Empty *Gonometa postica* cocoons function as nest sites and shelters for arboreal ants

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Highlights

• Arboreal ants of different species were observed sharing trees and cocoons.

• Ants prefer wider cocoons containing small holes in trees containing scale insects.

• Ant abundance was lower in cocoons occupied by other invertebrates.

ABSTRACT

Arboreal ants use a variety of plant structures as nesting sites, but may also nest in structures created by arboreal ecosystem engineers. We observed, for the first time, ants using empty cocoons of the economically important silk moth species, *Gonometa postica*, as shelter and nesting sites. Individual trees and individual cocoons were occupied predominantly by one dominant ant species, although in some cases by co-occurring ant species. Ant abundance and occurrence were positively related to cocoon size and the presence of scale insects on branches of the trees, and negatively influenced by cocoon occupancy by other invertebrates. Ants also preferred cocoons containing only small parasite holes as opposed to cocoons containing large moth emergence holes, suggesting that ants select cocoons based on cocoon characteristics. Further, these results reveal that other arboreal invertebrates appear to benefit from cocoon production. Empty cocoons could be functioning as nest sites and shelters for arboreal invertebrates, and they could create favourable habitats for other invertebrates on *Vachellia erioloba*. Therefore, *G. postica* acts as an autogenic ecosystem engineer and current silk harvesting practices, which partly rely on harvesting empty *G. postica* cocoons, may have potential local and large-scale implications for inter-specific interactions in these arboreal systems.

Keywords: Biogenic arboreal nests, cocoon-spinning species, *Crematogaster* sp., Kalahari, *Vachellia erioloba*

1. Introduction

Ecosystem engineers alter their environment in such a way that it benefits themselves or, either directly or indirectly, other organisms by creating, modifying or maintaining habitats (Jones et al., 1997; Breitburg et al., 2010). Consequently, ecosystem engineers promote habitat heterogeneity and can affect patterns and processes at the individual, population and community level. Indeed, by increasing local habitat patchiness, ecosystem engineers can alter population dynamics and support different species compared with equivalent environments from which they are absent (Jones et al., 1997; Dangerfield et al., 1998). Autogenic ecosystem engineers alter the environment via their own physical structures (e.g. plants, mussels or biofilm-producing microbes) (Jones et al., 1997; Dangerfield et al., 1998). In contrast, allogenic ecosystem engineers, such as soil cast-creating earthworms, tree-felling elephants and dam-building beavers (Jones et al., 1997; Breitburg et al., 2010), transform materials from one physical state into another (Dangerfield et al., 1998).

In arboreal systems, there are many examples of allogenic herbivorous invertebrate ecosystem engineers, including leaf-tying, leaf-rolling and leaf-folding caterpillars, leaf miners and wood-boring beetles (Fukui, 2001; Lill and Marquis, 2003; Lima et al., 2013). The shelters that they create within trees are frequently used by other taxa as refuges against negative bottom-up (e.g. plant chemical defences) or top-down (e.g. predation) effects (Fukui, 2001). These shelters, through their provisioning of new physical structures and novel microhabitat conditions in trees, may influence the abundance, survival and distribution of other species, and can therefore shape local patterns of species diversity (Fukui, 2001; Lill and Marquis, 2003; Cornelissen et al., 2016).

Arboreal ants are canopy-dwelling invertebrates that form part of important protective ant-plant mutualisms in both temperate and tropical regions (Heil and McKey, 2003). In these regions, they structure a multitude of biotic interactions (Moreau et al., 2006) and can be

ecologically dominant and diverse. Arboreal ants use a wide variety of structures as nesting sites (Beattie and Hughes, 2002). These include plants structures such as specialized thorn domatia (Campbell et al., 2013a), other domatia in hollow stems, leaf pouches, petioles (Heil and McKey, 2003), and natural plant cavities (Dejean et al., 2012), as well as structures created by other organisms, such as leaf shelters constructed by lepidopteran larvae (Nakamura and Ohgushi, 2003). These structures serve many functions, including the provision of favourable conditions for rearing brood, sheltering the queen and providing refuges for workers against abiotic environmental conditions or natural enemies (Blüthgen and Feldhaar, 2010). In some cases, the structures that house arboreal ants can be considered ecosystem engineered structures if these structures are created, modified or maintained by other organisms and are able to ameliorate abiotic stress for the ants, provide ants with protection from natural enemies or increase ant survivorship (Cornelissen et al., 2016).

In this study, we report on the use by arboreal ants and other invertebrates of the empty cocoons of the economically important silk moth species, *Gonometa postica* Walker 1855 (Fig. 1) (Hartland-Rowe, 1992; Veldtman et al., 2002, 2007). The larvae of *G. postica* forage on the foliage of host trees for approximately two months before spinning cocoons (Hartland-Rowe, 1992). During foraging *G. postica* is involved in direct antagonistic interactions with arboreal ants (chiefly *Crematogaster* sp.); the ants display aggressive behaviour towards foraging *G. postica* larvae and remove the larvae from trees (Campbell et al., 2013b). This behaviour may be contingent on the presence of scale insects (e.g. Styrsky and Eubsnks, 2007).

However, we document here that this negative ant-caterpillar interaction can be followed by an indirect positive interaction, where empty *G. postica* cocoons serve as ant sheltering and nesting sites (similar to thorn domatia), potentially protecting ants and other invertebrates against environmental extremes and natural enemies by creating a unique, sheltered

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environment. Therefore, the empty cocoons can be considered autogenic ecosystem engineered structures, which create a new abiotic state that increases habitat heterogeneity in trees (Lill and Marquis, 2003; Cornelissen et al., 2016). Thus, this study examines, for the first time, the ecological function of empty *G. postica* cocoons as potential nests and shelters for arboreal ants and other invertebrates.

The aims of this study were to first characterise the patterns of ant species occurrence and co-occurrence within cocoons and trees. Second, we assessed whether ant species presence and abundance within cocoons is affected by cocoon characteristics. Good evidence exists that nest site (e.g. domatia) selection for arboreal ants is influenced by nest architecture (Fincke, 1999; Thomas, 2002; Campbell et al., 2013a). We thus examined how cocoon characteristics (e.g. cocoon length and width, and cocoon hole type) along with other variables (e.g. cocoon aspect, time of day sampled and the presence of other invertebrates in the cocoons) affected 1) ant species presence and 2) ant abundance. Last, we tested whether ant species presence and abundance is mediated by the presence of scale insects. These produce liquid food rewards for ants in return for protection against natural enemies (Heil and McKey, 2003; Gibbs and Cunningham, 2009) and may mediate arboreal ant distributions and behaviour towards herbivores (Gibbs and Cunningham, 2009). Therefore, we related ant species abundance and occurrence within cocoons to the presence of scale insects on the trees, the incidence of ants tending scale insects and the time of day that the observations were made.

Fig. 1. An emerged *Gonometa postica* cocoon and associated ants on *Vachellia erioloba*. Scale insects are also visible on the bottom right of the twig. Photograph: Isabelle Buyens.

2. Methods

2.1. Gonometa postica

Gonometa postica is one of two indigenous silk moth species in southern Africa. The species has been extensively harvested, though little is known its biology (Veldtman et al., 2002). It occurs mainly in northern areas of South Africa but also in Namibia, Botswana and East Africa (Raath et al. unpublished data). The life cycle of *Gonometa* species is complex, characterised by two generations per year, one in early spring (September) and the other in mid-summer (December-January) (Delport, 2006; Veldtman et al., 2007). Their populations are considered to be eruptive, reaching very high densities over large areas during outbreak periods. It is unclear whether population eruptions occur after populations are exposed to ideal conditions or if eruptions are initiated through the dispersal of individuals that belonged to previously eruptive populations (Delport, 2006). Eruptions have also been observed following periods of drought, possibly because drought conditions are unfavourable for larval

parasites (Hartland-Rowe, 1992). In contrast, large population crashes have been observed after heavy periods of rainfall. Therefore, *G. postica* displays sporadic and unpredictable population outbreaks, and high spatial and temporal variability in population size and extent (Veldtman et al., 2007).

2.2. Sampling

Fieldwork was conducted over an area of approximately 5 km^2 on the Oppiknoppi Guest Farm, near Hotazel in the Northern Cape Province, South Africa (26°39'48"S, 22°43'04"E). The farm lies in the Kalahari, which is an arid component of the savanna biome (Knobel and Bredenkamp, 1999). The area receives about 400 mm rainfall p.a. and is characterised by deep, sandy soils. Dominant trees at the site, *Vachellia erioloba*, *Senegalia mellifera* and *Boscia albitrunca*, were sparsely scattered between a variety of grass and shrub species.

   Gonometa postica cocoons were collected from *V. erioloba* trees in December 2014 and January 2015. *Vachellia erioloba,* one of *G. postica*'s main host plants in southern Africa, was the only plant species on which cocoons were found in abundance (Hartland-Rowe, 1992; Veldtman et al., 2002, 2007). None of the cocoons was occupied by *G. postica* at the time of sampling, and cocoons were probably from a previous outbreak of the species, two years prior to the sampling period (2012/2013). Sampling was conducted in the mornings between 5:30 and 12:00, and in the late afternoon between 14:00-18:00. All sampled trees were located at more than 20 m from farm roads to minimise road effects. Trees were sampled on transects of variable lengths. For each transect, a starting point (focal tree) was randomly selected and sampled (Fig. A.1. in Supplementary Material). Thereafter, the two nearest neighbouring trees were also selected and sampled. Trees were sampled in such a way that the nearest neighbour of one focal tree was not the nearest neighbour of another focal tree. Thereafter, the next focal tree (located within a 90° angle in the direction of the transect

and at least 10 m away from the previous focal tree) was sampled along with its two nearest neighbours. This selection procedure was repeated by walking along the length of the transect (see Catana, 1963). Only trees ranging in height from 1.5 m to 5 m were sampled because no cocoons were found on trees less than 1.5 m in height and it was not possible to accurately count and sample cocoons on trees exceeding 5 m.

The cover (present on 0%, <1%, 0-10%, 10-15%, 15-20%, 20-25%, 25-30%, 30-40% and > 40% of branches) of scale insects per tree was visually estimated, and whether scale insects were tended by ants (i.e. the presence and absence of scale insect-ant interactions) was recorded. If there was tending, the morphospecies of ants that were tending scale insects were recorded. *Vachellia erioloba* can form swollen thorn domatia. These form part of protective ant-plant interactions (Heil and McKey, 2003): the plants provide ants with specialised, pre-formed nesting sites (domatia) in return for protection against a range of herbivores. Therefore, the presence of swollen thorn domatia (see Campbell et al., 2013a) was also recorded for each tree.

Every *G. postica* cocoon that could be reached by hand or with a 1 m pole was collected from sampled trees. For each collected cocoon, aspect (i.e. whether the cocoon was collected from the north or south sides of the host tree) and the time of collection were recorded. Cocoons that contained one or more small holes (mean diameter ± SD = 2.68 ± 1.71 mm) were categorized as parasitized, although we acknowledge the possibility that some of these small holes may have been created or modified by the ants themselves (e.g. see Federle et al., 2001). The majority of *G. postica* parasites are wasps (Hymenoptera, in the families Ichneumonidae, Chalcididae, Eurytomidae, Perilampidae and Eupelmidae) while some belong to the Diptera within the family Tachinidae (see Veldtman et al., 2004). Cocoons containing a larger hole (mean diameter = 6.72 ± 2.12 mm) towards the apex of the cocoon (with a characteristic three-fold split) were considered to be "emerged" (i.e. cocoons from

which fully-developed moths had emerged). Cocoons that contained both a large hole towards their apex and small holes were considered as emerged with secondary holes (i.e. holes potentially created by ants or other invertebrates following moth emergence).

Sampled cocoons were frozen to kill invertebrate occupants. The length and width of each collected cocoon were measured using a digital calliper, and the cocoons were cut open and the abundance, morphospecies and life stage of ants (adults, juveniles and eggs) within each cocoon recorded. Reference specimens of the morphospecies were collected from all sampled cocoons. The presence and identity of other invertebrates, broadly classified as Araneae (spiders), Coleoptera (beetles) or Lepidoptera (caterpillars), within the cocoons were also recorded.

2.3. Statistical analyses

Ant abundance data were both zero-inflated and overdispersed. Data were therefore analysed using hurdle models, which involve two analyses (Rose et al., 2006). One analysis tests for trends in the positive (count) data with a linear model, whereas the other compares zeros to non-zeros with a binary model. All hurdle models were run as generalized linear mixed effects models (hurdle GLMMs), with tree identity as a random effect to account for multiple cocoons being collected from some trees. A truncated negative binomial distribution with a log-link function was fitted to all analyses on count data to correct for overdispersion (Rose et al., 2006), and all binary models were fitted using a binomial distribution and the logit-link function.

To ascertain if ants were selecting *G. postica* cocoons based on cocoon characteristics, a hurdle GLMM was run to test whether ant morphospecies abundances and presence-absence within cocoons were influenced by cocoon aspect, cocoon length and width, and cocoon hole type. Also included as predictors were the occurrence of other invertebrates within the cocoons and time of day that the cocoons were sampled (with a quadratic term), as these may

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have affected ant abundance or occurrence. Most morphospecies were infrequently recorded within cocoons. Therefore, this analysis was only conducted for *Crematogaster* sp. 1. A third GLMM hurdle model was run to test whether ant abundance and occurrence within cocoons was related to the presence of scale insects on the trees, the presence of ants tending scale insects and the time of day that the observations were made. For this analysis, total ant abundance was used as response variable. No cocoon characteristics (mentioned above) were included as predictors for this analysis.

For each component of the hurdle models, predictor variable selection was done by forward stepwise regression, which selected the best models based on model AIC scores. Data were analysed in R v.3.0.2 (R Core Team, 2013) using the glmmADMB package.

3. Results

3.1. Morphospecies occurrence within trees and G. postica *cocoons*

Thorn domatia were absent from the majority (n =173) of the *V. erioloba* trees (n = 197) surveyed in this study, and when thorn domatia were present *G. postica* cocoons were also present. The mean number of *G. postica* cocoons collected per tree was 5.9 ± 4.1 (mean ± SD). Of these, 2.6 ± 2 were occupied by ants. These are not the true mean value because only cocoons that could be reached by hand or through the use of a 1 m pole were collected. Cocoons at the very tops of the trees (which could not be reached) were not collected. Five ant species, including two *Crematogaster* species were identified in the collected cocoons (Fig. 2; Table 1). *Cataulacus* sp. and *Crematogaster* sp. 1 were the most abundant ant species per cocoon on average (Fig. 2a); however, the highest total mean ant abundance was observed when the two *Crematogaster* species co-occupied cocoons. *Crematogaster* sp. 1 had the highest number of brood within cocoons (Fig. 2b) followed by *Cataulacus* sp. and the

Crematogaster spp. co-occupants. No brood was found in cocoons occupied by *Crematogaster* sp. 2 and *Nesomyrmex* sp.
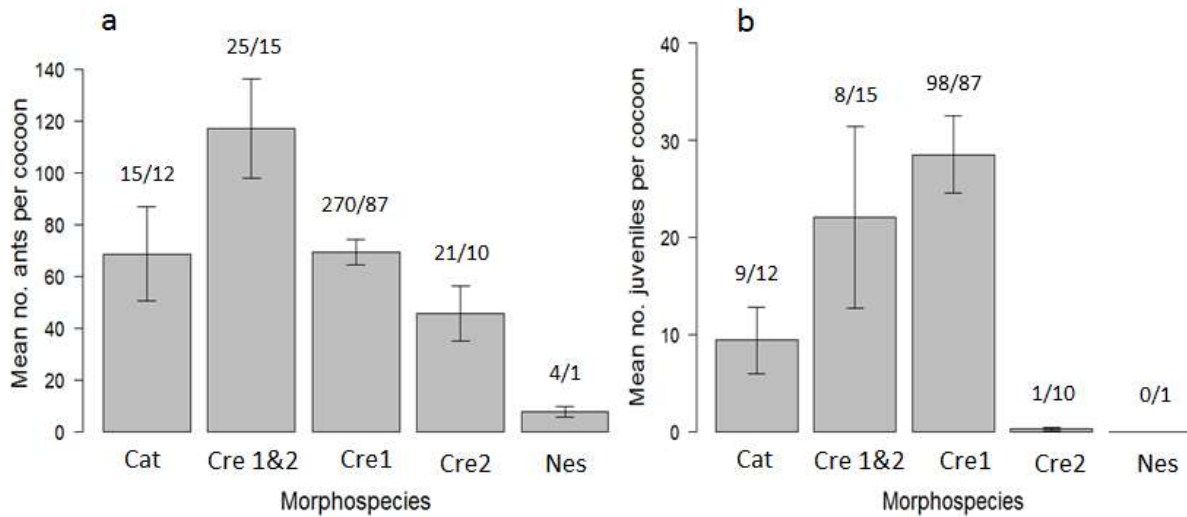

Fig 2. a) Mean (± SE) abundance of ant morphospecies per ant-occupied *Gonometa postica* cocoon (n = 336 cocoons). b) Mean (± SE) abundance of brood ants for *Cataulacus* sp. (Cat) *Crematogaster* sp. 1 (Cre1), *Crematogaster* sp. 2 (Cre2), *Crematogaster* spp. co-occupants (Cre 1&2) and *Nesomyrmwx* sp. (Nes). The number of cocoons and trees (n/n) from which each morphospecies and juveniles morphospecies was recorded is indicated above the bars.

Trees with cocoons were most commonly occupied by a single ant species (n = 73 of 124, *cf.* 59%), with fewer of these trees co-occupied by two species (n = 52 of 124, *cf.* 42%) and only four of these trees co-occupied by three ant species (Table 1). *Crematogaster* sp. 1 was dominant, occupying cocoons on 87 trees (*cf.* 70%) in total of which 66 (*cf.* 53%) of the trees were exclusively occupied by this species (without any other ant species).

Crematogaster sp. 1 was also the most commonly encountered ant species within *G. postica* cocoons, occurring in 270 (*cf.* 80%) of the 336 ant-occupied cocoons. On average, this species occurred in 2.1 ± 2.4 cocoons per tree. The remaining morphospecies each occurred in less than 25 of the sampled cocoons (Table 1), although the two *Crematogaster* morphospecies occurred together within 25 of the 336 ant-occupied cocoons. *Nesomyrmex*

sp. and *Camponotus* sp. were rarely recorded in cocoons on the trees, occupying n = 4 and n = 1 of the total 336 ant-occupied cocoons respectively (Table 1). About half (*cf.* 52%) of the cocoons sampled (n = 366 of n = 702) were unoccupied by ants; however, 88 (*cf.* 24%) of these unoccupied cocoons were occupied by other invertebrates (spiders, caterpillars and/or beetles). *Crematogaster* sp. 1 most often co-occurred in cocoons with other invertebrates (n = 37 of 702).

Table 1. The number of trees (n = 124) on which each ant morphospecies occurred, and the number of trees that were exclusively occupied by the ant species (i.e. other ant species were not recorded on the tree). Cocoons occupied: total number of cocoons (n = 702) occupied by each ant morphospecies. Shared occupancy with other invertebrates of 1) trees: the number of trees in which both cocoons occupied by the ant species and cocoons occupied exclusively by other invertebrates were recorded; and 2) cocoons: the number of cocoons that were co-occupied by the ant morphospecies and other invertebrates. Ants occupied a total of 336 cocoons, co-occupied 25 cocoons with other ant species and co-occupied 41 cocoons with other invertebrates. A total of 194 cocoons contained neither ants nor other invertebrates

Morphospecies	Trees occupied		Cocoons occupied	Shared occupancy with other non-ant invertebrates	
	Total	Exclusively	Total	Trees	Cocoons
Crematogaster sp. 1 (Myrmicinae)	87	66	270	27	37
Crematogaster sp. 2 (Myrmicinae)	10	4	21	3	0
Crematogaster sp. 1 and *Crematogaster* sp. 2 co-occupants	15	1	25	5	3
Cataulacus sp. (Myrmicinae)	12	1	15	5	1
Camponotus sp. (Formicinae)	1	1	1	0	0
Nesomyrmex sp. (Formicinae)	1	0	4	0	0

3.2. *The effect of cocoon characteristics and scale insects on ant abundance and occurrence*

Due to most morphospecies being only infrequently recorded within cocoons, analyses testing the effect of cocoon characteristics on ant abundance and presence-absence were only conducted for *Crematogaster* sp. 1 (Table A.1 in Supplementary Material). The analyses

yielded similar results to those when all ant species were analysed together (Table A.2 in Supplementary Material). Cocoons containing only small holes, had higher abundances of *Crematogaster* sp. 1 than cocoons containing only emergence holes (p = 0.031; Table A.1). *Crematogaster* sp. 1 was significantly more abundant in cocoons from which other invertebrates (i.e. spiders, caterpillars and beetles) were absent (p < 0.001). The abundance of *Crematogaster* sp. 1 was also positively affected by cocoon width (p < 0.01; Table A.1), while species occurrence was negatively related to cocoon length (p = 0.033; Table A.1).

Both *Crematogaster* species were most frequently observed tending scale insects but tending by the *Camponotus* species was also observed on some of the trees. The presence of scale insects on *V. erioloba* trees, the incidence of ants tending scale insects and the time of day that the cocoons were sampled were either not included in the minimal adequate models or had no significant effect on ant abundance in *G. postica* cocoons (Table A.3 in Supplementary Material). However, there was a higher incidence of ant presences in cocoons if scale insects were present on the tree.

4. Discussion

Our results demonstrated a novel ecological role of a cocoon-spinning lepidopteran species, with ants and other invertebrates using *G. postica* cocoons as nesting sites and for shelter. Empty *G. postica* cocoons can therefore be considered as ecosystem engineered structures (see Lill and Marquis, 2003; Lima et al., 2013; Cornelissen et al., 2016) because they create a new abiotic state within trees that is different from the unmodified abiotic conditions. Arboreal ants are territorially dominant and often occur on myrmecophytes, which they protect from herbivores in exchange for food rewards or nesting sites (Heil and McKey, 2003; Palmer et al., 2008; Stanton and Palmer, 2011; Campbell et al., 2013b). Thorn domatia were rarely recorded on the *V. erioloba* individuals sampled in this study; however, ants appeared to secondarily occupy and house their brood within vacant *G. postica* cocoons. This

was surprising because arboreal ant species belonging to the *Crematogaster* genus have been observed to behave aggressively towards *G. postica* on *V. erioloba* by removing larvae from the trees (Campbell et al., 2013b). This suggests that the direct negative interaction between ants and *G. postica* is followed by an indirect commensal interaction, where (abandoned) *G. postica* cocoons benefit ants who gain shelter and nesting sites from the cocoons.

4.1. Ant morphospecies occurrence and co-occurrence in trees and cocoons

Certain ant species are known to nest exclusively in myrmecophytes (Palmer et al., 2000; Heil and McKey, 2003), occupying individual trees in the absence of other ant species. In some cases different species share a myrmecophyte, coexisting with other ant species in the same tree (Raine et al., 2004; Campbell et al., 2013a; Campbell et al., 2015). In this study, trees and cocoons were predominantly occupied by *Crematogaster* sp. 1, but in some cases simultaneously by multiple ant species. *Crematogaster* species frequently dominate the trees in which they nest and are very territorial in colony defence (Stanton and Palmer, 2011). However, in this study, shared occupancy of cocoons was observed for *Crematogaster* sp. 1 and *Crematogaster* sp. 2. Ant co-occupancy of nest sites (parabiosis) has also been reported elsewhere, e.g. from ant gardens in the Neotropics and Paleotropics (Orivel et al., 1997). Disadvantages to sharing shelters include decreased fitness through reduced pupal mass (Lill et al., 2007) and increased competition during foraging which leads to decreased food retrieval (Menzel et al., 2014). However, co-occupancy of nests by ant species could also enhance defence against mutual enemies (Sagata et al., 2010), and in ant gardens, two ant species may even forage together or feed one another (Menzel and Blüthgen, 2010). Moreover, ant species may benefit from co-occupancy through shared pheromone trails leading to food sources. Whether the relationship between the *Crematogaster* spp. in this study is mutualistic remains to be determined.

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Larger trees appeared to have more cocoons and ants; however, approximately half of all cocoons were unoccupied by ants or other invertebrates (see also Sagata et al., 2010; Campbell et al., 2015). While this could be due to low cocoon occupancy (perhaps because ants use the cocoons opportunistically as shelter and nesting sites); it may also be because ants migrate between shelters to track microclimates (Jones and Oldroyd, 2007), or due to recent changes in colony sizes (Palmer, 2003).

4.2. Morphospecies abundance and occurrence in cocoons as a function of cocoon characteristics

Ant colonies can select nests based on the quality of each nesting site relative to others (Thomas, 2002). Of the occupied *G. postica* cocoons, ant abundance and occurrence were highest and most apparent in cocoons that contained only parasite holes (the smallest hole types within the cocoons). Similarly, Pratt and Pierce (2001) found that the cavity-dwelling ant species, *Leptothorax curvispinosus*, preferred cavities that had small entrance holes. A preference for cocoons with smaller holes could be because these cocoons show greater thermal buffering and higher humidity levels (see Jones and Oldroyd, 2007). Indeed, desiccation (Hood and Tschinkel, 1990) and heat (Roces and Núñez, 1989) are important stresses for ants, especially in arid environments. Cocoons with smaller holes may also provide refuge from competitors and predators to the ants and their brood (Blüthgen and Feldhaar, 2010), because nests with smaller entrance holes can be more effectively defended (Palmer, 2003).

Ant abundance was greater in wider cocoons, in agreement with studies that show that domatium size constrains colony size (Thomas, 2002; Campbell et al., 2013a). Larger nests can support more individual ants and brood (Campbell et al., 2013a). Conversely, ants were less likely to occur in longer cocoons, indicating that nest selection is also influenced by nest

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shape, which can affect microclimatic parameters such as the amount of solar radiation reaching the nest surface (Hubbard and Cunningham, 1977).

4.3. Scale insect presence

Ant occurrence in cocoons was positively related to the presence of scale insects. Honey-dew-producing homopterans play an important role in structuring arboreal ant communities (Blüthgen et al., 2004; Styrsky and Eubanks, 2007) because they represent a key resource for the ants (Davidson et al., 2003). Both *Crematogaster* species were the most commonly encountered species tending the scale insects on the trees in this study, matching observations from other studies (Campbell et al., 2013b). This is further supported by observations that dominant ant species usually monopolize honeydew sources, making their co-occurrence with other scale insect-tending ant species rare (Blüthgen et al., 2004). Moreover, when scale insects were present on the trees, ants were nearly always observed tending them. These results suggest that on top of cocoon characteristics, the presence of scale insects on trees is another important factor for nest site selection by arboreal ants.

4.4. Conclusion

Our results suggest that *G. postica* cocoons increase tree structural complexity to the benefit of arboreal invertebrates. The fact that the cocoons constitute a habitat utilized by other species suggests that *G. postica* is indeed an autogenic ecosystem engineer (Lill and Marquis, 2003; Wright and Jones, 2006; Lima et al., 2013). Ecosystem engineering effects can occur at fine and broad scales and for short to long time periods (Wright and Jones, 2006). Due to the sporadic nature of *Gonometa* populations through space and time (Veldtman et al., 2007), the ecosystem engineering effect that the cocoons provide will likely vary spatially and temporally, occurring in an area in some years and not in others. The exact spatial scale at which *G. postica* cocoons are functioning as nest sites and shelters for arboreal invertebrates

is unknown. However, this phenomenon has been observed in the region of, but at significant distances from, the study area (> 50 km, pers. obs. MJR & MG) and in Namibia (> 600 km from the study area, pers. obs. HC). Moreover, *Gonometa postica* cocoons persist for at least two years within this environment, providing shelter and nest sites for ants and other invertebrates from the time of moth emergence until the cocoon degrades or falls off the tree. What remains to be determined is whether the cocoons significantly impact populations of ants and other invertebrates that utilize the structures, or whether these empty cocoons only function as opportunistic shelters and nest sites.

The shelter and nesting site function of *G. postica* cocoons could have implications for the harvesting of cocoons from the wild. Currently, silk industries in southern Africa are mainly reliant on harvesting empty *G. postica* cocoons or the pupal stage of the species (Veldtman et al., 2007). Such harvesting could impact upon the multiple species interactions occurring within these arboreal systems. Removal of cocoons could, for example, lead to increased myrmecophyte defoliation (or even mortality; see Moraes and Vasconcelos, 2009) of *V. erioloba* through the breakdown of mutualisms (Palmer et al., 2008). Ant-scale insect associations may also be sensitive to cocoon harvesting (see Feldhaar et al., 2000).

Therefore, depending on the spatial extent and permanence of the effect of the presence of empty *G. postica* on arboreal invertebrates, silk industries may have to be limited to harvesting a proportion of cocoons per tree. If cocoon collection cannot be regulated to maintain the ecological interactions in these arboreal systems, silk industries should focus on rolling out and improving semi-captive and artificial rearing techniques (Ngoka et al., 2008.). That way both *G. postica* populations and the species' greater ecological role can be maintained.

5. Acknowledgements

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Supplementary Material.

Table A.1. Results from the minimum adequate mixed effect hurdle models testing the effects of cocoon characteristics on (a) *Crematogaster* sp. 1 abundance (n = 270 cocoons, n = 88 trees, p < 0.05) and (b) *Crematogaster* sp. 1 presence-absence (n = 336 cocoons, n = 95 trees, p < 0.05) in *Gonometa postica* cocoons. Bold p-values indicate significant effects. Abbreviations: P = cocoons containing one or more small parasite holes; E = emerged cocoons and ES = emerged cocoons with secondary holes; Pr = other invertebrates present and Ab = other invertebrates absent

a. Fixed effects	Level	Estimate	SE	z value	p-value
(Intercept)	-	2.434	0.376	6.470	**< 0.001**
Width	-	0.097	0.019	5.090	**< 0.001**
Hole type	P > ES > E	-	-	-	**0.031**
Time of day	-	-0.016	0.010	-1.620	0.105
Other invertebrates	Pr > Ab	-	-	-	**< 0.001**
Random effect	SD	Variance			
(1|Tree)	0.471	0.222			

b. Fixed effects	Level	Estimate	SE	z value	p-value
(Intercept)	-	-1.189	0.691	-1.720	0.085
Length	-	-0.085	0.040	-2.130	**0.033**
Random effect	SD	Variance			
(1|Tree)	3.124	9.757			

Table A.2. Results from the minimum adequate mixed effect hurdle models testing the effects of cocoon characteristics on (a) overall ant abundance (n = 339 cocoons, n = 95 trees, p < 0.05) and (b) presence-absence (n = 702 cocoons, n = 124 trees, p < 0.05) in *Gonometa postica* cocoons. Bold p-values indicate significant effects. Abbreviations: P = cocoons containing one or more small parasite holes; E = emerged cocoons and ES = emerged cocoons with secondary holes; Pr = other invertebrates present and Ab = other invertebrates absent; N = north aspect and S = south aspect

a. Fixed effects	Level	Estimate	SE	z value	p-value
(Intercept)	-	2.562	0.335	7.650	**< 0.001**
Width	-	0.090	0.017	5.330	**< 0.001**
Hole type	P > ES > E	-	-	-	**0.018**
Time of day	-	-0.016	0.009	-1.680	0.094
Other invertebrates	Pr > Ab	-	-	-	**< 0.001**

Random effect	SD	Variance			
(1|Tree)	0.451	0.203			

b. Fixed effects	Level	Estimate	SE	z value	p-value
(Intercept)	-	-1.189	0.691	-1.720	0.085
Hole type	P > E = ES	-	-	-	**< 0.001**
Time of day	-	-0.026	0.016	-1.590	0.111
Other invertebrates	P > A	-	-	-	**< 0.001**
Length	-	0.033	0.018	1.880	0.061
Aspect	N = S	-	-	-	0.086

Random effect	SD	Variance			
(1|Tree)	0.830	0.688			

Table A.3. Results from the minimum adequate hurdle models, testing the effects of presence or absence of scale insects, the incidence of ants tending scale insects on the trees and time of day that sampling took place on (a) total ant abundance (n = 99 trees, p = 0.033) and (b) ant presence-absence (n = 195 trees, p < 0.05) within all *Gonometa postica* cocoons per tree. Bold p-values indicate significant effects. Abbreviations: Pr = present and Ab = absent

a. Variable	Level	Estimate	SE	z value	p-value
(Intercept)	-	5.391	0.163	33.010	**< 0.001**
Ants tending scales	Pr = Ab	-	-	-	0.052
Time of day	-	-0.013	0.009	-1.420	0.154

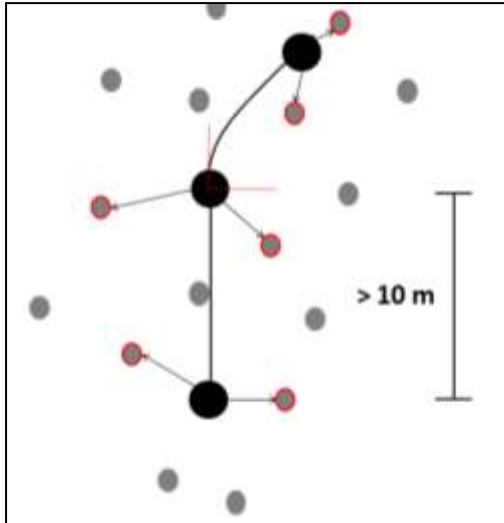| b. Variable	Level	Estimate	SE	z value	p-value
(Intercept)	-	-1.334	0.362	-3.680	**< 0.001**
Scale insects	Pr > Ab	-	-	-	**< 0.001**
Time of day	-	0.038	0.020	1.940	0.052

Fig A.1. Schematic diagram illustrating the tree sampling procedure. A focal tree (black dots) was randomly selected and sampled. The two nearest neighbouring trees (grey circles highlighted in red) were also selected and sampled such that the nearest neighbour of one focal tree was not the nearest neighbour of another focal tree. The next focal tree (located within a 90° angle in the direction of the transect and at least 10 m away from the previous focal tree) was sampled along with its two nearest neighbours.