Invasion impacts vary across the diel cycle: hemipterans supercharge ant ecosystem functions and restructure local invertebrate communities

Mark K. L. Wong[1,2,3*], Zohara Scott[2], Farhan Bokhari[2], Julian Kalau[4], Raphael K. Didham[3] and Melissa L. Thomas[2]

[1] School of Life and Environmental Sciences, The University of Sydney, Camperdown, NSW, 2006, Australia

[2] Harry Butler Institute, Murdoch University, Murdoch, 6150, WA, Australia

[3] School of Biological Sciences, The University of Western Australia, Crawley, WA, 6009, Australia

[4] Chevron Australia Pty Ltd, Level 2, The Esplanade, Perth, WA, 6000, Australia

*Corresponding author; email: markwong.research@outlook.com

Abstract

Biological invasions threaten biodiversity and ecosystem functions, often causing cascading effects across trophic levels. Yet how these impacts vary over the fundamental day–night cycle remains largely overlooked. On Barrow Island, a high-conservation-value reserve off northwestern Australia, we examined how infestations of the non-native scale insect *Saissetia miranda* (Hemiptera: Coccidae) on a dominant native tree species – the fig *Ficus brachypoda* – influenced native arboreal invertebrate communities and ant-mediated ecosystem functions in a natural matched-pairs experiment, comparing scale-infested versus uninfested sites. We observed the ecologically dominant native meat ant *Iridomyrmex sanguineus* collecting carbohydrate-rich honeydew from the non-native scale insects on fig trees. Although the meat ants are primarily diurnal, their nocturnal foraging activity increased by 164% at infested sites. Scale-infested sites supported higher abundances of arboreal invertebrates (~28% higher overall). In particular, scale infestations boosted the nighttime abundances of moth and cockroach species, which were observed feeding on excess honeydew, as well as spiders, possibly preying on these groups. Moreover, we uncovered knock-on effects on ant-mediated ecosystem functions in the brown and green food webs of infested sites. On the ground, the higher nocturnal ant activity contributed to a 207% increase in the mass of protein baits scavenged by ants during the night. In the canopy, there was a nearly fivefold increase in ant attacks on insect herbivores, as well as a 35% reduction in leaf damage across diel periods. Our findings show that non-native hemipterans can trigger carbohydrate-rich pulses in ecosystems, reshaping ant behaviour and amplifying both ant–herbivore interactions and higher-order effects on multitrophic communities. Critically, these impacts are not uniform across the diel cycle, but disproportionately affect nocturnal assemblages. Recognising the temporal dimension of invasion impacts is crucial for understanding and managing their full ecological consequences.

Introduction

A major concern with biological invasions is their far-reaching cascading effects on species and ecosystem functions, extending across multiple trophic levels (Ehrenfeld, 2010; Simberloff et al., 2013). The temporal dimensions of such impacts – exactly when they emerge, intensify and diminish – can have important implications for understanding and managing invasions. Although many species vary strongly in their behaviour, physiology, and interactions over the fundamental day–night (diel) cycle (Kronfeld-Schor & Dayan, 2003; Wong & Didham, 2024), a pervasive bias in ecological research towards daylight hours has left nocturnal communities and their contributions to ecosystem processes underexplored (Gaston, 2019). The consequences of invasive species for nocturnal biodiversity and functions may therefore be systematically underestimated. Given that many ecological interactions – such as herbivory, predation, and scavenging – vary with time of day (Cox & Gaston, 2024), invasion impacts are unlikely to be temporally uniform.

The sap-sucking insects of the order Hemiptera are among the most diverse and widespread invertebrate invaders, with at least 1,691 species known to have spread to non-native regions globally (Liebhold et al., 2024). Non-native hemipterans often exert disproportionate ecological impacts through mutualisms with ants which feed on the carbohydrate-rich honeydew they excrete (Styrsky & Eubanks, 2007). While such ant-hemipteran associations are indeed ‘novel’ in a coevolutionary sense (Simberloff & Von Holle, 1999), they can nevertheless have broad ecological effects. Many studies in managed systems show that such interactions not only alter ant behaviour but can also lead to cascading effects on ant–herbivore dynamics, plant health and the structure of multitrophic food webs (e.g. Powell, 2009; Tena et al., 2013; Kulikowski, 2020; Anastasio et al., 2021; reviewed in Styrsky & Eubanks, 2007; Nelson & Mooney, 2022). These wide-ranging effects reflect the central role of ants in ecosystem functioning, as they regulate green food webs by dispersing seeds and suppressing herbivores, and brown food webs through scavenging and nesting activities that drive decomposition, nutrient cycling and soil turnover (Rocha et al., 2024).

Islands are global hotspots for biological invasions (Roy et al., 2023) and have long served as model systems for uncovering their ecological mechanisms (Simberloff & Wilson, 1969). One well-documented example of a hemipteran invasion in this context is the co-invasion of the scale insect (*Coccus celatus*) and yellow crazy ant (*Anoplolepis gracilipes*) on Christmas Island (O’Dowd & Lake, 2003). The carbohydrate subsidies provided by the honeydew of *C. celatus* supported exceptionally high densities of *A. gracilipes*, driving severe ecological impacts. On the forest floor, these included the decimation of native crab populations and consequent transformation of forest structure through the release of seedling recruitment and reduced litter breakdown. In the canopy, excess honeydew promoted sooty mould proliferation, extensive tree dieback, and large-scale alterations to forest composition (O’Dowd & Lake, 2003). Yet aside from this classic case study, the ecological consequences of non-native hemipterans on islands, and particularly their interactions with native ants, remain poorly understood. Conceivably, such associations may generate similarly strong but context-dependent effects, especially when involving ecologically dominant native ant species.

Moreover, whether novel ant–hemipteran interactions disproportionately impact specific diel communities and ecosystem functions is poorly known. Many ant species show strong diel foraging patterns (Ohyama et al., 2024; Middendorp et al., 2025), which can strongly influence the nature and extent of their ecosystem functions (Houadria et al., 2016). In natural ant–hemipteran pairs, tending can modify ant diel activity, for instance leading to higher ant abundance around aphid colonies at night (Depa, 2024). While such mutualisms can shift ant diel activity, the effects of interactions with non-native hemipterans are unknown. Potentially, these novel interactions could alter the timing and magnitude of ant impacts on other species and ecosystem processes, but whether diurnal or nocturnal communities are disproportionately affected remains unclear. Understanding these temporal dynamics is crucial to assessing the ecological consequences of hemipteran invasions and their ant partners.

We investigated diel variation in the impacts of a recent hemipteran invasion on Barrow Island, a 23,500-ha nature reserve off the northwest coast of Australia. The island is of considerable ecological significance, supporting numerous endemic species and remaining one of the largest land masses globally without established non-indigenous vertebrates (Scott et al., 2017). The predominant habitat is spinifex grassland, with individuals of the dominant tree species – a native fig (*Ficus brachypoda*) – occurring patchily within this landscape (Fig. 1). The discrete patches of fig trees are integral to the island's biodiversity as they provide vital trophic and structural (i.e. refuge and nesting habitats) resources for numerous invertebrates and vertebrates (Lynch et al., 2019).

In a recent survey of 94 fig trees across Barrow Island in 2022, high densities of the non-native Mexican black scale *Saissetia miranda* (Hemiptera: Coccidae) were documented on 39 trees and found to be associated with the occurrence of sooty mould (Thomas & Framenau, 2023). The Mexican black scale is globally widespread, recorded from 40 countries spanning all major zoogeographic regions, including Africa, Asia, the Americas, and Europe, as well as oceanic islands such as Hawaii, Fiji, Galapagos and Cape Verde (García Morales et al., 2016). Although the ecological impacts of Mexican black scale remain poorly studied, there have been recent anecdotal reports of damage to *Ficus carica* in Iran (Moghaddam & Watson, 2024). Moreover, the closely related congener *Saissetia oleae* is a major pest of citrus and olive that reduces growth and yield through still poorly understood physiological mechanisms (dos Santos et al., 2022). While no clear impacts of Mexican black scale and sooty mould on the health of fig trees on Barrow Island have yet emerged (Thomas & Framenau, 2023), the potential knock-on effects of interactions between the scale and native ants on the island's biodiversity and ecosystem functions are unknown.

We focused our investigation on the effects of the scale infestation on local invertebrate communities as well as ant-mediated ecosystem functions occurring on and around the ecologically pivotal fig trees of Barrow Island. Specifically, we studied (i) the composition of the local ant community and their foraging activity, (ii) the composition of multitrophic invertebrate communities in the canopy, (iii) the performance of two crucial ant-mediated ecosystem functions for the brown and green food webs: ant scavenging on insect biomass on the ground, and ant attacks on herbivores in the canopy, and (iv) leaf damage from herbivory in the canopy. We leveraged a natural matched-pairs experimental design, comparing the study parameters for scale–infested trees to adjacent uninfested controls. To test for diel variation in invasion impacts, we conducted observations during both the day and night. We hypothesised that the presence of non-native scale insects would increase nocturnal ant diversity and activity (Depa, 2024), thereby enhancing nighttime rates of ant scavenging and attacks on canopy herbivores, ultimately reducing overall leaf damage and altering the composition of nocturnal invertebrate communities.

Methods

Study period and sites

The study was conducted between 20 August and 25 September 2024, coinciding with the peak activity period of Mexican black scale and associated sooty mould outbreaks (Thomas & Framenau, 2023). We employed a natural matched-pairs experimental design with the two geographic regions of Barrow Island (northern and southern) as a blocking factor. We sampled a total of 20 paired sites (40 sites in total) relatively evenly distributed across these blocks (nine site-pairs in the northern block, eleven site-pairs in the southern block; Fig. S1). We first selected an infested site by identifying a fig tree hosting feeding populations of Mexican black scale on at least one-third of its canopy. Such trees were usually straightforward to locate, as the sooty mould associated with Mexican black scale typically enveloped the canopy, giving the trees a distinctly dark and conspicuous appearance (Fig. 1). For each infested site, we then selected a paired control site comprising a fig tree of comparable stature located at least 50 m away, verifying that it had not been previously infested in 2022 or 2023 using data from Thomas and Framenau (2023). The 50 m separation was chosen to minimise overlap in local ant communities and the low overlap was confirmed during the ant survey (see below). Surveys of all study parameters (below) were conducted at all 20 site-pairs during the day (0900–1500 h), and at a subset of 10 site-pairs (five northern block, five southern block) at night (2000–0000 h). All measurements for a given focal parameter (listed below) were conducted by the same observer across the entire study, with paired infested and control sites measured within the same hour to ensure consistency and minimise observer bias.

Although a minimum distance of 50 m between infested and control sites was expected to minimise overlap in ant communities, colonies of the abundant meat ant *Iridomyrmex sanguineus* occasionally established satellite nests only 5–10 m apart. To ensure independence, we confirmed colony identity prior to baiting by reciprocally translocating meat ant workers between sites and testing for antagonistic interactions with the resident meat ants.

Ant community composition and trophic preferences

We assessed ant communities using baits representing two key trophic resources required for colony maintenance and reproduction: carbohydrates and insect protein (Feldhaar, 2014). Each bait type was presented as standardised cubes of agar jelly, with carbohydrate baits made from 15% sugar solution and protein baits from 15% cricket powder solution, each set in 0.8% agar. We used agar-based baits because they retain structural integrity under high temperatures and allow resources to be presented in consistent amounts and configurations, thereby facilitating accurate comparisons of ant trophic preferences and resource removal. We cut the baits into standardised cubes (2 mm on each side; ~0.06 g) that could be readily carried by ants.

At each focal tree we established five bait stations on the ground around the crown perimeter, spaced approximately 2–4 m apart. Each station consisted of two petri dishes with small side openings to permit ant entry: one dish containing 16 cubes of carbohydrate bait, the other 16 cubes of protein bait (Fig. 1). Baits were exposed for 30 minutes, during which we recorded the species identities and abundances of all ants recruiting at 10-minute intervals to determine community composition as well as species' preferences for specific resources. We collected representative specimens of each species for identification using taxonomic keys (Heterick, 2021) in the laboratory. Using an infrared thermometer (Matador M207), we recorded the ground surface temperature at each bait station during each survey.

Arboreal invertebrate community composition

We sampled invertebrates in the canopy of the fig tree in each site only after the ant baiting and predation assays (below) were completed so as not to disrupt ant activity. Each site was surveyed using two complementary methods (Fig. 1). First, one researcher conducted a 10-minute manual search of the canopy, collecting invertebrates by hand into vials containing 100% ethanol. Second, another researcher performed systematic sweep-netting of all branches. Specimens were bagged and frozen immediately, then stored in 100% ethanol. This combination of sampling methods ensured broad coverage of canopy invertebrates across body sizes, mobility, and conspicuousness. To maximise consistency, the same researchers performed their respective tasks at all sites. Specimens collected using both methods were combined into a single pooled sample per site for all subsequent processing and analyses. All specimens were bagged and frozen immediately, then sorted and stored in ethanol. Taxonomic identifications to order, family, species, or morphospecies level were conducted using the Barrow Island invertebrate reference collection currently housed at Murdoch University, Western Australia.

Ant ecosystem functions in brown and green food webs

To quantify the scavenging of insect biomass by ants, we measured the mass of protein bait removed during the 30-minute period. Pilot trials confirmed that this duration was sufficient for ants to completely remove all protein baits during both day and night sampling.

To quantify ant predation pressure on canopy herbivores, we used model caterpillars fashioned from green moulding clay (after Roslin et al., 2017) (Fig. 1). Five caterpillars were attached to the terminal branches of each tree, spaced evenly around the canopy's circumference and placed arbitrarily across both lower and upper canopy positions. After 30 minutes of exposure, caterpillars were examined for signs of ant attack, typically conspicuous paired mandible impressions. We recorded the number of bite marks per caterpillar (attack severity) and the proportion of caterpillars attacked per site (attack incidence). We then multiplied the measure of incidence by the mean value of severity to obtain an incidence–severity measure of ant predation pressure at each site that was used for analysis.

Foliar herbivory

We assessed foliar herbivory on the fig tree at each site by visually surveying the entire canopy and estimating damage across leaves encountered throughout this inspection (Fig. 1). Specifically, we estimated (i) the incidence of herbivory, expressed as the percentage of leaves showing evidence of herbivore damage, and (ii) the severity of damage, quantified as the average proportion of leaf area removed on damaged leaves (after Smith et al., 2005). Rather than sampling a fixed number of leaves, the observer conducted a systematic visual scan of the canopy and integrated observations across all visible foliage to generate these whole-tree estimates. All assessments were made by the same observer across sites to ensure consistency. Unlike the other study parameters, which were assessed during both day and night, foliar herbivory was measured once per site, as this metric reflects cumulative leaf damage rather than instantaneous herbivore activity and was not expected to change appreciably within a 24-h period. We multiplied measures of incidence by severity to obtain an incidence–severity measure of foliar herbivory for analysis.

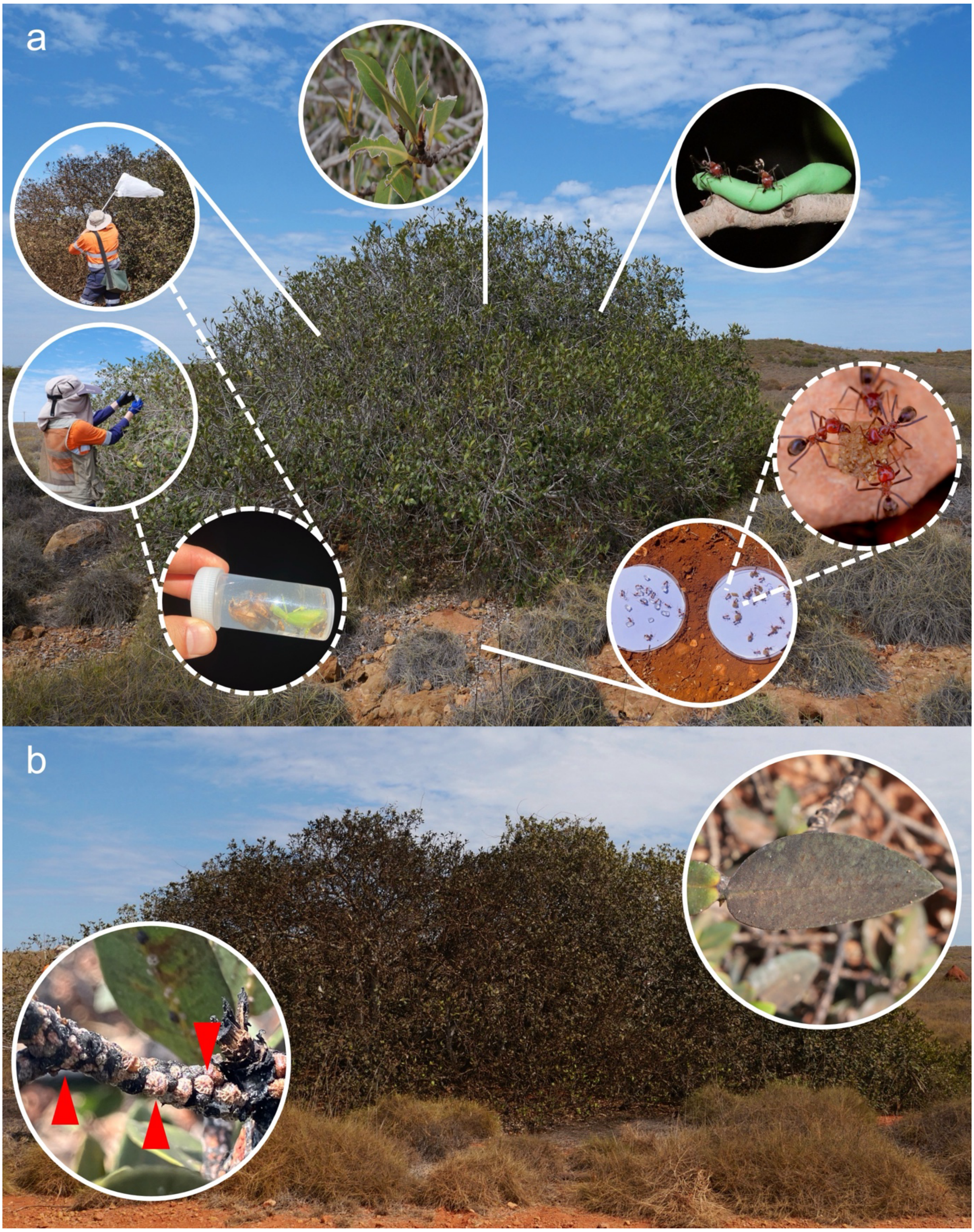

Figure 1. Study system and sampling methods. (a) Illustration of sampling methods at each site, which centred on a native fig tree (photograph shows a control site with a fig tree lacking the non-native Mexican black scale). Sampling methods included (anti-clockwise from bottom right): baiting ant communities with carbohydrate and insect protein-enriched agar on the ground; assessing ant attacks on herbivore models in the canopy; assessments of foliar herbivory in the canopy; and sampling canopy invertebrates by sweep netting and direct sampling. (b) An infested site, comprising a fig tree infested with Mexican black scale (left inset: red arrows). Infested fig trees were typically enveloped in black sooty mould (right inset), giving their canopies a distinctly darker shade.

Statistical analysis

Ant community and foraging patterns of dominant ants

We tested whether ant species richness (the total number of ant species recorded at baits in each site during a particular diel period) was significantly influenced by infestation status (the presence of Mexican black scale on the fig tree), the specific diel period, or an interaction between the two factors using a Poisson generalised linear mixed effects model (GLMM) with a logit link. The model included fixed effects for infestation status (infested vs. control), diel period (day vs. night), and their interaction. Random intercepts for site-pair (20 in total) and region (northern vs. southern) were included to account for repeated measures and spatial variation.

We also tested the effects of infestation status and diel period on the foraging activity and trophic preferences of the dominant ant species, the meat ant *I. sanguineus* using generalised linear mixed models. Foraging activity was quantified as bait occupancy by the meat ants. At each site and sampling period, five bait stations were deployed, and occupancy was modelled as a binomial response (number of baits occupied vs. unoccupied) with a logit link. Fixed effects included infestation status, diel period, and their interaction. Site-pair and region were included as random intercepts. Trophic preferences were assessed by analysing meat ant recruitment to carbohydrate versus protein resources. The response variable was the mean number of meat ant workers observed across all baits of a given resource type in each site during each baiting session. Recruitment was modelled using a Gamma error distribution with a log link. Fixed effects included infestation status, resource type, diel period, and all interactions. Site-pair and region were included as random intercepts.

Arboreal invertebrate community richness and composition

We tested whether invertebrate richness (total number of orders, families, or species) and abundance recorded at each site during a given diel period was influenced by infestation status, diel period, or their interaction. Separate Poisson GLMMs were fitted for order-, family-, species-level richness, and abundance, with infestation status, diel period, and their interaction as fixed effects, and site-pair and region as random intercepts. We also tested whether invertebrate community composition differed between control and infested sites using permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarities calculated from site-level community matrices of taxonomic order abundances. Infestation status (control vs. infested), diel period (day vs. night), and their interaction were included as fixed factors, with site-pair included as a blocking factor in the model. A SIMPER analysis was used to identify the taxa that contributed most to compositional dissimilarity. Patterns in community composition were visualised using non-metric multidimensional scaling (NMDS) ordinations derived from the same dissimilarity matrix.

Ecosystem functions in brown and green food webs

We tested the effects of infestation status and diel period on ant-mediated scavenging in the brown food web and on the incidence–severity of ant attacks on canopy herbivores in the green food web. We also examined whether the incidence–severity of foliar herbivory on fig trees varied with infestation status.

Scavenging by ants was quantified as the proportion of protein baits removed at each site and analysed using a generalised linear mixed-effects model with a binomial error distribution and logit link. The response was specified as the number of protein baits removed versus not removed, with infestation status, diel period, and their interaction as fixed effects, and site-pair and region as random intercepts. Ant scavenging was quantified using protein bait removal because protein foraging by ants is more closely associated with predatory and scavenging behaviour, whereas carbohydrate foraging primarily reflects exploitation of sugar resources such as honeydew and would be strongly confounded by the presence of scale insects (Davidson, 1997). The incidence–severity of ant attacks on canopy herbivores was analysed using a generalised linear mixed model with a Tweedie error distribution and log link, with the same fixed and random effects. The incidence–severity of foliar herbivory was log transformed for normality and analysed using a linear mixed-effects model with infestation status as a fixed effect and site-pair and region as random intercepts.

All data were analysed in R version 4.3.0 (R Core Team, 2023). Linear and generalised linear mixed models were built using *lme4* (Bates et al., 2015) and *glmmTMB* (McGillycuddy et al., 2025), respectively. Model estimates were back-transformed to the original scale to aid interpretation and reported as multiplicative changes (i.e., percent differences) in the results. PERMANOVA and SIMPER analyses were conducted using *vegan* (Oksanen et al., 2013).

Results

Ant community and foraging patterns of dominant ants

A total of 16 ant species representing five subfamilies were collected (Table S1). Ant species richness did not vary significantly between scale-infested and control sites, nor between diel periods (Fig. 2a; Table S2). Among the ant species, the meat ant *I. sanguineus* was numerically dominant, occurring at all sites and comprising a mean of 95.7% (± 10.9 SD) of all individuals recorded at baits per site.

Foraging activity of the meat ant (measured as the proportion of baits occupied) was significantly influenced by diel period, declining sharply at night ($\beta=-2.69$, $P<0.001$). However, at scale-infested sites, this decline was mitigated, as indicated by a significant interaction between infestation status and diel period ($\beta=1.40$, $P=0.04$). At control sites, meat ant foraging declined by 66% from day (mean bait occupancy rate=0.83) to night (mean=0.28). In contrast, nocturnal foraging activity was higher at scale-infested sites (mean=0.74), representing a 164% increase relative to control sites (Fig. 2b).

The trophic preference of the meat ant was influenced by infestation status and diel period. Recruitment, measured as the mean number of workers recruiting over the baiting session, was significantly lower to protein resources than to carbohydrate resources ($\beta=-0.44$, $P=0.002$), while scale infestation increased overall recruitment ($\beta=0.60$, $P=0.01$).

Recruitment to protein resources declined at night relative to the day, as indicated by a negative interaction between resource type and diel period ($\beta=-0.88$, $P=0.008$). However, the nocturnal reduction in recruitment to protein was moderated by infestation status, as reflected by a positive three-way interaction between infestation status, resource type and diel period ($\beta=0.76$, $P=0.06$) (Table S3). Specifically, at protein resources during the night, mean recruitment increased from 1.8 workers at control sites to 8.2 workers at scale-infested sites (Fig. 2c).

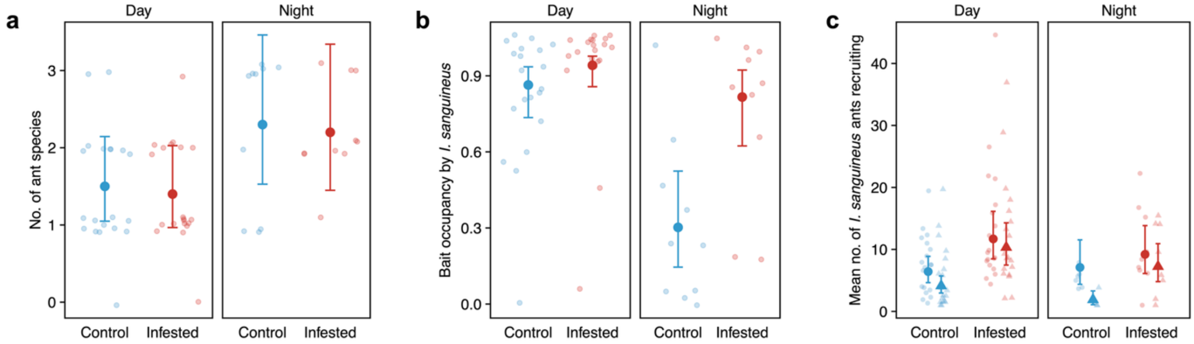

Figure 2. Effects of scale infestation and diel period on ants on Barrow Island. (a): Ant species richness neither varied significantly with infestation status nor with diel period. (b): Bait occupancy of the dominant meat ant *I. sanguineus* was significantly higher at infested sites at night. (c): The mean number of meat ant workers recruiting to protein resources (triangles) was consistently lower than that to carbohydrate resources (circles), but nocturnal recruitment to protein resources was higher at infested sites. In all plots, points indicate predicted mean values and error bars indicate 95% confidence intervals (CIs).

Arboreal invertebrate community richness and composition

A total of 857 individual invertebrates were collected. These comprised 104 species from 70 families in 12 taxonomic orders, including numerous spiders (Araneae), cockroaches (Blattodea), flies (Diptera), wasps (Hymenoptera), moths (Lepidoptera), crickets (Orthoptera) and other invertebrates (Table S4). While there were no significant effects of infestation status, diel period, or their interaction on the richness of invertebrate orders, families, or species at a site (Table S2), a GLMM showed that invertebrate abundance was 28% higher at scale-infested sites ($B=0.25$, $P=0.003$). Additionally, a PERMANOVA model showed that the composition of the invertebrate community in a site (i.e. the relative abundances of individuals of different species) was significantly influenced by infestation status ($F_{1,56}=2.76$, $R^2=0.04$, $P=0.002$) and diel period ($F_{1,56}=4.33$, $R^2=0.07$, $P=0.001$). Collectively, diel period and infestation status explained 11% of the compositional dissimilarity among invertebrate communities, as reflected by the overlap observed in the NMDS ordination (Fig. S2). Compositional dissimilarity was primarily driven by changes in the abundances of a subset of invertebrate species. As indicated by SIMPER analysis, 54% of the average dissimilarity between scale-infested and control invertebrate communities was attributable to differences in the abundances of 10 species representing eight orders (Fig. 3). In particular, one spider (Araneae), two cockroaches (Blattodea), and one moth (Lepidoptera) species were more abundant at scale-infested sites at night, whereas one fly (Diptera), ant (Hymenoptera), and beetle (Coleoptera) species were more abundant at scale-infested sites during the day (Fig. 3).

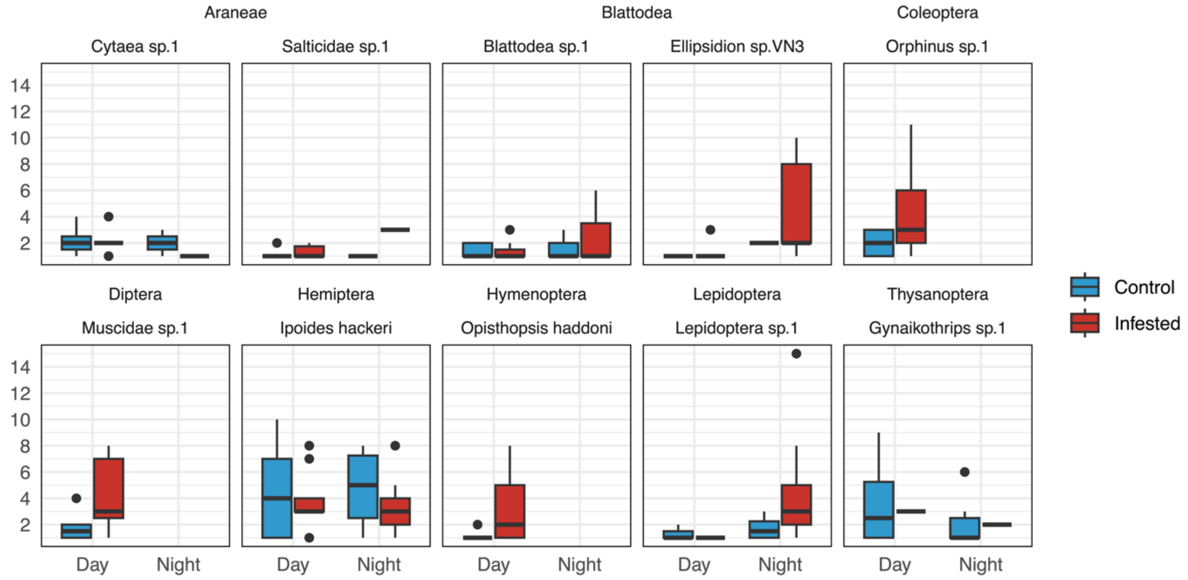

Figure 3. Plots showing sample-level species abundances, by scale-infestation status and diel period, for the 10 invertebrate species (from eight orders) that together accounted for approximately 54% of the average dissimilarity between control and scale-infested sites based on SIMPER analysis. Black bars in boxplots indicate median values and boxes represent interquartile range.

Ecosystem functions in brown and green food webs

Ant scavenging was significantly influenced by both diel period and infestation status. Overall, a shift from day to night had a significant negative effect on scavenging (β=-1.51, $P < 0.001$), while scale infestation had a significant positive effect (β=1.05, $P < 0.001$), with a smaller positive interaction term (β=0.43, P=0.004) (Table S2). Consequently, scale infestation increased the mean mass of protein bait removed by ants, with similar absolute increases in mass removed during day and night (day: 3.13 g vs 1.90 g in controls; night: 1.87 g vs 0.61 g in controls), but substantially stronger proportional effects at night (day: +65%; night: +207%).

Scale infestation also had a significant positive effect on the incidence–severity of ant attacks on canopy herbivores (β=1.31, P=0.002). The incidence–severity of ant attacks in infested sites was nearly fivefold higher (mean=3.52) than in control sites (mean=0.59). Attacks did not vary significantly with diel period (Fig. 4b).

Scale infestation had a significant negative effect on the incidence–severity of foliar herbivory on the fig trees (β=-1.08, P=0.003). The incidence–severity of foliar herbivory on fig trees in infested sites (mean=2.0) was 35% lower than in control sites (mean=3.07) (Fig. 4c).

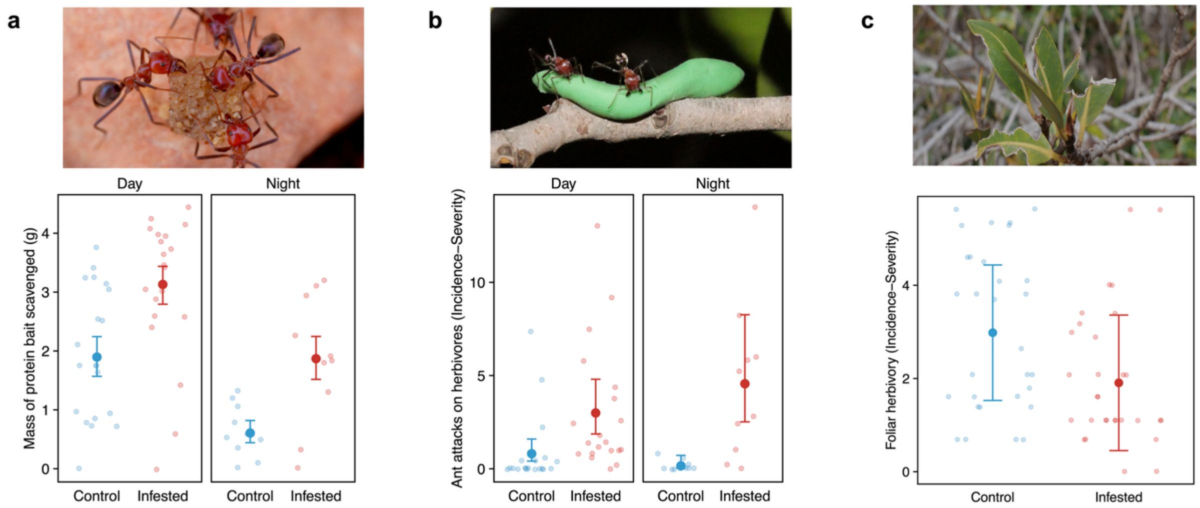

Figure 4. Effects of *S. miranda* infestation status and diel period on ecosystem functions on Barrow Island. (a): The mass of protein baits removed by scavenging ants was significantly higher during the day as well as at infested sites. (b): The incidence–severity (proportion of model caterpillars attacked × mean bite marks per caterpillar) of ant attacks on canopy herbivores was significantly higher at infested sites. (c): The incidence–severity (percentage of leaves damaged × mean proportion of leaf area removed per damaged leaf) of herbivory on leaves of fig trees was marginally lower at infested sites. In all plots, points indicate predicted mean values and error bars indicate 95% confidence intervals (CIs).

Discussion

Despite being widespread globally, the ecological consequences of hemipteran invasions remain poorly resolved outside of a handful of case studies. Our findings demonstrate that invasions by non-native hemipterans on islands can trigger short-term cascading effects that influence multitrophic interactions and ecosystem processes across both brown and green food webs. These effects were associated with the carbohydrate-rich honeydew produced by the non-native Mexican black scale *S. miranda*, which supported strong nocturnal activity of the dominant native meat ant *I. sanguineus* and altered its trophic foraging. The resulting changes in ant activity had temporally variable impacts across the diel cycle, with disproportionate consequences for nocturnal assemblages, including shifts in the abundance of multiple canopy invertebrate taxa.

Carbohydrate subsidies amplify ant foraging and alter trophic preferences

The strongest effect of scale infestations was the creation of a carbohydrate subsidy in the form of honeydew. Carbohydrates are critical for fuelling ant activity, and honeydew provision is known to stimulate higher recruitment and prolonged foraging in both native and invasive ants (Styrsky & Eubanks, 2007; Nelson & Mooney, 2022). In our study, honeydew presence coincided with sustained nocturnal activity of the meat ant, a period when foraging otherwise declined sharply at control sites.

Davidson (1997) proposed that surplus carbohydrates in ant colonies can be allocated to activities that enhance acquisition of limiting protein resources. Our results are consistent with this hypothesis: at infested sites, meat ant colonies allocated a greater share of foragers to protein resources at night. This suggests that carbohydrate subsidies did not only attract workers to honeydew itself, but also enhanced overall colony capacity for acquiring limiting nitrogenous nutrients necessary for brood development and colony growth (Feldhaar, 2014). In other words, access to abundant honeydew may have allowed colonies to redirect foraging effort toward protein resources, illustrating a mechanistic link between carbohydrate subsidies and altered trophic allocation.

Cascading effects onto ecosystem functions in brown and green food webs

The behavioural changes of meat ants had clear consequences for ant-mediated ecosystem functions. In the brown food web, enhanced nocturnal activity translated into a 207% increase in ant scavenging of insect protein baits, offsetting the typical nocturnal decline in scavenging observed at control sites. This suggests that honeydew subsidies can not only increase total rates of nutrient recycling via scavenging but also redistribute them across diel periods. In the green food web, ant attacks on model herbivores were more than fourfold higher at infested sites, and leaf damage was reduced, consistent with strengthened top-down control by ants. While the herbivory reduction was not statistically significant, the direction of the effect aligns with previous studies demonstrating honeydew-fuelled increases in ant protection of plants (Tena et al., 2013; Anastasio et al., 2021). Taken together, these findings show that hemipteran–ant associations can amplify both brown and green food web processes, with consequences for plant–herbivore dynamics and energy flows through detrital pathways.

Effects on nocturnal multitrophic communities

Beyond direct effects on ants and their functions, scale infestations also restructured arboreal invertebrate communities, but these changes were concentrated at night. Moths (Lepidoptera) and cockroaches (Blattodea) were more abundant on infested trees during nocturnal surveys, with spiders (Araneae) likewise increasing, possibly reflecting greater prey availability. One possible explanation is that reduced ant activity in the canopy at night freed up honeydew for other insects, or lowered the risk of ant aggression. However, our assays indicated that ant attack rates on model herbivores in the canopy remained consistently high during both day and night on infested trees (Fig. 4b). This suggested that ant pressure did not diminish sufficiently at night to account for the observed shifts.

Instead, the predominance of nocturnal responses is more likely to reflect the intersection of two processes: intrinsic diel activity patterns of canopy invertebrates and temporal variation in resource availability. Many insects are adapted to exploit cooler nighttime conditions and reduced exposure to vertebrate predators such as birds (Wong & Didham, 2024), which likely concentrates activity at night. At the same time, honeydew subsidies generated by scale insects may not be temporally constant. Plant physiological processes and phloem quality can vary across the diel cycle, potentially influencing sap-feeding activity and honeydew excretion rates. If honeydew availability is elevated at night, this would further amplify nocturnal aggregation and feeding by canopy invertebrates. However, we did not quantify diel variation in honeydew production by *S. miranda*, and resolving whether subsidy supply itself varies over the diel cycle represents an important avenue for future work. Together, these mechanisms suggest that non-native hemipterans not only introduce novel carbohydrate subsidies into ecosystems, but also modulate when those subsidies are most strongly expressed and utilised.

Broader implications and future research

One limitation of our study was the relatively brief observation window within a single season. Hemipteran populations often fluctuate with plant phenology, climatic conditions, and their own life cycles (Bodino et al., 2019; Santos et al., 2019), which may in turn modulate their levels of honeydew production and ecological impacts. Future research should therefore examine invasion impacts across multiple seasons and years, testing whether the strength and timing of honeydew-mediated subsidies vary not only over the diel cycle but also across seasonal and interannual scales. Such work would provide a more complete picture of how hemipteran invasions interact with temporal dynamics to shape communities and ecosystem functions. Another key direction for future research would be to quantify honeydew production and composition by the non-native scale insect and experimentally test its role in shaping ant–hemipteran associations and downstream community impacts, thereby establishing a mechanistic link between honeydew availability and observed trophic restructuring.

In summary, our results highlight that the ecological impacts of non-native hemipterans are strongly context-dependent, emerging not only from novel associations with ants but also from the temporal structuring of ecological processes. By disproportionately altering nocturnal interactions and communities, non-native scale insects reshaped an ecological domain typically underrepresented in invasion studies. Critically, if our surveys had been restricted to daylight hours, the strongest community-level effects would not have been detected. This underscores the need to integrate nocturnal perspectives into invasion ecology more broadly.

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