

# Roads increase population growth rates of a native leaf-cutter ant in Neotropical savannahs

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## Summary

1. A challenge in applied ecology is understanding the responses of native species to roads, which are ubiquitous drivers of environmental heterogeneity. While most studies highlight their negative effects, the potential for native species to increase in abundance near roads has been underappreciated, and the demographic mechanisms underlying abundance changes remain unclear. Elucidating these mechanisms requires first determining how demographic vital rates and life-history stages interact to influence population growth. One can then assess how roads alter the relative importance of the alternative demographic pathways – increased performance of early vs. late life stages – suggested as the principal drivers of increased population growth.

2. We parameterized demographic models with 3 years of census data and conducted perturbation analyses to evaluate how proximity to roads altered abundance and demography. To do so, we used the leaf-cutter ant *Atta laevigata* as our model organism. Leaf-cutters are native ecosystem engineers and dominant herbivores in Neotropical ecosystems and also amongst the longest lived insects in nature. Our study was conducted in Cerrado savannahs, where road networks are rapidly expanding and *Atta* species are major agricultural pests.

3. We found that 35–45% of adult colonies were located within 15 m of roads, which is significantly closer than expected at random. Population growth rates ( $\lambda$ ) were  $>1$  both near and far from roads, but  $\lambda$  near roads were significantly (41%) higher. Elasticities of  $\lambda$  to early survival and growth rates were proportionally much higher than those of adult stages, irrespective of habitat. Life-table response experiment results indicate that the higher  $\lambda$  near roads was due primarily to the much higher colonization and early-life performance there.

4. *Synthesis and applications.* Road networks are proliferating throughout biodiversity-rich regions. Developing conservation and management guidelines for species whose abundance is altered by roads requires understanding the demographic mechanisms that underpin these changes. We demonstrate that the higher growth rate of roadside *Atta laevigata* populations is due to increased early-life performance. Thus, the expansion of road networks could have major ecological and economic consequences by facilitating the increased abundance of ecosystem engineers and agricultural pests. Accounting for *A. laevigata* early life stages and careful planning of road placement should improve management strategies of protected areas and agricultural systems in Neotropical savannahs.

**Key-words:** *Atta laevigata* ants, anthropogenic disturbances, Brazilian Cerrado, demography, elasticities, life-table response experiments, long-lived organisms, population dynamics, roads, superorganisms

## Introduction

Roads are increasingly prevalent drivers of environmental heterogeneity in many landscapes (Trombulak & Frissell 2000; Laurance, Goosem & Laurance 2009), and globally

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at least 25 million km of new roads are expected by 2050 (Laurance *et al.* 2014). They can fragment populations, elevate risk of individual mortality and alter behaviour related to dispersal and reproduction (Trombulak & Frissell 2000; Vasconcelos *et al.* 2006; Shepard *et al.* 2008; Laurance, Goosem & Laurance 2009). This has led many to conclude that roads will have detrimental impacts on the population dynamics of most species (Trombulak & Frissell 2000; Laurance, Goosem & Laurance 2009), and indeed, declines or extinctions of species such as large mammals and birds have been documented in their vicinity (Oliveira, Alberts & Francisco 2011). However, the potential for roads to benefit some native species (e.g. Rytwinski & Fahrig 2007) because of either 'bottom-up' (e.g. increases in food availability, altered microclimate) or top-down changes (e.g. low predator abundance) (Rytwinski & Fahrig 2013) has been largely overlooked in the ecological literature.

Documenting changes in abundance is the essential first step in testing the hypothesized impacts – positive or negative – of roads on species. However, identifying any conservation or management actions that must be taken in response to these changes requires quantifying how disturbances modify the population growth rate (i.e.  $\lambda$ ) and the vital rates that shape it (Heppell, Crouse & Crowder 2000; Bruna, Fiske & Trager 2009; Crone *et al.* 2011). Although studies quantifying how abundance changes with proximity to roads are becoming more common (e.g. Rytwinski & Fahrig 2012), almost nothing is known about the particular demographic mechanisms underlying the observed changes in abundance. This is because few studies evaluating the population-level impacts of roads have done so with a comprehensive demographic approach that evaluates and integrates the effects of these disturbances across a range of life-history stages. Demographic studies have typically found that adult survivorship and growth have the largest influence on  $\lambda$  (Ramula *et al.* 2008; Burns *et al.* 2010), including in human-modified systems such as fragmented landscapes (reviewed in Bruna, Fiske & Trager 2009). However, recent work has found that vital rates related to reproduction and recruitment can have demographic impacts comparable in magnitude to those of 'adult' stages (Maclean *et al.* 2011; Caughlin *et al.* 2014). Elucidating why abundance changes near roads therefore requires quantifying the relative influence of different demographic pathways and life-history stages.

Insects figure prominently in studies of population dynamics (Wallner 1987; Yamamura *et al.* 2006) and are important bioindicators of disturbance (Cole 2009). However, while road-driven changes in insect abundance could potentially have large effects on ecosystems – in many systems, they are the primary herbivores, pollinators, predators or seed dispersers – their size and often cryptic biology make them challenging to use as model organisms for demographic research. Notable exceptions are ants and other eusocial insects, for which a colony can be

considered a long-lived 'superorganism' that survives, grows and reproduces over multiple years and hence is functionally equivalent to the individual in a population (Hölldobler & Wilson 1990).

We used a species of leaf-cutter ant – *Atta laevigata* (F. Smith) – as a model system with which to evaluate mechanisms by which roads influence the abundance and population growth rates of long-lived organisms. This and other *Atta* species are keystone species and ecosystem engineers throughout the Neotropics (Hölldobler & Wilson 1990; Keller 1998). They are the dominant herbivores both numerically and in terms of biomass consumption (Costa *et al.* 2008; Leal, Wirth & Tabarelli 2014), exert strong effects on population-, community-, and ecosystem-level processes (Terborgh *et al.* 2001; Farji-Brener & Ghermandi 2008; Mundim *et al.* 2012) and are arguably the region's most important agricultural pest (Hölldobler & Wilson 1990). They also have a number of traits that make them ideal superorganisms with which to conduct demographic studies. First, individual demographic units (i.e. colonies) are readily identified and surveyed in the field, even if they have interdigitating foraging trails (Costa *et al.* 2008). Secondly, their colonies are founded and maintained by a single queen (i.e. they are monogynic), meaning one can track the demographic history of individual 'propagules' from foundation forward. Thirdly, ecologically relevant proxies for colony size and life-history stage are straightforward to define and measure (Costa *et al.* 2008; see Appendix S1 in Supporting Information), which simplifies the construction of demographic models. Finally, colonies can persist for 10–20 years, which surpasses the life span of ~85% of ant species included in a recent review (Keller 1998) and many vertebrate taxa.

Surveys have found *Atta* colonies are more common in successional habitats (Vasconcelos & Cherrett 1995; Meyer, Leal & Wirth 2009; Dohm *et al.* 2011) such as those near roads, but these surveys were either one-time 'snapshots' of abundance (Dohm *et al.* 2011) or counted only large colonies (Meyer, Leal & Wirth 2009). It is therefore unclear whether the observed differences in abundance were a transient phenomenon (Meyer, Leal & Wirth 2009) or whether they are driven by how disturbance influences *Atta* demography. For example, queens preferentially attempt to establish colonies on dirt roads, which despite increased rates of predation ultimately translates into higher abundance of incipient colonies there (Vasconcelos *et al.* 2006; Vieira-Neto & Vasconcelos 2010). Alternatively, the greater abundance of larger, reproductive colonies in disturbed areas could be because they have higher rates of survivorship and growth there. Road verges have more of the pioneer plants (Vasconcelos, Araújo & Bruna 2014) typically preferred as substrates by established colonies for growing their fungal food source (Vieira-Neto & Vasconcelos 2010); there may also be fewer predators of large colonies (e.g. armadillos, army ants) near roads due to roadkill or behavioural avoidance (Rao 2000; Shepard *et al.* 2008).

Here, we use demographic models parameterized with 3 years of census data to evaluate the relative importance of two pathways – increased juvenile recruitment vs. elevated adult survivorship and growth – hypothesized to alter the demography of leaf-cutter ants along roadsides. To do so we addressed the following questions:

1. Does leaf-cutter ant density increase or decrease with increased proximity to roads?
2. Is the population growth rate ( $\lambda$ ) higher near roads than away from them?
3. Are these differences the result of changes in the survivorship and growth of large colonies or the recruitment and establishment of new ones?

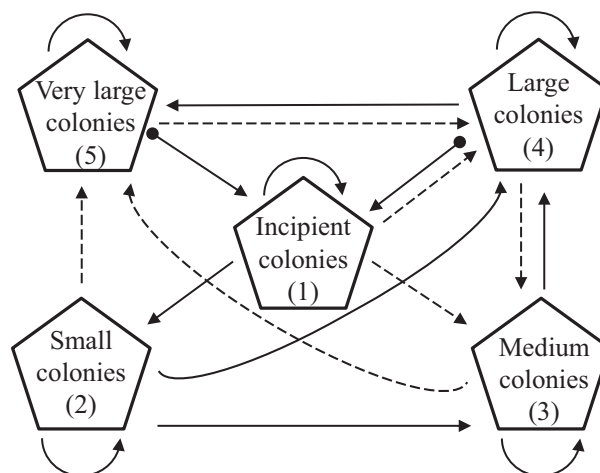
We show that roadsides favour early stages of colony life history, resulting in greater colony abundances and population growth rates. Our results suggest that some native species can benefit demographically from disturbances such as those created by road construction. Furthermore, our results suggest that for long-lived organisms, the early stages of life history can often have demographic impacts comparable to later ones.

## Materials and methods

### STUDY SPECIES AND LIFE CYCLE

Leaf-cutter ants (*Atta* spp.) are widely recognized as dominant herbivores in Neotropical rain forests, but they are 3–6 times more abundant and consume relatively more primary productivity in the Cerrado savannahs (Costa *et al.* 2008). These ants are functional herbivores, harvesting fresh plant tissue to cultivate symbiotic fungus gardens that are its main food source (Hölldobler & Wilson 1990). While some *Atta* species are region-specific, others (e.g. *A. laevigata*, *A. sexdens*) are widely distributed throughout South American forests and savannahs (e.g. Costa & Vieira-Neto 2015).

The life cycle of a colony is similar across *Atta* species (Hölldobler & Wilson 1990; Fig. 1) and begins with thousands of male and female alates leaving their natal nests for a nuptial flight, during which they mate several kilometres above-ground. After mating, females land and actively search for sites to found their nests. Mortality during this stage is extremely high for *Atta* (Vasconcelos *et al.* 2006; Vieira-Neto & Vasconcelos 2010). Colonization in *Atta* species is haplometrotic – new colonies are founded after a single-mated female (Fig. S1a) digs a nest up to 15 cm deep and seals its entrance with soil removed during excavation. Excavation occurs at clear sites; recolonization of previous nests was never observed. The colony then enters the claustral phase, during which the nest entrance remains sealed (Fig. S1b), while the queen raises its first brood and grows a new fungal culture using nutrients derived from her wing muscles and fat reserves. The claustral phase lasts for approximately 3 months and ends when the first workers emerge and start foraging. Colonies in this transition are classified as incipient (stage 1) and can be identified by small pellets of soil deposited by ants around the nest entrance that form a circular mound ca. 2–5 cm in diameter (Fig. S1c). A larger and deeper (ca. 1 m deep) second chamber is only built when the new but still small colony (stage 2) is approximately 1 year old (Fig. S1d). Its construction is followed by a rapid and noticeable increase in nest mound size due to the deposition of



**Fig. 1.** The life cycle graph of *Atta laevigata* leaf-cutter ants. Arrows indicate potential transitions between stages, including regression, persistence, growth and contributions to colonization from reproductive colonies (arrows with closed circles; stages 4 and 5). Dashed lines indicate rarely observed transitions.

excavated soil. It is therefore possible to distinguish colonies that are less than 1 year old (stage 1) from those that are older (stage 2) based on nest mound sizes and characteristics, although on very rare occasions regression from stage 2 to 1 can occur. Following these stages, colony growth accelerates as more workers become available for foraging. After 24 months, the colony usually opens more entrances and the mound grows in a non-circular fashion as the first few major workers emerge. These colonies now begin to leave obvious foraging trails, defining a ‘medium-sized’ colony (stage 3, Fig. S1e). Finally, adult colonies have nest mounds  $>2$  m<sup>2</sup>, producing reproductive individuals and large numbers of major workers (cf. Vasconcelos & Cherrett 1995). They are divided into large (2–15 m<sup>2</sup> in area, stage 4) and very large ( $>15$  m<sup>2</sup>, stage 5) nests (Fig. S1f) based on survival probabilities and reproductive output (cf. Morris & Doak 2002).

### STUDY REGION AND SITE

The Brazilian savannah known as the Cerrado is the second largest biome in South America, comprising an area of approximately 2 million km<sup>2</sup> (Klink & Moreira 2002). This biodiversity hot spot is a mosaic of vegetation types ranging from open grasslands to forests and is characterized by a marked seasonality, with a May–September dry season and an October–April wet season. Over the past 50 years, this biome has been dramatically altered by agriculture and other forms of human occupation, resulting in a rapidly expanding network of paved and unpaved roads (Klink & Moreira 2002; Vasconcelos, Araújo & Bruna 2014).

We conducted our study at the Panga Ecological Station (19°10'S 48°23'W), a 404-ha reserve located 30 km south of Uberlândia, Minas Gerais, Brazil (Vasconcelos *et al.* 2006). The dominant leaf-cutter ant in the reserve and the focus of our study is *Atta laevigata*, although there are also occasional colonies of *Atta sexdens* (Costa *et al.* 2008). Medium and adult colonies of these species are easily distinguishable in the field, and younger colonies can also be differentiated based on worker morphology. Our demographic surveys were conducted in a 19-ha area of the reserve dominated by woodland savannah and

surrounded by 2.1 km of dirt roads. These roads are 4-m wide and at least 30 years old (Vieira-Neto & Vasconcelos 2010); the roads continued to be maintained following the establishment of the reserve in 1985 but traffic is now limited to researchers and their vehicles. While *A. laevigata* queens establish nests on roadside verges, they do not nest in the roads themselves (Vasconcelos *et al.* 2006).

#### DEMOGRAPHIC SURVEYS AND MODELS

In June–August 2005, we identified all adult colonies (>2 m<sup>2</sup>) in our 19-ha area. We then established 10 demographic plots of 30 × 30 m – five traversed by a road and five ≥150 m from any road – in which we identified all colonies of prior life-history stages (<2 m<sup>2</sup>). We permanently marked and mapped each mound and estimated mound area using the formula for an ellipse (Costa *et al.* 2008). We repeated censuses annually for two additional years, when we searched for any new nests while also monitoring the status of previously marked colonies. We considered nests dead if there was an excess of leaf-litter, spider webs or other debris in the entrances, if no sign of worker activity was detected after disturbing the nest, and if signs of excavation were absent. We conducted post-breeding demographic censuses (Morris & Doak 2002), surveying the populations a few months after the annual reproductive event.

We evaluated how road proximity influenced adult colony density by testing whether the average observed distance from the nearest road was different from what would be expected at random. To do so, we generated randomly distributed points within our study area using ArcGIS 10.2 and measured the distance from each point to the nearest road. The number of points generated was equivalent to the number of observed adult nests found and mapped in the area in each study year. We then used a two-way ANOVA to compare the average distance to roads of random and observed points in all years.

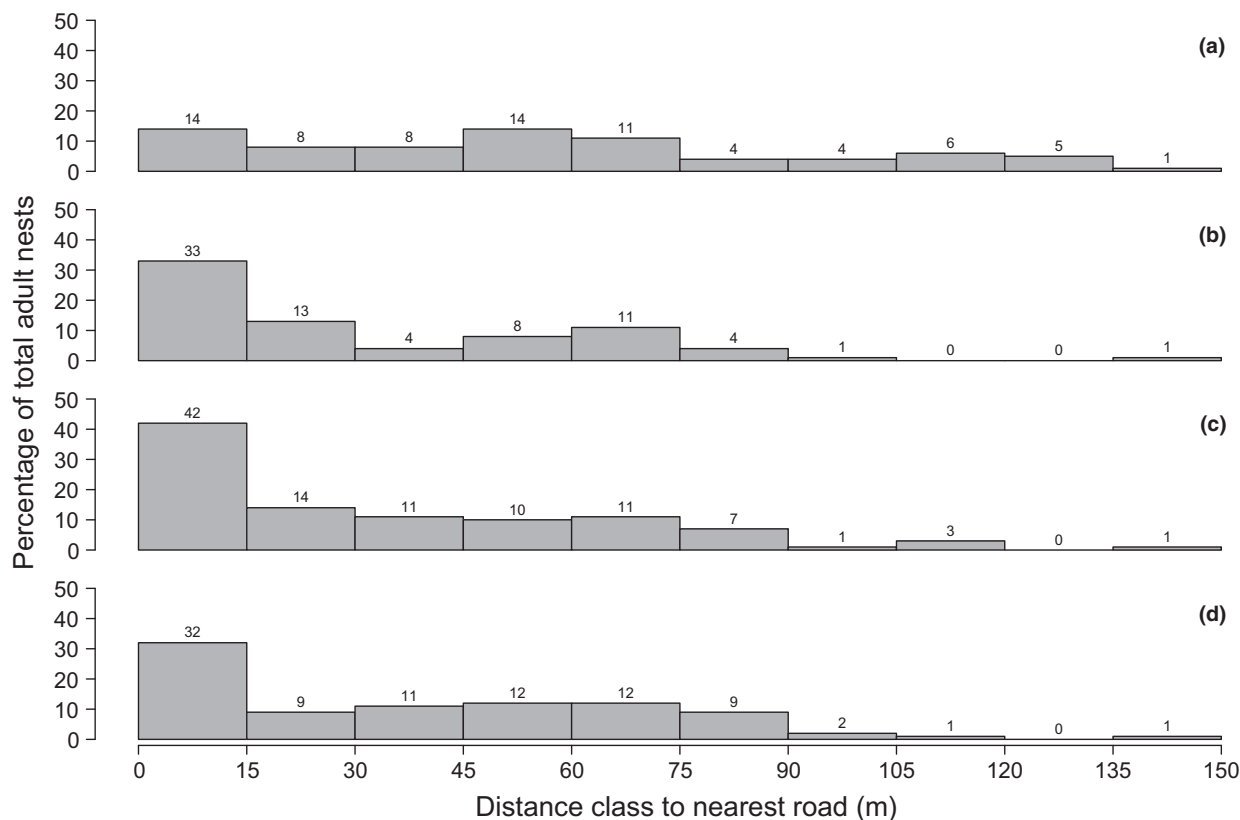
To assess the effect of road proximity on *Atta* demography, we constructed and parameterized deterministic matrix models (Caswell 2001; Morris & Doak 2002). These models have been frequently used in population and conservation biology to determine the growth rate of populations and the underlying mechanisms that shape them (Morris & Doak 2002). To do so, we assigned individual colonies to five stage classes, two of which were reproductive (i.e. adults), based on their size and other unique biological characteristics for the different stages of *A. laevigata* colony life history (Fig. 1). We then calculated the transition probabilities between stage classes (e.g. probability of a colony in stage 1 to reach stage 2). These probabilities are conditional, for example a stage 1 colony's growth to stage 2 was conditional on it first having survived in stage 1 for a year – and are given by the product of stage-specific vital rates (Caswell 2001; Morris & Doak 2002; Table S1) as in the following equation:

$$LCA = \begin{bmatrix} \text{Incipient} & \text{Small} & \text{Medium} & \text{Large} & \text{Very large} \\ (345) & (124) & (113) & (264) & (61) \\ s_1 p_1 & s_2 r_2 & s_3 f r_{32} & N_{q4} Q_{suc} & N_{q5} Q_{suc} \\ s_1 (1-p_1) g_1 & s_2 p_2 & s_3 r_3 & s_4 f r_{42} & s_5 f r_{53} \\ s_1 (1-p_1) f g_{12} & s_2 (1-p_2) g_2 & s_3 p_3 & s_4 r_4 & s_5 f r_{52} \\ s_1 (1-p_1) f g_{13} & s_2 (1-p_2) f g_{22} & s_3 (1-p_3) g_3 & s_4 p_4 & s_5 r_5 \\ s_1 (1-p_1) f g_{14} & s_2 (1-p_2) f g_{23} & s_3 (1-p_3) f g_{32} & s_4 (1-p_4) g_4 & s_5 p_5 \end{bmatrix}$$

where text above the matrix indicates the total number of colonies for each stage class. In the matrix, contributions to stage *i* (rows) in year *t* + 1 come from individuals in stage *j* (columns) in year *t*. The letters within the matrix represent the vital rates, where *s<sub>i</sub>* = survival (colonies from year *t* alive in year *t* + 1), *p<sub>i</sub>* = persistence (surviving colonies that did not grow or regressed between years), *g<sub>i</sub>* = growth (colonies at stage *i* that grew one stage), *f g<sub>ij</sub>* = fast growth (colonies at stage *i* that grew *j* stages), *r<sub>i</sub>* = regression (colonies at stage *i* that regressed one stage), *f r<sub>ij</sub>* = fast regression (colonies at stage *i* that regressed *j* stages), *N<sub>qi</sub>* = number of alates (i.e. potential future queens) produced by adult colonies (stages 4–5) and *Q<sub>suc</sub>* = a composite rate of queen performance for reproductive stages.

Survival, persistence, growth and regression were calculated using survey data. Since colony size and local resource availability influence queen production in some ant species (Boulay *et al.* 2007) but no such data are available for *Atta* species, we used a randomly generated Poisson distribution to calculate *N<sub>q</sub>*. For stage 5 colonies, this distribution had mean = 3000 based on literature reviews of *Atta* biology (Autuori 1950; Mariconi 1970). How reproductive output changes with colony size is unknown in *Atta*, but in other ant species, it has been shown to increase as colonies grow (Hee *et al.* 2000; Bono & Herbers 2003). We therefore assumed that stage 4 colonies had a reproductive output 50% lower than that of stage 5 following a similar average size difference between these two stages. We then drew reproductive output values from a Poisson distribution with a mean = 1500 alates. In addition, the probability of reproduction (Liautard *et al.* 2003) and reproductive output (Bono & Herbers 2003) can be higher in optimal conditions and habitats for other ant species, but there are no similar data available for *Atta* species. Thus, we were conservative in assuming that all adults reproduced and that reproductive means were the same near and far from roads. The remainder parameters were derived from field experiments in each habitat (Vasconcelos *et al.* 2006; Vieira-Neto & Vasconcelos 2010; Table S2). *P<sub>sp</sub>* is the probability of a queen surviving pre-foundation predation, *S<sub>cf</sub>* is the probability of a queen successfully founding the colony, *C<sub>s</sub>* is the probability of a colony surviving the claustral phase, with the composite *Q<sub>suc</sub>* thus given by *P<sub>sp</sub>* × *S<sub>cf</sub>* × *C<sub>s</sub>*.

Using data from our demographic plots, we constructed habitat × year projection matrices simulating two conditions: a population of colonies on and near dirt roads (NR, colonies <15 m from the roads) and one far from roads (FR, colonies >15 m from roads). This cutoff distance was based on adult colony distribution (Fig. 2b–d) and is within the 15–30 m width of roadside typically observed in the region (Vasconcelos, Araújo & Bruna 2014). We calculated the deterministic asymptotic population growth rates (*λ*) for each matrix. Bias-corrected 95% confidence intervals (Caswell 2001; Morris & Doak 2002) were obtained by creating 1000 randomized populations with the same number of individuals observed in each stage as in our original sample and



**Fig. 2.** Percentage of adult nests (>2 m<sup>2</sup> and reproductive) within each distance class (in metres) to the nearest road. Letter 'a' denotes average data from randomly generated points within the area in each year, whereas letters 'b-d' are associated to observed census data in years 1–3, respectively. Numbers above bars represent the number of nests in each distance class.

calculating  $\lambda$  for each of these populations. We then determined whether the observed differences in  $\lambda$  between habitats were statistically significant using two-tailed randomization tests (Caswell 2001).

Finally, we calculated the elasticities of  $\lambda$  to perturbations in the lower-level vital rates and conducted a fixed-design one-way life-table response experiment (LTRE; Caswell 2001) to determine the contribution of each vital rate to the observed differences in  $\lambda$  (i.e.  $\Delta\lambda$ ) between populations NR and FR; the FR population was used as the 'control' matrix. We were unable to construct a robust stochastic model due to low abundances of some stages in plots that rendered plot-specific bootstrapping and randomization procedures impossible. Thus, we pooled data from all plots and years for our analyses and constructed summary matrices representing a single average time step. This corrects for the disproportionately large effect of vital rates and life stages with low sample sizes on the structure of randomized populations used to estimate confidence intervals of  $\lambda$  (Caswell 2001). We built population models using a modified version of the package popbio (Stubben & Milligan 2007) for R (R Core Team 2015).

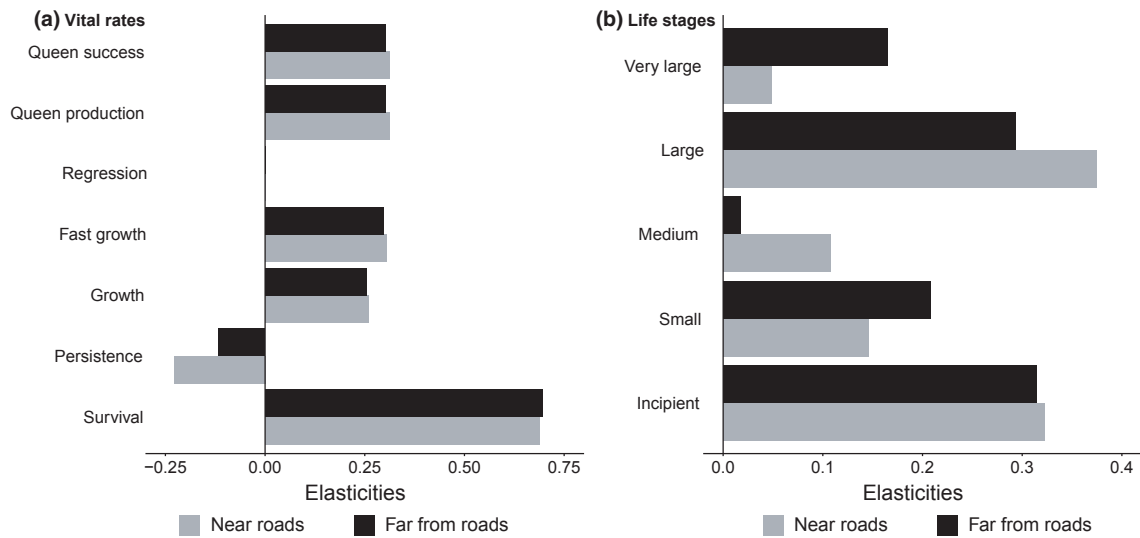
## Results

Pooling across years, we mapped a total of 907 colonies across all stage classes, of which 469 were located near roads. We found, 35–45% of the adult colonies were located within 15 m of roads (Fig. 2b–d). This is significantly closer than the average distance from roads of

randomly distributed adult colonies ( $F_{1,522} = 38.479$ ,  $P < 0.001$ , Fig. 2a, Table S3, Appendix S3).

Projected population growth rates were >1 both near roads ( $\lambda_{NR}$ ) and far from roads ( $\lambda_{FR}$ ). However,  $\lambda_{NR}$  was ~41% higher than  $\lambda_{FR}$  (2.72 vs. 1.94). Bootstrapped confidence intervals for  $\lambda_{NR}$  (2.24–3.18) and  $\lambda_{FR}$  (1.53–2.27) were relatively large. Nevertheless, the probability of randomly observing such a large difference between  $\lambda_{NR}$  and  $\lambda_{FR}$  was extremely small ( $P = 0.021$ ). Our results thus support the hypothesis that proximity to roads will increase population growth rates.

The positive effects of roads were primarily due to the performance at early life stages. Overall, the elasticities of  $\lambda$  to survival and growth rates of early stages were proportionally much higher than those of later stages, with survival having the largest effect on population growth (Fig. 3a). This was true irrespective of habitat, although values varied less near roads (Fig. 3b). These results are further supported by our LTRE analysis. Overall, the LTRE contributions to the observed difference between  $\lambda_{NR}$  and  $\lambda_{FR}$  ( $\Delta\lambda$ ) of regression terms were mostly negligible. While the contributions of fertility and survivorship terms were mostly positive those of persistence and growth were variable, and their summed contributions were consistently negative. However, our results clearly indicate that the higher  $\lambda$  near roads was

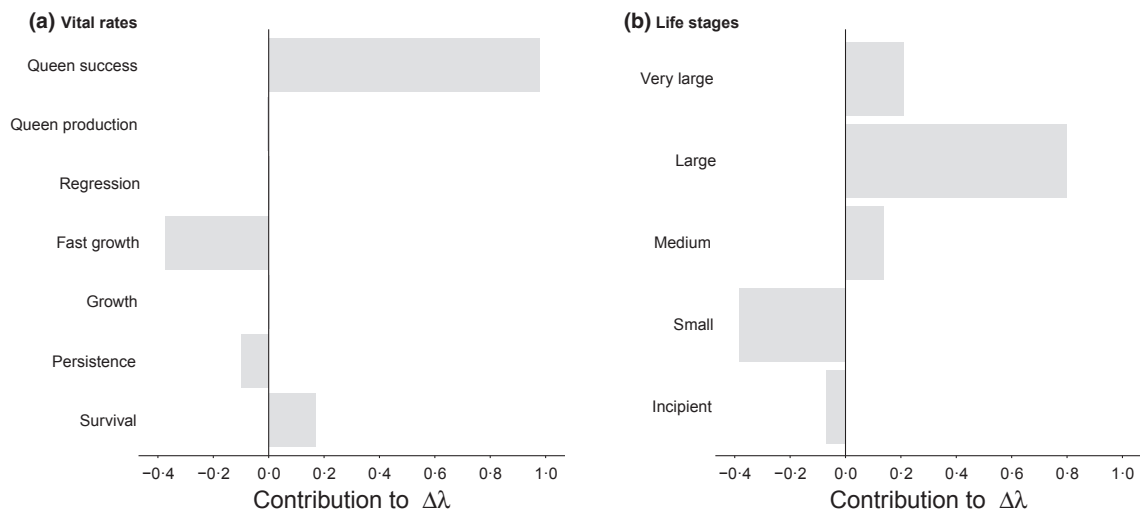


**Fig. 3.** Elasticities of  $\lambda$  to (a) vital rate and (b) life-stage transition changes in *Atta* populations near (grey bars) and far (black bars) from roads over three years in the Brazilian Cerrado savannah. Data from all years were pooled for model parameterization.

primarily due to terms related to the increased establishment and survival of incipient colonies. The summed contributions to  $\Delta\lambda$  of pre-establishment success were fivefold greater than those of survival and at least threefold greater than those of growth or persistence (Fig. 4a).

Of particular note are the very large LTRE contributions of fertility rates for stages 4 and 5, which are composed of a combination of parameters reflecting performance during establishment of pre-incipient colonies (Appendix S2). In addition, there were large and positive contributions of fast growth, especially of colonies at stages 1 or 2. The contribution to  $\Delta\lambda$  of colony growth (of all stages) was frequently positive, albeit small (Fig. 4a). There was also a similar but negative contribu-

tion to  $\Delta\lambda$  of stage 2 survival, indicating greater survivorship of small colonies away from roads. In contrast, the contribution of stage 1 survival to  $\Delta\lambda$  was positive rather than negative, and the persistence of colonies in all stages made lower and mostly negative contributions (Fig. 4a). When summing stage-specific contributions, we found that early stages made consistently negative contributions to  $\Delta\lambda$ , while the contributions of reproductive stages were consistently positive, mostly due to the large effect of queen success. Overall, the largest contribution by far was of stage 4 – twofold greater than that of stages 1 and 2 combined (Fig. 4b). The sum of LTRE contributions was within 6% of the observed values of  $\Delta\lambda$ , indicating the adequacy of the models (Caswell 2001).



**Fig. 4.** Results of one-way LTRE analyses showing the contributions of (a) vital rates and (b) life stages to the observed difference in population growth ( $\Delta\lambda$ ) between leaf-cutter ant populations near (NR) and far (FR) from roads in two transition years in a Neotropical savannah. Positive contributions indicate that the value of a given vital rate in the treatment population matrix (NR) is higher than in the control matrix (FR), and vice versa. Data from all years were pooled for model parameterization.

## Discussion

Roads have been suggested to benefit primarily exotic and pioneer species. However, our results demonstrate that a native, long-lived superorganism can also increase in density dramatically near roads. Our results also highlight the important role that early life stages can play in the population dynamics of long-lived organisms. We suggest that increases in dispersal and recruitment driven by anthropogenic changes to landscapes, such as the expansion of road networks, may play a critical but underappreciated role in the expansion of some native species (Vasconcelos *et al.* 2006; Suarez-Esteban, Delibes & Fedriani 2013) similar to those observed for exotic ones (Gelbard & Belnap 2003). Because our focal species is an important ecosystem engineer, road-driven changes in population dynamics could also have important implications for ecosystem dynamics: unpaved roads like those we studied represent ~88% of Brazil's 1.72 million km road network (DNIT 2015).

Demographic studies have generally found that in long-lived organisms, the survivorship and growth of stages that are reproductive or pre-reproductive have the greatest demographic impact (Franco & Silvertown 2004). For example, a review of the habitat fragmentation effects on plant populations found that for trees and other perennial plants the survivorship and growth of adult individuals have the largest elasticities (Bruna, Fiske & Trager 2009), with an additional study showing that these rates are temporally less variable (Burns *et al.* 2010). In addition, a review of population dynamics of 200 invasive and native plant species has shown that the elasticities of growth and fecundity of invasives and survival of natives have a greater effect on  $\lambda$  (Ramula *et al.* 2008). Similarly, in many long-lived animal species, changes in the survival of subadults and adults have the largest effects on population growth (e.g. Crowder *et al.* 1994; Dudas, Dower & Anholt 2007). Our results show a very different pattern, with the largest impacts on the population growth of our native focal species originating from vital rates related to early stages. This is underscored by the proportionally lower elasticities of survival and growth of reproductive adults and the high elasticities of early survival rates. While similar results have been observed in savannah trees (Maclean *et al.* 2011), studies demonstrating similar patterns in animals are rare or not directly comparable (e.g. Karraker, Gibbs & Vonesh 2008), especially regarding long-lived superorganisms. Previous work has suggested that another long-lived ant species, the western harvester ant *Pogonomyrmex occidentalis*, can favour roadside habitats and use it as conduits for their range expansion (Demers 1993). However, no demographic or causal mechanism has been suggested, and no direct test has been made. Given that *P. occidentalis* and *Atta* species have similar reproduction and colony foundation strategies (cf. Hölldobler & Wilson 1990), we hypothesize the demographic mechanisms revealed here could be char-

acteristic of other social insects, particularly those often favoured by anthropogenic alterations of the environment. Thus, further studies should investigate whether this pattern holds in other species groups.

Roads have long been recognized as a disturbance with major ecological impacts. Not surprisingly, the majority of studies have demonstrated negative effects of roads on animal species ranging from arthropods to mammals (reviewed in Trombulak & Frissell 2000). It is frequently asserted that most common dangerous effects are related to the preference of roads and roadsides by animals as foraging or breeding habitat resulting in increased rates of mortality, that is roads are ecological traps (e.g. Battin 2004). However, our results show no indication that roads are ecological traps for leaf-cutter ants. In fact, habitats close to roads positively affected population growth – our LTREs revealed that the greater preference for roads by queens founding nests and high early-colony performance there (Vasconcelos *et al.* 2006; Vieira-Neto & Vasconcelos 2010) have population-level consequences. This may stem in part from their being superorganisms, and hence, more resilient to the elevated risk of mortality to individual colony members to roadkill or increased predation than other organisms.

We also found consistently positive and high contributions near roads of terms for fast colony growth (e.g. colonies moving from stage 2 to stage 4 in a single transition year). Rapid growth near roads could be indicative of either a release from food limitation (i.e. increased resource availability) or that foraging workers are more easily able to find and harvest plants (i.e. increased resource accessibility). Leaf-cutter ants harvest a diverse array of plant species, but they often have strong preferences for a select subset of available plants (Blanton & Ewel 1985). In addition, young colonies have even narrower diets due to constraints on their foraging ability, resource availability and environmental conditions (Wetterer 1994). A recent survey in the region where we conducted our study found that while roadside verges can harbour up to 70% of the plant species present in nearby Cerrado – including many of those preferred by *Atta* colonies – plant abundance near roads was 60% lower (Vasconcelos, Araújo & Bruna 2014). Increased resource availability near roads is therefore not the mechanism responsible for more rapid colony growth there unless there has been a major shift in roadside community composition towards *Atta*-preferred species. Instead, we hypothesize resources on roadsides are more accessible, which would allow colonies to shift their resource allocation from foraging to growth and enhance the survival of resource-limited incipient colonies (Vieira-Neto & Vasconcelos 2010).

Leaf-cutter ants are regarded as keystone species (Fowler *et al.* 1989) and ecosystem engineers (Leal, Wirth & Tabarelli 2014) throughout the Neotropics. Their nest construction alters soil properties (Moutinho, Nepstad & Davidson 2003), surface microclimate (Meyer *et al.* 2011), creates new sites for plant establishment and invasion (Farji-Brener & Ghermandi 2008) and provides shelter

and foraging sites for animals (Fowler *et al.* 1989). In addition, their selective plant harvesting can alter nutrient cycling (Moutinho, Nepstad & Davidson 2003) and the survival and reproduction of plant species (Mundim *et al.* 2012), which could ultimately alter plant demography and community composition. Leaf-cutter ants are also major crop pests (Fowler *et al.* 1989), which results in losses of millions of dollars and the widespread application of insecticides (Zanetti *et al.* 2014). Our results suggest that the proposed increases in road networks throughout their range – c. 7500 km over the next 20 years in the Cerrado alone (cf. Passos 2012) – could lead to dramatically increased abundance and the expansion of their range. This could have major ecological as well as economic consequences that remain almost entirely unexplored.

We demonstrate that enhanced colony establishment and the performance of juvenile life stages strongly influence the demography and population dynamics of *Atta laevigata*. However, other mechanisms may also do this, either individually or in concert. Plant diversity and predation pressure are potential drivers of ant demography, as they have been shown to influence leaf-cutters at the individual colony level (Rao 2000; Rao, Terborgh & Nunez 2001; Terborgh *et al.* 2001). Furthermore, density-dependent recruitment, survival and growth could influence habitat selection and spatial distribution, especially when taking into account ontogeny (Caughlin *et al.* 2014). Thus, the interplay between density-dependent and density-independent mechanisms could have further implications for *Atta* populations. Differences in queen production by colonies near and far from roads, and whether or not roads are paved could also influence vital rates. While beyond the scope of this study, we aim to evaluate these issues in future work. Finally, it is important to emphasize that the focal roads in our study were unpaved. While unpaved roads are ubiquitous throughout natural areas, agricultural landscapes and the developing world, it is important to conduct studies that evaluate whether the results can be generalized to paved roads as well.

Studies on the demographic effects of roads on animal species are still relatively rare, and recent work has mostly focused on their negative impacts on vertebrate species either via elevated adult (Mumme *et al.* 2000; Boulanger & Stenhouse 2014) or juvenile (Karraker, Gibbs & Vonesh 2008) mortality. This pattern extends to invertebrates and a recent review of the effects of roads on insects states they are mostly deleterious (Munoz, Torres & Megias 2015). To our knowledge, this is the first study to demonstrate that the population growth rate of a native keystone superorganism can be strongly and positively enhanced by proximity to roads. As revealed by the high elasticities and LTRE contributions, this effect was driven not by individuals in later life-history stages but by juveniles, which contrasts sharply with the dominant paradigm describing the demography of long-lived species. We suggest this pattern might be more prevalent than previously thought and propose data bases such as

COMADRE and COMPADRE may be useful to evaluate the extent to which this paradigm is actually upheld. However, given the paucity of studies on the demography of ants and other insects, direct comparisons of our results with those for similar organisms are challenging. We therefore urge for further studies evaluating the demographic mechanisms underlying the population dynamics of insects, which are key bioindicators, can have major detrimental impacts on native and agricultural systems and provide fundamental ecological services.

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## Data accessibility

Demographic and road distances data: Dryad Digital Repository doi: 10.5061/dryad.1s4f2 (Vieira-Neto, Vasconcelos & Bruna 2016).

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## Supporting Information

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

**Appendix S1** Life cycle of an *Atta laevigata* leaf-cutter ant colony.

**Figure S1** Life stages of a leaf-cutter ant (*Atta laevigata*) colony.

**Appendix S2** Parameter values used for the construction of demographic models.

**Table S1** The 33 lower-level vital rates (LLVR) calculated from three census years used to parameterize matrix population models of *A. laevigata* leaf-cutter ants near and far from roads in the Brazilian Cerrado savannahs.

**Table S2** Parameters used to calculate fertility rates for *A. laevigata* populations near (NR) and far (FR) from roads.

**Table S3** Results of a two-way ANOVA comparing the mean distance to the nearest road of adult field colonies of *A. laevigata* observed (O) in three subsequent years to that of randomly generated locations (R) for each year within the study site.

**Appendix S3** Initial distribution of adult *Atta laevigata* colonies in the study site.