 2015). Nevertheless, the net demographic effect of natural canopy disturbances on *P. quinquefolius* was unknown.

## STUDY AREAS

We took advantage of natural canopy disturbance events that occurred at five long-term research sites, each containing natural populations of *P. quinquefolius*. Due to the economic and conservation values of *P. quinquefolius*, generic site descriptors (NY, WKY, EKY) have replaced actual location names. While the canopy disturbances were noted during censuses, we did not anticipate a comparative study of canopy disturbance effects; therefore, changes in PPF and in canopy structure following each disturbance were estimated using data collected after each disturbance event.

### NY – Forest tent caterpillar defoliation

The affected range, frequency and intensity of some phytophagous insect outbreaks are predicted to increase with the changes in temperature and precipitation associated with climate change (Williams & Liebhold 1995; Harrington, Woiwod & Sparks 1999; Logan, Régnière & Powell 2003; Battisti *et al.* 2006; Dukes *et al.* 2009; Klutsch *et al.*

2009; Bentz *et al.* 2010). An example of this is the recent widespread tree mortality observed in the western United States caused by bark beetle outbreak (Bentz *et al.* 2009). Another example is forest tent caterpillars (FTC; *Malacosoma disstria*), which feed on leaves of an array of broadleaf trees (Dukes *et al.* 2009). Insect defoliation thins the tree canopy, thus allowing more sunlight to reach the understorey until refoliation occurs. Soil nutrient inputs increase as well due to frass deposition (Hunter 2001; Frost & Hunter 2004). The study site was located in eastern New York (NY), U.S.A. In May–June, 2006, heavy FTC defoliation resulted in the loss of up to 100% of the deciduous canopy cover over parts of the population for several weeks in mid-growing season. Refoliation occurred gradually in July and August.

Although we did not quantify the change in the understorey light environment due to FTC defoliation in 2006, we estimated the upper limit of the effect by quantifying PPF before and after canopy leaf-out in spring, 2016. Three 30-m transects were established on April 13, 2016 and PPF was measured at 10 evenly spaced points along the transect (mean of three measurements per point) on a clear day between 11:30:00 and 12:30:00. The measurements were repeated on a clear day between 11:30:00 and 12:30:00 at the same points on June 19, 2016, after canopy closure. The data were transformed, and light levels were compared for the two time points using a two-way ANOVA without replication (independent variables; Time of Measurement and Sample Point).

### WKY – Ice storm

Like insect defoliation, ice storms are common recurrent disturbance events in many temperate forests (Irland 2000; Darwin *et al.* 2004; Roberts 2004; Vowels 2012). Ice storms can cause breakage of tree limbs, crowns and even boles, leading to abrupt changes in tree stand and canopy structure (Irland 2000). The duration of an ice storm's influence on the understorey can vary depending upon storm severity. Roberts & Gilliam (2003, 2014) predicted that small canopy gaps created by ice storms would create a light environment that favours shade-tolerant understorey plants, while larger canopy gaps would favour shade-intolerant species. Three western Kentucky, U.S.A. (WKY) study sites containing *P. quinquefolius* populations experienced heavy damage from ice storms in January 2009. A protracted freezing rain event deposited c. 5 cm of ice, leading to loss of tree limbs and whole crowns (Vowels 2012). The pre- and post-disturbance light environments were not quantified for the three WKY study sites at the time surrounding the ice storm event. However, another study assessed damage from the same ice storm in two nearby sites and found that the mean percentage of trees damaged in the canopy, mid-storey and understorey by the ice storm was 10.47%, 16.42% and 17.24% respectively (Vowels 2012; K.M. Vowels, personal communication). Further, the majority of damage caused by the ice storm fell within the severe category as opposed to moderate or light damage, and pole size trees (10 cm < dbh < 25 cm) were more susceptible to ice storm damage than large trees or saplings (Vowels 2012; K.M. Vowels, personal communication).

### EKY – Lightning strike

Severe thunderstorms may produce hail, tornado activity and, more frequently, lightning strikes, any of which can affect tree canopy integrity. Lightning is the most common of these in temperate deciduous forests, and can produce a variety of structural and physiological damages (Taylor 1971). Moreover, climate models predict increases

in the frequency of severe thunderstorms (Trapp *et al.* 2007; Brooks 2013).

In late spring, 2012, lightning killed two dominant trees within a single *P. quinquefolius* population in eastern Kentucky, U.S.A. (EKY), opening the canopy over portions of the population. A LI-COR LI-189 light meter (LI-COR Environmental, Lincoln, NE, USA) was used in summer 2015 to measure PPFD ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) along four transects that extended in each cardinal direction from the centre of the canopy gap. Light measurements were taken at 0, 2, 4, 6, 8, 10 and 12 m intervals from the gap centre. These transects were designed to determine 'affected' areas and 'unaffected' areas in the population, based on the influence of the gap on light. Light levels dropped sharply at 8 m and beyond, thus the individuals that fell within the 8-m radius of the origin were deemed affected by the canopy gap, while unaffected individuals fell outside the same radius.

### Comparison of canopy disturbance effects

This study was by necessity not experimental and therefore was unreplicated and did not control for possible confounding factors. However, the study sites had some environmental characteristics in common, including an overstorey dominated by *Acer saccharum*, and intermediate phosphorus and potassium levels relative to other sites with *P. quinquefolius* (Table 1). Perhaps most importantly, all sites contained long-persistent populations of *P. quinquefolius*, which coincidentally had been censused formally for several years prior to each disturbance. Thus, while replicated forest defoliation experiments might have been ideal, such a large-scale study is impractical, and we were fortunate to have a large, long-term data set on natural populations for comparative purposes.

The three disturbance events (NY, WKY and EKY) were qualitatively different. FTC defoliation at the NY population resulted in a strong, but short-term enhancement of PPFD accompanied by a pulse of nutrient inputs by frass. Photosynthetic photon flux density was c. 25 times greater in the understorey before leaf-out ( $F = 134.73$ ,  $P < 0.0001$ ); a magnitude expected to be similar to the difference in PPFD experienced before and after the defoliation event in 2006. By contrast, ice damage to the tree canopy at WKY represented a spatially variable disturbance with longer lasting effects. Nevertheless, the increase in light following the ice storm event was lower than the increase observed in the NY population during the FTC defoliation event. Lightning damage at EKY represented a strong effect in the

'affected' area of the population, but like the ice storm damage at WKY, the disturbance pattern was somewhat more variable than was observed at the defoliated NY population.

### PANAX QUINQUEFOLIUS CENSUS

*Panax quinquefolius* plants were labelled with an aluminium tag so that each individual could be accurately identified each census year. Census data were collected twice annually; once in the spring to assess emergence and leaf area, and once in the fall to assess reproduction. We collected data on plant emergence, leaf number, length and width of the longest leaflet on each leaf (cm), reproductive status (Reproductive: Y/N) and number of seeds produced.

Individual survival was determined by observing plant emergence. Two criteria were used to establish death of a plant: (i) new seedlings were considered dead if they did not re-emerge the growing season following their initial emergence; (ii) All older plants were considered dead if they did not emerge for two consecutive growing seasons. The 2-year waiting period was necessary because plants whose roots or shoots had been damaged prior to spring census may lie dormant for one growing season and re-emerge the following season.

Leaf area was calculated using a previously established regression equation based on the allometric relationship between total leaf area and length and width of the longest leaflet on each leaf (Souther & McGraw 2011b). Leaf area of all leaves was summed to yield total leaf area of an individual.

### ASYMPTOTIC POPULATION GROWTH RATE

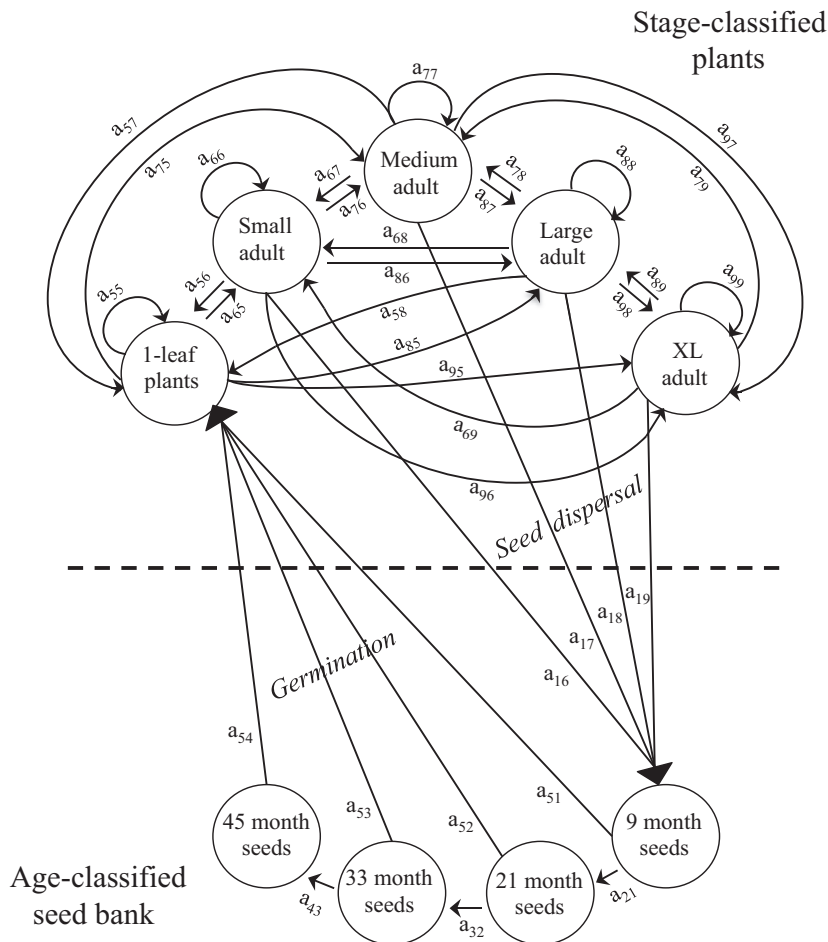
Separate population projection matrices (Caswell 2001) were parameterized for each of the three disturbance types for the nine transition periods from 2004 to 2013. To obtain a sample size sufficient for demographic analyses, the three WKY populations, which were all within 50 km of each other, were pooled.

Data from annual censuses and seed cage experiments were used to parameterize elements of nine-stage transition matrices (Fig. 1) for each population for each transition year ( $t$  to  $t + 1$ ; from 2004 to 2013). The matrices included four seed age classes and five post-germination stage classes. Matrix transition elements ( $a_{ij}$ ) represented the number of class  $i$  individuals derived from class  $j$  individuals over the span of 1 year. Seed classes represented viable seeds present in the soil at the spring census; therefore, they were 9, 21, 33 and

**Table 1.** Characteristics of each site, including dominant overstorey species, soil pH, phosphorus, potassium and calcium levels in the soil (M-moderate, H-high, VH-very high), site elevation and aspect

Site	Overstorey	Soil pH	P	K	Ca	Elevation (m)	Aspect
NY	<i>Acer saccharum</i> <i>Pinus</i> sp.	4.4	M	H	M	469	Flat
WKY <sub>1</sub>	<i>Acer saccharum</i> <i>Diospyros virginiana</i>	6.1	M	H	VH	150	North
WKY <sub>2</sub>	<i>Acer saccharum</i> <i>Fagus grandifolia</i> <i>Liriodendron tulipifera</i>	6.0	M	H	H	121	North
WKY <sub>3</sub>	<i>Acer saccharum</i> <i>Fagus grandifolia</i> <i>Diospyros virginiana</i>	5.8	M	H	VH	152	South
EKY	<i>Acer saccharum</i> <i>Quercus alba</i> <i>Fraxinus</i> sp.	5.1	M	H	VH	304	Northwest





**Fig. 1.** Life cycle stages used for demographic modelling and analysis. The seed bank classes (stages 1–4) were based on seed ages, while the stage-classified portion of the model was based on leaf number for one-leaf plants (stage 5) or leaf area for adults (stages 6–9). Arrows indicate all possible life stage transitions. Stage transition probabilities ( $a_{ij}$ ) represent the number of individuals ( $i$ ) in each stage at the spring census in year  $t + 1$  per individual size ( $j$ ) at the spring census in year  $t$ .

45 months old. To parameterize the seed bank transition probabilities in each matrix ( $a_{21}$ ,  $a_{32}$ ,  $a_{43}$ ), mean seed survival was estimated from mean values obtained from two serial seed cage experiments performed on these populations (McGraw & Furedi 2005; Souther & McGraw 2011b). Because it was impractical to repeat these studies annually, seed survival transitions within the seed bank were assumed to be constant for a given population across years.

Stage 5 in the matrix represented one-leaf plants. The probability of a seed germinating and producing a one-leaf new plant (transitions  $a_{51}$ ,  $a_{52}$ ,  $a_{53}$  and  $a_{54}$ ) was calculated as:

$$a_{5j} = \frac{G_i}{S_j}$$

where  $G_i$  equals the mean number of germinants ( $t + 1$ ) and  $S_j$  equals the mean number of viable seeds at time  $t$ .

Because the photosynthetic capacity and reproductive effort of *P. quinquefolius* depends more on leaf area than age, analyses of *P. quinquefolius* have used stage-based demographic models (Bierzychudek 1982; Charron & Gagnon 1991; Nantel, Gagnon & Nault 1996; Van der Voort & McGraw 2006; McGraw *et al.* 2013). We also used a stage-based matrix to represent post-germination growth of individuals. The first post-germination growth stage included all one-leaf plants (stage 5). The placement of one-leaf individuals into a separate non-adult class is appropriate because, unlike adults, flowering is extremely rare for one-leafed individuals. The partitioning of individuals into adult stages (small – stage 6, medium – stage 7, large – stage 8 and extra-large – stage 9) was determined by dividing adults into four groups of comparable size ( $n$ ) based on the leaf area

of each adult individual. Transition probabilities ( $a_{ij}$ ) within stages 5–9 represented stage stasis ( $a_{ij}$ , where  $i = j$ ), growth to a larger stage ( $a_{ij}$  where  $i > j$ ) or reduction to a smaller stage ( $a_{ij}$  where  $i < j$ ). The seed stratification requirement (over two winters) precluded direct transition from a reproductive individual (stages 6, 7, 8 and 9) to a one-leaf plant (stage 5).

The fertilities of each individual stage 6 through 9 ( $a_{16}$ ,  $a_{17}$ ,  $a_{18}$ ,  $a_{19}$ ) were determined as follows:

$$a_{ij} = v \frac{\sum S_j}{n_j}$$

where  $v$  is a constant (0.9289), representing the proportion of seeds remaining viable from dispersal to the next growing season (9 months; Souther & McGraw 2011b),  $S_j$  is the number of seeds produced in August of year  $t$  by individuals in stage  $j$  ( $j = 6, 7, 8$  and  $9$ ) and  $n_j$  is the total number of individuals in stage  $j$  at the spring census of year  $t$  (Caswell 2001). For each transition period in each disturbance type, the finite rate of population growth ( $\lambda$ ) was calculated as the dominant eigenvalue of the transition matrix (**A**) (Caswell 2001).

To allow comparisons of population growth rate between transition periods, pseudovalues ( $\phi_i$ ) of the finite rate of population increase were determined (McGraw 1989; Vavrek, McGraw & Yang 1996; Chandler *et al.* 2015). The mean pseudo-value of  $\lambda$  ( $\bar{\phi}_i$ ) provides an unbiased estimate of  $\lambda$ , and pseudovalues can be used as replicates for statistical analyses and estimates of standard errors (McGraw 1989; Vavrek, McGraw & Yang 1996; Chandler *et al.* 2015). For each matrix that was assembled, to determine a  $\phi_i$ , each individual  $i$

within the matrix was removed stepwise, and a new  $\lambda$  minus individual  $i$  was determined. Each missing individual's contribution to overall population growth was then calculated as the pseudovalue ( $\phi_i$ ) of population growth rate as follows:

$$\phi_i = n\lambda_{\text{all}} - (n-1)\lambda_{-i}$$

where  $n$  is the total number of individuals,  $\lambda_{-i}$  is the population growth rate when individual ( $i$ ) is removed and  $\lambda_{\text{all}}$  is the population growth rate when all individuals are included (McGraw 1989; Vavrek, McGraw & Yang 1996; Chandler *et al.* 2015). Pseudovalues of  $\lambda$  ( $\phi_i$ ) were then used to compare population growth one transition period prior to the disturbance and one transition period after the disturbance for each disturbance type. Normality was improved by transformation when possible, and nonparametric Welch's ANOVAs were used when normality could not be improved.

#### LIFE TABLE RESPONSE EXPERIMENTS

Life table response experiments (LTREs) are retrospective analyses that evaluate the controls over population growth rate differences (Caswell 2001), an approach that can be particularly powerful when comparing the same population under different conditions. In the present implementation, LTREs were performed to determine the transition parameters ( $a_{ij}$ ) most responsible for the observed differences in population growth rate ( $\lambda$ ) one transition period before and one transition period after the defoliation at the NY population, the ice storm damage at the WKY population and the lightning strike at the EKY population. We wanted to examine whether these qualitatively different canopy disturbances affected demographic transitions in similar ways.

#### STOCHASTIC POPULATION GROWTH RATE

By employing iterative simulations, stochastic demographic models can be used to evaluate how variations in matrix elements caused by environmental change can affect population growth (Morris & Doak 2002; Hunter *et al.* 2010). Stochastic population growth rates ( $\lambda_s$ ) were calculated for each of the populations using both Tuljapurkar's approximation and simulations (Morris & Doak 2002; MathWorks 2015). We first calculated stochastic population growth rate for the NY and EKY populations by executing 50 000 simulations that used only the eight matrices in which the disturbance of interest did not occur (minus disturbance). We used a similar procedure for the WKY population, however; only seven 'undisturbed' matrices were utilized in the WKY simulation. The matrix two transition periods after the disturbance event was excluded from the 'undisturbed' set of matrices to control for the residual effects of the ice storm on the population during that period. For all three populations, each **A** matrix in these simulations had an equal probability of selection. We performed another set of simulations in which the disturbance matrices were included (plus disturbance). The probability of selecting the disturbance matrices was equivalent to the observed disturbance probabilities. We calculated the observed probability of each of the three disturbances occurring in a given place at a given time by dividing the number of occurrences observed by the total population years of data collected at all 30 of our long-term research sites ( $n = 461$ ). The probability of disturbance was then subtracted from the total probability, one, and the remainder was equally divided such that matrix selection was equally probable among the remaining undisturbed matrices.

#### TRANSIENT POPULATION DYNAMICS

Natural disturbances and other stochastic environmental events disrupt the stable state of a population (Hastings 2001; Koons *et al.* 2005; Ezard *et al.* 2010; Tremblay, Raventos & Ackerman 2015). Transient population dynamics can be used to determine how populations vary as a function of these disturbances, in the absence of a stable stage distribution (Hastings 2001; Koons *et al.* 2005; Ezard *et al.* 2010; Tremblay, Raventos & Ackerman 2015). Transient population models were constructed in an effort to determine what, if any, effects these disturbance events had on short-term population dynamics. Previously developed MATLAB code (Box 7.3; Morris & Doak 2002) was used as a basis of stochastic simulations. An average matrix was formed from the undisturbed matrices for each disturbance type, and the initial population state vector was calculated as the right eigenvector of the average matrix. Matrices for the transition period that encompassed the ice storm and the transition period directly following were excluded from the calculation of an average undisturbed matrix at WKY. The exclusion of the second matrix was necessary to control for residual effects of the ice storm on the WKY population. The numbers of individuals in the above-ground stages were relativized to  $N = 100$  and were added to the total seed count to yield initial population size. For each disturbance type, we first projected population size 15 years into the future by running 10 000 simulations using only the matrices in which the disturbance of interest did not occur (- disturbance). Each **A** matrix in these simulations had an equal probability of selection each year. Then, we re-ran the projections with a single 'disturbance matrix' introduced at  $t = 5$ . We chose to introduce the disturbance matrix at  $t = 5$  in order to clearly illustrate how estimates of mean population size changed both multiple years before and multiple years after disturbance, and to clearly depict such patterns. Mean population sizes ( $\pm$ SE) were plotted for the two sets of projections for each of the three disturbance types to visualize the transient effects.

#### DISCRETE STAGE-MODEL VS. INTEGRAL PROJECTION MODEL

We considered formulating the adult components of our population projection model using an integral projection model approach, which has certain advantages over discrete-stage models (Ramula, Rees & Buckley 2009) but for the purposes of this study, we elected to use a model with four seed age classes, one seedling class, and four discrete adult classes for the following reasons: (i) the seedling (one leaf) class has distinct survival and growth patterns as it is in the establishment phase, where rooting depth and microsite determine early success, (ii) the smallest adult class rarely produced seeds, and therefore allocation and growth had distinctive behaviour warranting a separate class from other adults, (iii) in comparing pre- and post-disturbance matrices with an LTRE, we felt the underlying causes of  $\lambda_s$  would be more clearly shown with a smaller set of meaningful size classes, (iv) due to its 'slow' life history and relatively low level of size variation, discrete stages adequately capture the broad patterns of between-year environmental effects and (v) prior demographic work with this species used this approach, and we wanted to make comparisons of our findings concerning natural disturbances with those previous studies of deer browse (McGraw & Furedi 2005), harvest (Van der Voort & McGraw 2006) and climate change (Souther & McGraw 2011a,b, 2014); thus, we did not want to confound methodological differences in making these comparisons.

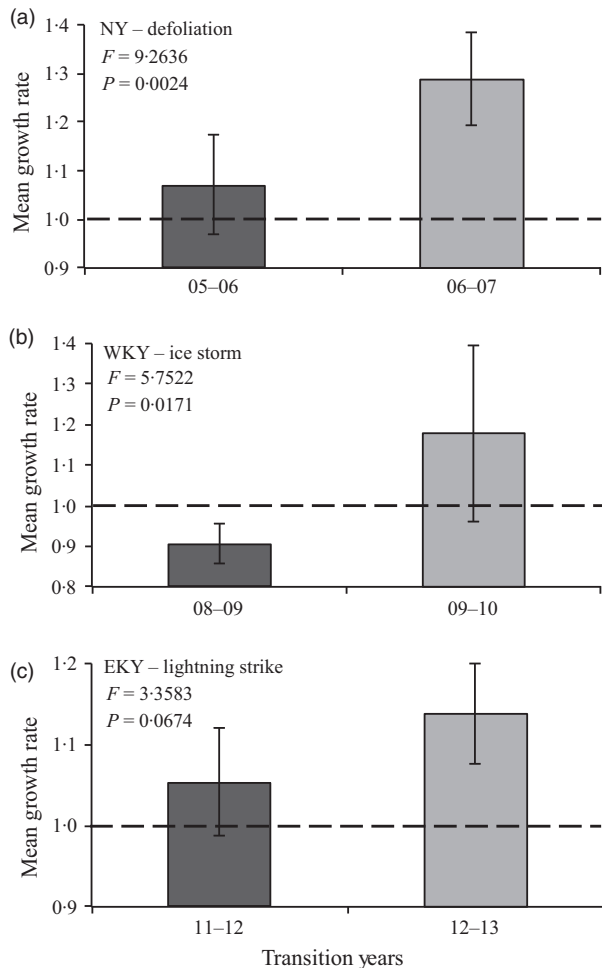
## Results

### ASYMPTOTIC POPULATION GROWTH RATE

#### NY – Forest tent caterpillar defoliation

The results from the FTC defoliation study supported the general pattern of population growth stimulation by canopy gap formation. A one-way ANOVA indicated that growth rate increased by 20.2% 1 year after defoliation relative to 1 year before defoliation (Fig. 2a). Mean population growth rates were  $>1$  in both transition periods, indicating that population sizes were increasing throughout the study period (Fig. 2a).

The LTRE revealed that change in the parameters reflecting greater growth from large to extra large individuals ( $\Delta a_{98} = 0.4152$ ;  $s_{98} = 0.2092$ ) and enhanced reproduction of



**Fig. 2.** Mean population growth rate ( $\bar{\phi}_t$ ) for the transition period not affected by canopy disturbance and for the subsequent transition period affected by canopy disturbance for: the NY population that incurred forest tent caterpillar defoliation (a), the WKY populations whose canopies were damaged by a severe ice storm (b) and the EKY population whose canopy was damaged by a lightning strike (c). The horizontal dashed line represents  $\lambda = 1$ , above which populations are growing and below which populations are decreasing.

extra large individuals ( $\Delta a_{19} = 4.2857$ ) contributed the most to  $\Delta\lambda$ , even though  $\Delta\lambda$  was not particularly sensitive to changes in the matrix element  $a_{19}$  (Table 2a;  $s_{19} = 0.0223$ ). The reduction in stasis of large adults ( $\Delta a_{88} = -0.4086$ ) and small adults ( $\Delta a_{66} = -0.4037$ ) led to a negative  $\Delta\lambda$ , but this was more than compensated for by the enhancement of  $\lambda$  by greater growth (Table 2a). Generally, the probabilities of an individual regressing or remaining static in stage were greater before defoliation. Conversely, the probability of individuals transitioning to larger stages was typically greater following defoliation. Although changes in population growth rate were most sensitive to transitions from one-leaf plants to medium adults ( $s_{75} = 0.4918$ ) and large adults ( $s_{85} = 0.6991$ ), these transitions were not substantial contributors to  $\Delta\lambda$  in the NY population (Table 2a). Transitions from the small adult stage ( $a_{56}$ ,  $a_{66}$ ,  $a_{76}$ ,  $a_{86}$  and  $a_{96}$ ) contributed the most to overall  $\Delta\lambda$  ( $\Sigma \Delta\lambda_{i6} = 0.0547$ ; Table 3a), reinforcing the importance of growth stimulation for enhanced population growth. Although the respective sensitivities were low, greater fertility of all reproductive stages ( $a_{16}$ ,  $a_{17}$ ,  $a_{18}$ ,  $a_{19}$ ) following defoliation did contribute positively to  $\Delta\lambda$ , with increases being the most pronounced in the largest size class.

#### WKY – Ice storm

Consistent with the pattern observed for FTC, a one-way Welch's ANOVA indicated that mean population growth rate ( $\bar{\phi}_t$ ) increased by 30.1% in the transition period following the ice storm relative to the transition period prior (Fig. 2b). While population size was decreasing by 9.4% the transition period prior to the disturbance ( $\lambda = 0.906$ ), population growth was increasing by 17.9% ( $\lambda = 1.179$ ) in the transition period that encompassed the disturbance (Fig. 2b).

Similar to the results obtained from the NY population, changes in matrix elements quantifying stasis and regression in size generally produced a negative  $\Delta\lambda$ , these probabilities were higher before the ice storm than afterwards at WKY populations (Table 2b). This pattern was especially pronounced in the stasis of one-leaf plants ( $\Delta\lambda_{55} = -0.0829$ ;  $s_{55} = 0.2444$ ). An exception was the stasis of extra-large individuals ( $a_{99}$ ), which was higher after the canopy was opened by the ice storm. Growth to a larger stage class was more commonly observed following the ice storm (Table 2b), as indicated by positive  $\Delta\lambda_{ij}$  for those transitions. Growth from large individuals to extra large individuals ( $\Delta a_{98} = 0.5653$ ;  $s_{98} = 0.1293$ ) was much greater following the ice storm ( $\Delta\lambda_{a_{98}} = 0.0731$ ). Changes in population growth rate were most sensitive to transitions from one-leaf plants to medium adults ( $s_{75} = 0.4472$ ), to large adults ( $s_{85} = 0.5690$ ) and to extra large adults ( $s_{95} = 0.7414$ ; Table 2b). Overall, the change in fates of medium-sized adults ( $a_{57}$ ,  $a_{67}$ ,  $a_{77}$ ,  $a_{87}$ ,  $a_{97}$ ) contributed the greatest positive  $\Delta\lambda$  among all stages (Table 3b). Fertility was higher for all reproductive stages ( $a_{17}$ ,  $a_{18}$  and  $a_{19}$ ) following the ice storm, but the enhanced fertility of extra large individuals produced the largest  $\Delta\lambda$  ( $\Delta a_{19} = 2.3323$ ,  $s_{19} = 0.0422$ ,  $\Delta\lambda_{a_{19}} = 0.0985$ ; Table 2b).

**Table 2.** Results of life table response experiments comparing matrices for the two transition periods surrounding a FTC defoliation event at the NY population (a), matrices for the two transition periods surrounding an ice storm at the WKY populations (b) and matrices for the two transition periods surrounding a death of canopy trees due to lightning strike at the EKY population (c). Transitions contributing most to  $\Delta\lambda$  are depicted in bold.

Vital rates ( $a_{ij}$ )	(a) NY – FTC defoliation			(b) WKY – Ice storm			(c) EKY – Lightning strike		
	Post-disturbance – Pre-disturbance			Post-disturbance – Pre-disturbance			Post-disturbance – Pre-disturbance		
	$\Delta a_{ij}$	$s_{ij}$	$\Delta\lambda$	$\Delta a_{ij}$	$s_{ij}$	$\Delta\lambda$	$\Delta a_{ij}$	$s_{ij}$	$\Delta\lambda$
$a_{55}$	-0.2074	0.1691	-0.0351	<b>-0.3393</b>	<b>0.2444</b>	<b>-0.0829</b>	-0.0938	0.1691	-0.0159
$a_{65}$	0.1146	0.3482	0.0399	-0.0223	0.3034	-0.0068	<b>0.1443</b>	<b>0.4375</b>	<b>0.0632</b>
$a_{75}$	0.0437	0.4918	0.0215	<b>0.1306</b>	<b>0.4472</b>	<b>0.0584</b>	-0.0015	0.7463	-0.0011
$a_{85}$	0	0.6991	0	0.0707	0.5690	0.0402	0	0.9074	0
$a_{95}$	0	0	0	0.0202	0.7414	0.0150	0	1.1916	0
$a_{16}$	0.1661	0.0269	0.0045	0	0	0	0.0399	0.0304	0.0012
$a_{56}$	0.0111	0.0641	0.0007	-0.2251	0.0642	-0.0144	-0.0879	0.0604	-0.0053
$a_{66}$	<b>-0.4037</b>	<b>0.1319</b>	<b>-0.0533</b>	-0.2900	0.0796	-0.0231	-0.0364	0.1563	-0.0057
$a_{76}$	0.0824	0.1863	0.0153	0.0779	0.1174	0.0091	0.0505	0.2667	0.0135
$a_{86}$	<b>0.2477</b>	<b>0.2648</b>	<b>0.0656</b>	0.2121	0.1494	0.0317	0.0343	0.3242	0.0111
$a_{96}$	0.0723	0.3640	0.0263	0.1515	0.1946	0.0295	0.0152	0.4258	0.0065
$a_{17}$	0.0884	0.0125	0.0011	0.1451	0.0534	0.0077	0.3262	0.0158	0.0052
$a_{57}$	0	0	0	-0.0862	0.0937	-0.0081	0	0.0314	0
$a_{67}$	-0.1551	0.0615	-0.0095	-0.1758	0.1163	-0.0204	0.1084	0.0813	0.0088
$a_{77}$	-0.1359	0.0869	-0.0118	-0.2603	0.1714	-0.0446	-0.1694	0.1387	-0.0235
$a_{87}$	0.0436	0.1235	0.0054	0.0289	0.2182	0.0063	-0.0129	0.1686	-0.0022
$a_{97}$	0.2487	0.1698	0.0422	0.4344	0.2842	0.1235	0.1097	0.2214	0.0243
$a_{18}$	1.5839	0.0154	0.0245	0.0900	0.0243	0.0022	0.5986	0.0154	0.0092
$a_{58}$	0	0.0368	0	0.0213	0.0426	0.0009	0	0.0306	0
$a_{68}$	-0.0161	0.0758	-0.0012	-0.1167	0.0529	-0.0062	0.0426	0.0792	0.0034
$a_{78}$	-0.0292	0.1071	-0.0031	-0.3936	0.0780	-0.0307	-0.0687	0.1351	-0.0093
$a_{88}$	<b>-0.4086</b>	<b>0.1522</b>	<b>-0.0622</b>	-0.0671	0.0993	-0.0067	-0.0491	0.1643	-0.0081
$a_{98}$	<b>0.4152</b>	<b>0.2092</b>	<b>0.0869</b>	<b>0.5653</b>	<b>0.1293</b>	<b>0.0731</b>	0.1566	0.2158	0.0338
$a_{19}$	<b>4.2857</b>	<b>0.0223</b>	<b>0.0957</b>	<b>2.3323</b>	<b>0.0422</b>	<b>0.0985</b>	-1.1644	0.0189	-0.0220
$a_{69}$	0.0208	0.1097	0.0023	-0.0952	0.0920	-0.0088	-0.0142	0.0972	-0.0014
$a_{79}$	-0.0217	0.1550	-0.0034	-0.2857	0.1356	-0.0387	0	0.1657	0
$a_{89}$	-0.0670	0.2203	-0.0148	0.0571	0.1725	0.0099	-0.0425	0.2015	-0.0086
$a_{99}$	0.0272	0.3028	0.0082	<b>0.3143</b>	<b>0.2248</b>	<b>0.0706</b>	0.0182	0.2646	0.0048

**Table 3.** Sum of the change in lambda for each vital rate one transition year before and after insect defoliation at the NY population (a), ice storm at the WKY populations (b) and tree death due to lightning strike at the EKY population (c). Each represents a sum of transitions from a single stage to any of four other stages ( $a_{i5}$ ,  $a_{i6}$ ,  $a_{i7}$ ,  $a_{i8}$ ,  $a_{i9}$ )

Vital rates ( $a_{ij}$ )	Post-disturbance – Pre-disturbance		
	$\sum \Delta\lambda_{\text{growth transitions}}$		
	(a) NY – FTC defoliation	(b) WKY – Ice storm	(c) EKY – Lightning strike
$a_{i5}$	0.0264	0.0239	0.0462
$a_{i6}$	0.0547	0.0328	0.0201
$a_{i7}$	0.0263	0.0566	0.0074
$a_{i8}$	0.0203	0.0305	0.0198
$a_{i9}$	-0.0076	0.0330	-0.0051

### EKY – Lightning strike

Population size was increasing ( $\lambda > 1$ ) in transition periods both before and after the lightning strike at the EKY population (Fig. 2c). However, a one-way Welch's ANOVA

revealed a trend which suggested that population growth rate was higher the transition period following the lightning strike than the transition period prior, resulting in a relative increase of 7.9% (Fig. 2c). While this increase was smaller than the previous two disturbance types, the pattern was the same.

The LTRE revealed that growth of one-leaf plants to small adults was greater following the lightning strike ( $\Delta a_{65} = 0.1443$ ) and that  $\lambda$  was sensitive to changes in that matrix element ( $s_{65} = 0.4375$ ), resulting in the largest  $\Delta\lambda$  among all transitions ( $\Delta\lambda_{a_{65}} = 0.0632$ ; Table 2c). Further, the sum of transitions from the one-leaf plant stage ( $a_{55}$ ,  $a_{65}$  and  $a_{75}$ ) contributed the most to overall  $\Delta\lambda$  ( $\sum \Delta\lambda_{i5} = 0.0462$ ; Table 3c). Fertility was generally higher for reproductive stages ( $a_{16}$ ,  $a_{17}$  and  $a_{18}$ ) following the lightning strike (Table 2c). However, the fertility of the extra large individuals ( $a_{19}$ ) was slightly lower following the lightning strike (Table 2c), a result that contradicts those of the other disturbed populations.

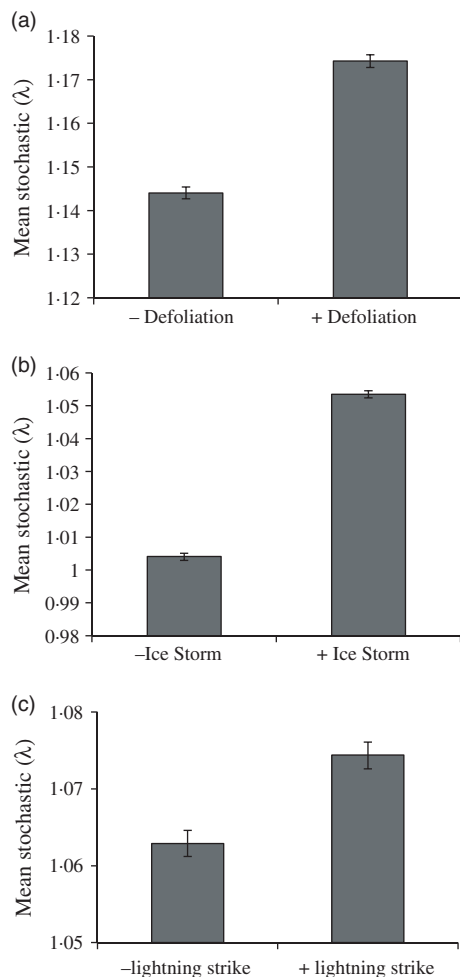
In the lowest severity canopy disturbance, lightning strike, the sum of transitions from the smallest stage class was most important in the  $\Delta\lambda$  (Table 3c). Conversely, as the severity of canopy disturbance increases, the sum of transitions from



increasingly larger stage classes had the greatest influence on the  $\Delta\lambda$  (Table 3a,b).

### Stochastic population growth rate

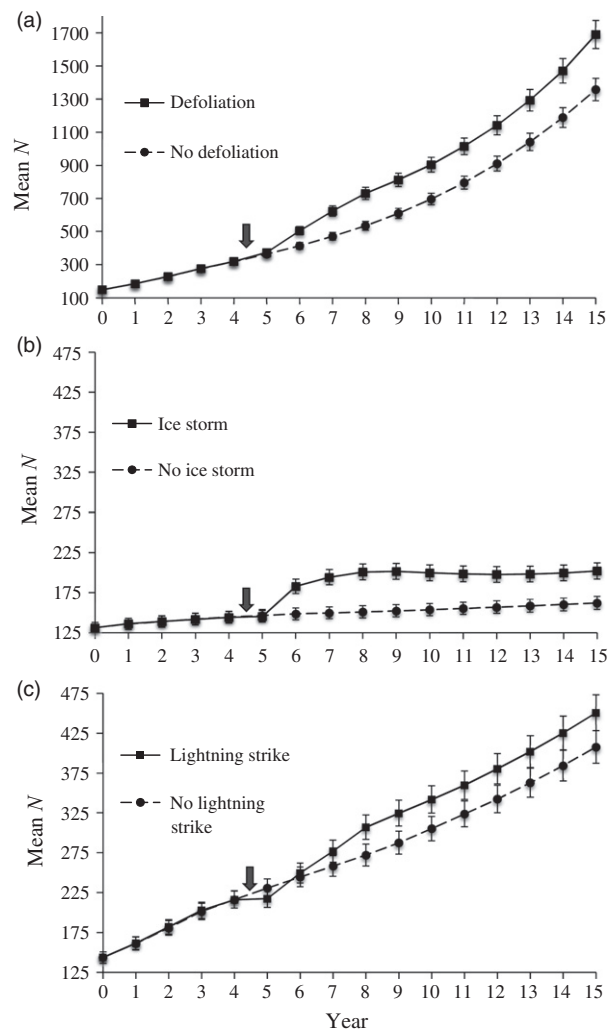
Stochastic population growth rates ( $\lambda_s$ ) increased significantly, albeit slightly, in all populations when the disturbance matrices were included (Fig. 3a–c). These data imply that these canopy disturbances are capable of increasing population growth even at their current rates of occurrence. The inclusion of the defoliation disturbance matrix increased  $\lambda_s$  by 2.6% at the NY population relative to the model that did not include the disturbance matrix (Fig. 3a). Stochastic population growth rate increased by 2.2% at the WKY population when the ice storm was included in the model compared to when the disturbance was excluded (Fig. 3b). Stochastic population growth rate increased by 1.1% at the EKY population when the lightning strike disturbance matrix was included in the model relative to when the disturbance matrix was excluded (Fig. 3c). The latter was the smallest increase in  $\lambda_s$  observed among all populations and disturbance types.



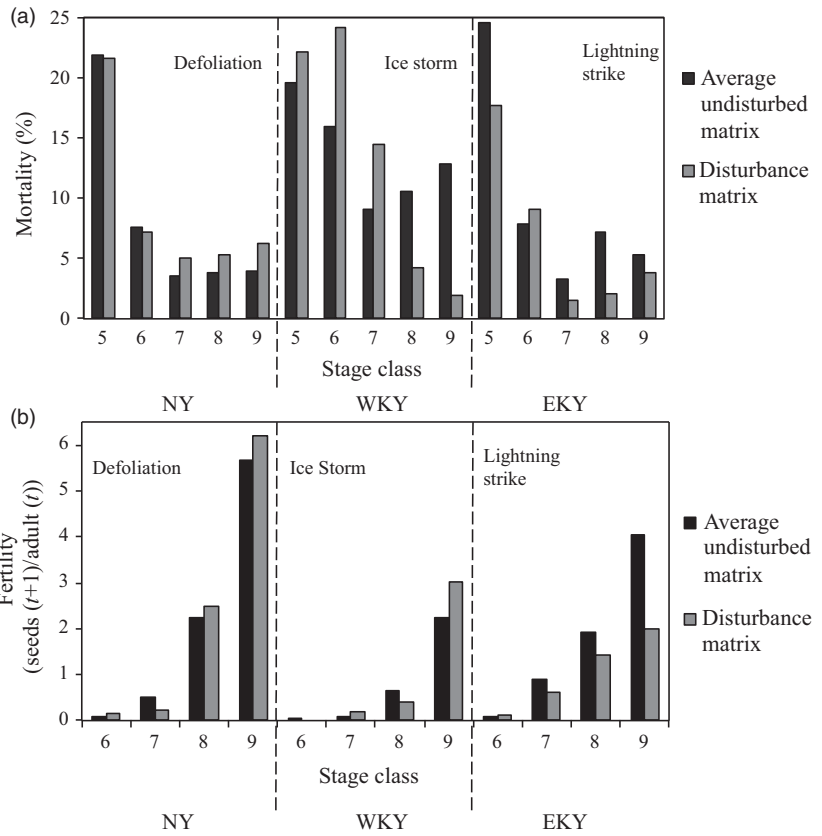
**Fig. 3.** Mean stochastic population growth rates ( $\pm 95\%$  CI) for: the NY population that incurred forest tent caterpillar defoliation (a), the WKY populations whose canopies were damaged by a severe ice storm (b) and the EKY population whose canopy was damaged by a lightning strike (c).

### Transient population dynamics

No differences in population size were observed between models with and without disturbance at year 5, which is the state of the population after multiplication by each respective disturbance matrix (Fig. 4a–c). However, the simulations including a disturbance matrix exhibited a significant increase in population size in year 6 (Fig. 4a–c). Contrasts in mortality and fertility were observed among the three populations that help to explain the lack of immediate year 5 numerical response (Fig. 5a,b). Fertility was higher in the NY and WKY disturbance matrix compared to the average undisturbed matrix, however, this increased fertility was offset by higher mortality (Fig. 5a,b). The opposite was observed in the



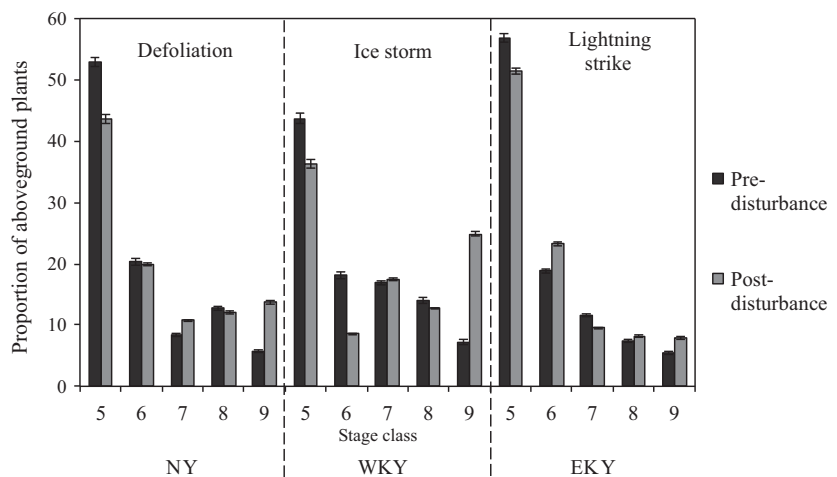
**Fig. 4.** Mean population size projected over 15 years using transient population dynamic simulations for the NY population that incurred forest tent caterpillar defoliation (a), the WKY populations that incurred canopy damage from an ice storm (b) and the EKY population that incurred canopy damage from a lightning strike (c). For each of the three disturbance types, 10 000 runs were performed with the disturbance matrices included in the model and 10 000 runs were performed with the disturbance matrices excluded. Vertical arrows represent the insertion of the post-disturbance matrix reflecting the canopy opening.



**Fig. 5.** Percent mortality for the average undisturbed matrix and for the matrix representing the disturbance period (a) and fertility for the average undisturbed matrix and for the matrix representing the disturbance period (b) for each of the three populations (NY, WKY and EKY). All above-ground stage classes (5, 6, 7, 8 and 9) are depicted in the figure that quantifies mortality (a), while only reproductive above-ground stage classes (6, 7, 8 and 9) are depicted in the figure that quantifies fertility (b).

EKY population where both mortality and fertility were lower in the disturbed matrix than in the average undisturbed matrix (Fig. 5a,b). Nevertheless, there was a consistent shift in stage class distribution from the pre-disturbance period (year 4) to the post-disturbance period (year 5) among all populations (Fig. 6). There was a decrease in the proportion of individuals that comprised the smallest above-ground stage (stage 5) between the pre-disturbance period (year 4) and post-disturbance period (year 5), coupled with an increase in the proportion of individuals that comprised the largest above-ground stage (stage 9) in the same period (Fig. 6). The observed shift to larger adults in the post-disturbance year led to stimulations

in seed production between years 5 and 6, thus explaining the rapid increases in population sizes observed in that interval. Population size increased at a relatively stable rate in the simulations that did not include a disturbance matrix (Fig. 4a–c). Further, while the size of the disturbed populations remained larger than their undisturbed counterparts following the disturbance year (year 6 and beyond), the rate of growth eventually returned to the same stable rate as observed in the undisturbed simulations (Fig. 4a–c). To compare relative stimulation of population size and growth in the three disturbance scenarios, we note that 3 years after disturbance, the mean population size of the simulations that incorporated a



**Fig. 6.** Proportion of plants in each of the five above-ground stages (5, 6, 7, 8 and 9) for the pre-disturbance period (Year 4) and the post-disturbance period (Year 5) for each of the three populations (NY, WKY and EKY).

defoliation event was 195 individuals larger (26.7%) compared with scenarios that did not incorporate the disturbance (Fig. 4a). Similarly, when compared with simulations that lacked each disturbance event, mean population size was 50 individuals larger (24.9%) in the populations affected by an ice storm (Fig. 4b), and 35 individuals larger (11.3%) in the population whose canopy was partially disturbed by a lightning strike (Fig. 4c). These results indicate that canopy disturbances can alter population dynamics in the short term and lead to increases in the overall population size that are sustained in a relatively undisturbed environment.

## Discussion

The post-disturbance patterns observed in all three populations support a general pattern of light-gap stimulated population growth, whether examining asymptotic or stochastic population growth rates. Further, transient population models revealed that after 15 years, population size was substantially higher in models that included one disturbance matrix compared to those that were comprised solely of undisturbed matrices, an increase that is caused by shifts in stage distribution to larger stage classes that are capable of producing more seeds. These results provide support for the idea that shade-tolerant herbs may be pre-adapted to take advantage of moderate canopy gap formation. These life-history responses may reflect long-term selection under dynamic canopies typical of old growth forests.

The transitions from larger stage classes had the greatest influence on  $\Delta\lambda$  at the two populations (NY and WKY) that incurred the most severe canopy disturbance. Larger plants appeared better able to withstand the stress caused by canopy disturbance than smaller plants. The brief but intense FTC defoliation event at the NY population elicited a strong growth response, likely due to a combination of increases in light resources and redistribution of nutrients from canopy leaves to the understorey in the form of frass deposition (Hunter 2001; Frost & Hunter 2004). In the year following defoliation, a few four-leaf plants transitioned to the unusually large five-leaf stage (<1 in 10 000 plants attain this size; J.B. McGraw, unpublished data). Additionally, the more open canopy caused by significant breakage of tree limbs and trunks from ice load at the WKY populations led to increased individual plant growth and consequently increased population growth rates.

While population growth rate was stimulated by the ice storm at WKY, leaves of plants that remained were noticeably thickened and showed signs of photooxidation (J.L. Chandler and J.B. McGraw, personal observations). Additionally, although fertility of surviving individuals increased directly following the ice storm, many of the berries that were produced desiccated prior to dispersal (J.L. Chandler and J.B. McGraw, personal observation), limiting both seed viability and the potential for long-distance dispersal via frugivorous birds (Hruska, Souther & McGraw 2014; Elza, Slover & McGraw 2015). Further, the above-ground portion of the plants at the WKY populations began senescing earlier in the fall than plants

in many other routinely censused populations that were not included in this study (J.L. Chandler and J.B. McGraw, personal observation), a pattern also observed in *Panax ginseng* grown under high irradiance (Parmenter & Littlejohn 2000). Nevertheless, the potential increases in photosynthesis and carbon storage for plants subjected to higher light levels appears to have more than compensated for the earlier senescence (Parmenter & Littlejohn 2000) and other signs of physiological stress.

While population growth rate did increase in response to a lightning strike, the increase was not as pronounced as in the other types of disturbance. One explanation for the smaller response is that only a small portion of the population was directly affected by the canopy gap, while the remainder experienced an undisturbed forest overstorey. Nevertheless, the growth stimulation of even a small portion of the population led to overall increases in population growth, indicating that even modest changes in light availability can result in significant, population growth stimulation.

Simulations in this study were performed under the assumption that each respective disturbance had only short-term effects on *P. quinquefolius*. However, in reality, the effects of all three disturbances could have persisted beyond one growing season in the form of residual soil nutrients from frass deposition and downed woody debris, and in the form of canopy openness that was sustained for longer than one transition period. As such, these results are conservative and may underestimate the stimulation of population growth following intermediate canopy disturbances.

Each of the three disturbance types discussed in this study are qualitatively different in terms of the mode of defoliation and the availability and duration of light in the understorey. Nevertheless, in each case we observed enhanced population growth, indicating that populations of *P. quinquefolius* can benefit from any of these types of intermediate-intensity canopy disturbances. However, the same pattern of increased population growth may not exist in populations exposed to far more intense canopy disturbances. The timber at a separate monitored long-term *P. quinquefolius* population was harvested in 2011 using a high-grade selection harvest, resulting in significant canopy loss (J.B. McGraw, unpublished data). Similar to the assertions of Roberts & Gilliam (2014), the large canopy gaps caused by the high-intensity timber harvest favoured the shade-intolerant, early successional species that eventually dominated the site (J.L. Chandler and J.B. McGraw, personal observations). Demographic analyses were not performed for this population, however, of those *P. quinquefolius* plants present in the population the growing season before the timber harvest, only 50% survived the five growing seasons after the harvest occurred (J.B. McGraw, unpublished data). Based on the observed increase in population growth following the three intermediate canopy disturbances in this study, and based on field observations that suggest populations are negatively affected by high-intensity canopy disturbances, we hypothesize that *P. quinquefolius* performance may be viewed as a parabolic function where performance is optimized at intermediate

levels of canopy disturbance. Of course, additional research quantifying population response to the highest spectrum of canopy openness is needed to support this hypothesis. Nevertheless, this hypothesis would suggest that, although *P. quinquefolius* and understory species like it are adapted to a low understory light environment, this guild is able to exploit moderate increases in light availability, and population performance increases as a result.

Different types of disturbances affect forests in different ways and to different degrees. Nevertheless, some of the most common types of forest canopy disturbances are linked to climate, and predictions indicate that changes in forest disturbance regimes will be exacerbated by future climate shifts (Ryan *et al.* 2008; Babst *et al.* 2014). In addition to insect defoliation, ice storms and lightning strikes, other climate-mediated disturbances that have the potential to alter the growth rates of understory plants include frost damage caused by emergence of plants prior to the passing of frost risk (Cannell & Smith 1986; Linkosalo *et al.* 2000; Jönsson *et al.* 2004; Souther & McGraw 2011a), wildfire (Babst *et al.* 2014), drought, herbivory (Parmesan 2006) and pests and disease (Parmesan 2006).

*Panax quinquefolius* is a long-lived obligate understory herb that exhibits the same slow life history as many other obligate understory species (McGraw *et al.* 2013). By using *P. quinquefolius* as a model species, we are able to better understand potential population-level responses of similar understory plants to disturbances. Our results suggest that this shade-adapted herb is able to utilize and benefit from the additional light produced by canopy disturbance. While this study was observational in nature, the inferences we offer were based on consistent, shared patterns of response. We conclude that moderate canopy disturbances could provide herb populations a temporary stimulus in population growth, resulting in larger population size and for rare to uncommon species, greater insulation from effects demographic stochasticity.

## Authors' contributions

J.C. and J.M. conceived the ideas and designed the methodology, J.M. and J.C. collected and analysed the data, and J.C. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Data accessibility

Data deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.562bg> (Chandler & McGraw 2016). *Panax quinquefolius* data for

scientists and the general public, along with description of annual *P. quinquefolius* census are available at: <http://www.wildginsengconservation.com>.

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