The secondary invasion of giant African land snail has little impact on litter or seedling dynamics in rainforest

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Abstract In the absence of empirical evidence, invasive species are often assumed to have negative impacts because of their conspicuously high abundance. The giant African land snail Achatina (Lissachatina) fulica is one such invader where its impact in natural ecosystems remains completely untested. On Christmas Island (Indian Ocean), A. fulica has become established across large tracts of rainforest following the impacts of invasive yellow crazy ant (Anoplolepis gracilipes) in mutualism with non-native scale insects. Yellow crazy ants facilitate the secondary invasion of A. fulica by extirpating native red land crabs (Gecarcoidea natalis) that are normally effective predators of A. fulica. We used a multifaceted approach to investigate some potential impacts of abundant A. fulica in invaded rainforest. Over the course of a wet season, diel activity transects showed that A. fulica consumed detrital material almost exclusively. However, stable isotope analysis did not confidently identify A. fulica as a predominantly detritivorous species. We found no statistically significant treatment effects of A. fulica exclusion on standing leaf litter and seedling recruitment processes during a 6-month manipulative field study. However, litter cover and biomass did remain slightly higher where A. fulica were excluded, albeit with overlapping confidence intervals with control plots. Our study constitutes the first empirical test for impact of A. fulica in a natural ecosystem and suggests that for Christmas Island rainforest, this species is not a damaging invader. Other studies will need to assess the impacts of A. fulica in other natural areas before these findings could be considered broadly applicable.

Key words: Achatina fulica, Christmas Island, exclusion experiment, invasional meltdown, stable isotope analysis, yellow crazy ant.

INTRODUCTION

Biological invasions are considered a major driver of environmental change (Didham et al. 2005; Tylianakis et al. 2008; Pyšek & Richardson 2010). The ubiquity of introduced species has generated important research on the ecology, mechanisms of spread and management of invasions (Simberloff 2009; Pyšek & Richardson 2010), yet the ecological impact of many introduced species remains poorly understood (Barney et al. 2013). The reported impacts of many common and widespread introduced species remain anecdotal and observational (Reaser et al. 2007), and in many cases, costly management is undertaken on the assumption that the species must be having negative effects (Barney et al. 2013, 2015). The precautionary principle drives much of this approach (Simberloff 2003; Cook & Thomas 2007), but it can also be attributed to the lack of an holistic framework for identifying the tipping point between a benign introduction and a high impact invader (Barney et al. 2013). For many introduced species, whether the presumption of impact is valid, or if some highly abundant invasive species actually have little to no impact, remains relatively unexplored (Yokomizo & Possingham 2009; Barney et al. 2013).

One such invader is the giant African land snail Achatina (Lissachatina) fulica Bowdich, 1822. Native to East Africa, A. fulica has successfully invaded and established high-density populations on most tropical mainland and many Indo-Pacific and other islands (Raut & Barker 2002). Their spread has been attributed to a number of factors, including accidental introductions through global commerce and trade, and deliberate introductions as a food resource (Mead 1961; Raut & Barker 2002; Thiengo et al. 2007; Cowie et al. 2008). An oviparous hermaphro-dite, A. fulica matures within 5–8 months, can grow to 15 cm or more in length, will lay an average of 1000 eggs during its lifetime, has a generalized diet and can tolerate a wide range of environmental conditions (Mead 1961; Raut & Barker 2002). These characteristics make A. fulica a very successful invader and it is recognized as an invasive species of global significance (Lowe et al. 2000). This designation is based primarily on the ability of A. fulica to reach high population densities, an observed broad diet...
that includes hundreds of plant species and detritus, and on some anecdotal accounts of impact in agricultural systems (Mead 1961; Raut & Barker 2002; Thiengo et al. 2007).

The impacts of Agrioxyris fulica on agriculture are potentially threefold: (i) these snails can cause a loss of productivity (either directly or indirectly), (ii) there can be labour and equipment costs associated with their control and (iii) there may be opportunity loss due to changes in regular cropping behaviour when A. fulica are present (Raut & Barker 2002). Although known to consume a wide variety of crop species, no quantitative assessment of impacts and costs at a large scale exists, and several researchers posit that the assumed severe impacts are the product of embellished and exaggerated accounts of damage in gardens and small-scale agriculture (Mead 1961; Raut & Barker 2002; Thiengo et al. 2007). There may also be temporal and spatial variability in which crop species are consumed, and how much is consumed (Mead 1961). Despite this lack of documented impact, significant control measures – including physical, chemical and biological – have been attempted with limited success across much of the species introduced range (Simberloff & Gibbons 2004; Thiengo et al. 2007; Colley & Fischer 2009).

Similarly to agricultural, the impact of A. fulica on natural ecosystems is also potentially threefold: (i) direct alteration through herbivory, (ii) indirect alteration of nutrient cycling via excessive plant material (both live and dead) consumption and (iii) potential impact on native land snails by direct competition and/or fouling the habitat with mucus and faeces (Raut & Barker 2002). Again, these impacts are assumed rather than based on quantitative information, which has led some to suggest that any lasting impact of A. fulica is not severe (Civeyrel & Simberloff 1996). Despite A. fulica continuing to spread (Thiengo et al. 2007; Green et al. 2011; Vogler et al. 2013), and complete eradication in many cases impossible (Thiengo et al. 2007), there remains a conspicuous lack of empirical research quantifying the impact of this species in natural systems.

Since around the year 2000, A. fulica has established high-density populations in rainforest on Christmas Island (Indian Ocean) as a consequence of the impacts of other successful invaders (Green et al. 2011). Assuming high density precipitates impact, we hypothesize that invasion by A. fulica significantly impacts the rainforest community on Christmas Island, probably through their generalist feeding behaviour. In our study we specifically asked: (i) Does A. fulica impact seedling recruitment, seedling survival and leaf litter cover or biomass? (ii) Are A. fulica more herbivorous or detritivorous in their feeding habits or diet? and (iii) Are these potential impacts related to diel activity patterns?

METHODS

Study system

Christmas Island (105°40'E, 10°30'S) is an isolated oceanic island, 360 km south of Java in the north-eastern Indian Ocean. The climate is tropical, with distinct wet (December–April) and dry (May–November) seasons (Falkland 1986). This limestone island rises in a series of cliffs and terraces to a central plateau (maximum elevation 360 m). Approximately 74% of the island (total area 135 km²) supports broad-leaved, structurally simple tropical rainforest (Du Puy 1993).

Achatina fulica was probably introduced to Christmas Island as a food resource during the Second World War (Sproul 1983). Until recently it was restricted to disturbed habitats (urban areas, roadsides and areas cleared for phosphate mining) and settled areas, and was unable to successfully invade intact rainforest because of strong biotic resistance provided by the endemic red land crab (Gecarcincoidea natalis) (Lake & O'Dowd 1991; Green et al. 2011). This naturally abundant land crab (~0.75 crabs m⁻²; Green 1997) plays a key functional role in shaping the forest understory structure by largely regulating seedling recruitment and litter decomposition (Green et al. 1997, 1999, 2008) and inhibits the entry of A. fulica into intact rainforest through opportunistic predation (Lake & O'Dowd 1991; Green et al. 2011).

However, much of the rainforest on Christmas Island has seen the local extinction of the red crab due to the impacts of other invaders. The yellow crazy ant (Anoplolepis gracilipes), a pantropical invader that has spread rapidly across the Indo-Pacific region (Wetterer 2005), has formed a mutualistic relationship with a number of non-native honeydew-secreting insects (Neumann et al. 2016) which has resulted in expansive high-density supercolonies on the island (O'Dowd et al. 2003; Abbott 2006). Where supercolonies have formed, red crabs are absent because of predation from abundant yellow crazy ants, which has led to considerable changes in forest understory structure (O'Dowd et al. 2003). Leaf litter is allowed to build up and persist throughout much of the year and there is a pulse recruitment of seedlings leading to greater habitat complexity (O'Dowd et al. 2003). Yellow crazy ants do not kill A. fulica (Green et al. 2011), so an indirect effect of invasion by ants and their scale insect mutualists has been the entry and spread of A. fulica into altered rainforest on the island (Green et al. 2011).

The invasion of A. fulica into the rainforest has progressed from multiple invasion fronts since 2001 (see Green et al. 2011). We identified a single experimental site in the southwest corner of the island (105°34'14"E, 10°29'43"S), where A. fulica density was high and thus provided a good chance of observing impacts. The rainforest at this site is of the type occurring on relatively shallow soils, is structurally mature and has never been cleared for phosphate mining. The canopy is between 20 and 30 m tall, and dominated by species including Dysoxylum gauchich sodium (Meliaceae), Inocarpus fagifer (Fabaceae) and Clusiaylon indicum (Euphorbiaceae). Seedling recruitment had occurred following red crab extirpation circa 2005, resulting in a complex understory between 2 and 7 m tall.

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A high-density yellow crazy ant supercolony was active at the site during the study.

Exclusion experiment

We conducted an exclusion experiment to test the hypothesis that highly abundant *A. fulica* affect seedling recruitment and standing leaf litter. The experiment consisted of 20-paired plots, each 2 × 2 m. Plots within pairs were a few metres apart, and pairs were irregularly spaced across the site, no closer than 20 m from each other. In each pair, *A. fulica* had unimpeded access to one plot (control) and were denied access to the other by a fence (exclusion).

Each exclusion fence was made from wire mesh (10 × 10 mm aperture) and secured to wooden corner posts. The fence was 0.8 m tall, with a 0.3-m-wide apron bent outwards and pegged to the ground to prevent snails from pushing their way underneath. The snails could climb on the vertical sides of the fences, but were prevented from climbing over the top by a 10 cm band of copper tape (Slugga) secured along both sides of the top. Overhanging vegetation was trimmed so that snails could not climb into the plots that way. Control plots were marked with wooden corner posts. The experiment was conducted over a single wet season for 6 months (December 2012–June 2013) when *A. fulica* was active. We did not observe the fences inhibiting small litter invertebrates (<10 mm in size) from gaining access to the exclusion plots, and there were no red crabs at the site due to the impacts of yellow crazy ants. Therefore, any treatment effect could be attributed to the exclusion of *A. fulica* >10 mm in size.

Plots were visited weekly to record *A. fulica* (<10 mm in size) density and maintain treatments. Density was recorded as the number of individuals within each plot (arboreal and terrestrial). Snails found in exclusion plots were recorded as the number of individuals within each plot (ar- boreal and terrestrial). Snails had free access to rain water and a source of calcium and proteins. Young and mature snails were marked with different colored skewsers (n = 5 each) and the sites were monitored for any uneaten leaves removed to ensure that snails were fed on a continuous diet of either fresh or decayed material. Snails had free access to rain water and a source of calcium and proteins. Young and mature snails were marked with different colored skewers (n = 5 each) and the site was monitored for any uneaten leaves removed to ensure that snails were fed on a continuous diet of either fresh or decayed material. Snails had free access to rain water and a source of calcium.

Diel activity

Belt transects were used to monitor diel activity of *A. fulica* at the experimental site. Three 50 × 1 m transects were established in April 2013 and surveyed monthly for 3 months. During each survey, the number of snails occurring on each transect was recorded during the morning (starting ~2 h after sunrise; 08:00–12:00 hours) and again at night (starting ~4 h after sunset; 20:00–24:00 hours). The position of each snail was recorded as either on the ground or on vegetation, and if the latter, at what height and on which species. Activity was recorded as either retracted within the shell (in) or extended out of the shell (out), and if the latter, the individual was moving, eating, engaged in mating or nothing. Food item (detritus, fresh leaf material, fruit) was noted when individuals were observed feeding.

Trophic position

In addition to direct observations of feeding (above), stable isotope ratios ($\delta^{13}$N and $\delta^{13}$C) were used to infer the trophic position and dietary source of *A. fulica* at the site of the exclusion experiment. This was undertaken in two ways. First, the stable isotope ratios from 10 field-collected *A. fulica* were compared against the isotopic baseline (fresh leaves and decaying leaf litter) and that of a known herbivore (Christmas Island stick insect *Ramulus nilpseudes*, n = 5), a detritivore (*Leptogoniulus sorornus*, n = 5) and a carnivore (spider *Nephila pilipes*, n = 4). Samples of fresh leaves were collected from four common species occurring in the understory (*C. indicum*, *D. gaudichaudiana*, *Hoya aldrichii* and *Ochrosia ackeringae* (Sapotaceae)). Samples of leaf litter were collected from five locations around the site. Samples were collected without regard to the state of decomposition because the stable isotope ratio of detritus material does not change through time (Meyer & Yeung 2011). All samples were hand collected from the field in July 2013 and preserved in 97% ethanol.

The second way in which we inferred trophic position was to compare the stable isotope ratios of field-collected *A. fulica* (above) against experimental *A. fulica* that were fed known diets. Forty mature snails (~40 mm length) were collected from the site and randomly assigned to one of two terrariums (60 × 30 × 40 cm) in a laboratory. Snails in one terrarium were fed a mix of fresh leaves from various species occurring at the site (most commonly *O. ackeringae*, *H. aldrichii*, *Aspenium nidus* (Aspleniaceae), *D. gaudichaudianum* and *Maclura cochinchinensis* var. *cochinchinensis* (Moraceae)), whereas snails in the other terrarium were fed leaf litter from a mix of species collected from the forest floor. New fresh leaves and litter were collected from the site weekly and stored in the fridge. Every 2–3 days, new leaves from the most recent collection were fed to the snails and any uneaten leaves removed to ensure that snails were fed on a continuous diet of either fresh or decayed material. Snails had free access to rain water and a source of calcium.

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(2–3 tennis ball-sized pieces of limestone collected from the site) throughout the experiment. After 3 months, all live individuals (fresh diet \( n = 8 \) of 20; detritus diet \( n = 16 \) of 20) were killed and tissue samples from the foot were collected for analysis. The experiment ran for 3 months. Samples from all field and experimental snails, and leaf and arthropod samples were returned to mainland Australia and analysed for \( \delta^{15}N \) and \( \delta^{13}C \) using an automated nitrogen carbon analyser system consisting of a 20–22 mass spectrometer and an elemental analyser (SERCON, UK).

Data analysis

Response variables (\( A. \) fulica density, leaf litter cover, bare ground cover, number of new seedling recruits, seedling mortality and total seedling recruits present) were modelled using generalized linear mixed models with Poisson distributions and logit link functions. Variables were modelled as a function of time and treatment with the replicate included as a random effect. Plots of residuals against fitted values, residual frequency histograms, quantile–quantile plots and residual variation box plots were examined to verify homogeneity and expected properties of residuals (Zuur et al. 2009). Tests for overdispersion were undertaken to assess if there was additional variance in the data than assumed by the Poisson distribution (Crawley 2013). If models were overdispersed, a random observation was included as a random effect. Response variables in which residuals were non-integers were modelled using a normal distribution. One-way ANOVA with Bonferroni post hoc tests was used to identify differences in \( \delta^{15}N \) and \( \delta^{13}C \) for \( A. \) fulica and samples of known trophic position. All analyses were performed using the lme4 (Bates et al. 2014) and statistics packages in R version 3.1.1 (R Core Team 2014).

RESULTS

Exclusion experiment

Despite occurring at high density (up to 6.25 snails \( m^{-2} \) on the control plots), \( A. \) fulica had no detectable impact on leaf litter or seedling dynamics. Coarse litter biomass decreased over the course of the wet season, but did not differ significantly between exclusion and control plots (Table 1; Fig. 1a). Similarly, there was no observed treatment effect on the percentage cover of leaf litter or bare ground (Table 2; Fig. 1b,c). There was a significant interaction between time and treatment for percentage leaf litter cover (Table 2), with cover in exclusion plots decreasing less rapidly (Fig. 1b). However, litter cover and biomass did remain slightly higher where \( A. \) fulica were excluded, albeit with overlapping confidence intervals with control plots (Fig. 1a,b).

The emergence of new seedling recruits was highest at the beginning of the experiment and decreased significantly over time (Table 2; Fig 2a). The exclusion of \( A. \) fulica had no effect on either the number of new seedling recruits (Table 2; Fig 2a) or seedling mortality (Table 2; Fig. 2b). The number of new seedling recruits present on a plot each month did not differ between treatments and did not change over the course of the experiment (Table 2; Fig. 2c).

Diel activity

In total, 585 diurnal and 635 nocturnal observations of \( A. \) fulica activity were made during the study. During the day, 96.9% of individuals were inside their shells, with the majority of those (73.7%) on the ground (Fig. 3). At night, 51.6% of individuals were out of their shell, with almost all of those (93.1%) on the ground. Of these active individuals, most were feeding (47.3%), and many were moving (29.0%) or simply doing nothing (21.9%). The consumption of dead leaves accounted for 95.8% of all feeding observations (\( n = 165 \)). Seven observations were of \( A. \) fulica consuming the fruit of \( O. \) ackeringae. \( Achatina fulica \) was not observed consuming fresh leaves. Individuals on vegetation (\( n = 214 \)) were observed on 14 different plant species; most commonly, \( Pandanus elatus \) (Pandanaceae) (25.7%), \( D. \) gauthierianum (15.0%) and \( I. \) fagifer (12.1%).

Trophic position

Stable isotope analysis revealed the carnivore (spider \( N. \) pilipes) to have a significantly higher \( \delta^{15}N \) (ANOVA; Table 1)

Table 1. Parameter estimates for predictors of coarse litter biomass on exclusion – control plots

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coarse litter biomass (g 0.016 m(^{-2}))</td>
<td>(Intercept)</td>
<td>5.59</td>
<td>0.47</td>
<td>11.93***</td>
</tr>
<tr>
<td></td>
<td>Time</td>
<td>−0.66</td>
<td>0.09</td>
<td>−7.73***</td>
</tr>
<tr>
<td></td>
<td>Treatment</td>
<td>0.75</td>
<td>0.43</td>
<td>−1.72</td>
</tr>
<tr>
<td></td>
<td>Time*Treatment</td>
<td>0.14</td>
<td>0.12</td>
<td>1.13</td>
</tr>
</tbody>
</table>

Results obtained by linear mixed models (LMM) with Poisson distribution using replicate as a random effect (***(** \( P < 0.001 \)).

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than all other groups (including fresh and detrital plant material), which did not differ from each other (Table 3). Carbon ratios ($\delta^{13}$C) did not differ among samples (ANOVA; $F_{7, 53} = 1.29, P = 0.27$) (Table 3). Nitrogen and carbon ratios for snails fed on exclusively fresh or detrital material and fresh or detrital plant material did not differ from each other (Table 3).

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detritus diets did not differ from each other or from snails collected from the field (Table 3).

**DISCUSSION**

We found no evidence that *A. fulica* in high density has any major impact on leaf litter cover and biomass or seedling recruitment in invaded rainforest on Christmas Island. *Achatina fulica* were found to be almost exclusively detritivorous, causing a small decrease in the amount of leaf litter present throughout the wet season, but not consuming those leaves at a rate that confidently separated their effect from natural decomposition. These findings are significant for two reasons. First, our study represents the only quantitative assessment of the impacts of *A. fulica* invasion in a natural ecosystem to date, and second, our findings demonstrate that the presumption of impact for highly abundant invasive species may sometimes be incorrect. These results support the contention of Civeyrel and Simberloff (1996) that described *A. fulica* in other areas as having little or no impact, and should therefore be considered a benign introduction.

Exclusion of *A. fulica* had no measurable treatment effect on the biomass or cover of leaf litter. This was surprising given that almost all feeding observations were of *A. fulica* consuming dead leaves from the forest floor. Elsewhere, *A. fulica* consume hundreds of plant species and are commonly referred to as a generalist feeder (Mead 1961; Raut & Barker 2002; Albuquerque et al. 2008). Our finding may not be the outcome of what *A. fulica* eats, but rather how much they eat. Anecdotal accounts describe high-density populations of *A. fulica* quickly consuming an entire crop of some agricultural species (Mead 1961; Raut & Barker 2002), but we found no study that quantified the amount of plant material they are capable of consuming. On Christmas Island, it seems individuals consume only a small proportion of detrital material available and therefore do not significantly alter standing leaf litter, even when in high densities. We observed a high proportion of *A. fulica* inside their shells during our diel surveys. Accounting for a species inactivity is important when considering niche opportunities and impacts of biological invasions (Shea & Chesson 2002). It is possible that high-density *A. fulica* have no significant impact on ground-layer dynamics in rainforest on Christmas Island because of high levels of inactivity.

The relative inactivity of *A. fulica* at our site may not be due simply to natural behaviours, but rather a response to the presence of an active yellow crazy ant supercolony. On Christmas Island, yellow crazy ants do not prey on *A. fulica* (Green et al. 2011), and

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Table 2. Parameter estimates for predictors of ground cover and seedling recruitment dynamics within our exclusion–control plots. Results obtained by generalized linear mixed models (GLMMs) with Poisson distribution using replicate as a random effect in all models.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground cover</td>
<td>(Intercept)</td>
<td>4.75</td>
<td>0.04</td>
<td>121.43***</td>
</tr>
<tr>
<td></td>
<td>Time</td>
<td>-0.08</td>
<td>0.01</td>
<td>-11.51***</td>
</tr>
<tr>
<td></td>
<td>Treatment</td>
<td>-0.02</td>
<td>0.03</td>
<td>-0.70</td>
</tr>
<tr>
<td></td>
<td>Time:Treatment</td>
<td>0.03</td>
<td>0.01</td>
<td>2.79***</td>
</tr>
<tr>
<td>Leaf litter (%)</td>
<td>(Intercept)</td>
<td>1.45</td>
<td>0.22</td>
<td>6.50***</td>
</tr>
<tr>
<td></td>
<td>Time</td>
<td>0.38</td>
<td>0.03</td>
<td>11.88***</td>
</tr>
<tr>
<td></td>
<td>Treatment</td>
<td>-0.12</td>
<td>0.18</td>
<td>-0.66</td>
</tr>
<tr>
<td></td>
<td>Time:Treatment</td>
<td>-0.07</td>
<td>0.05</td>
<td>0.14</td>
</tr>
<tr>
<td>Bare ground (%)</td>
<td>(Intercept)</td>
<td>2.15</td>
<td>0.50</td>
<td>4.25***</td>
</tr>
<tr>
<td></td>
<td>Time</td>
<td>-0.38</td>
<td>0.08</td>
<td>-4.80***</td>
</tr>
<tr>
<td></td>
<td>Treatment</td>
<td>-0.16</td>
<td>0.34</td>
<td>-0.47</td>
</tr>
<tr>
<td></td>
<td>Time:Treatment</td>
<td>0.01</td>
<td>0.10</td>
<td>0.10</td>
</tr>
<tr>
<td>New emergents/month</td>
<td>(Intercept)</td>
<td>-0.17</td>
<td>0.41</td>
<td>-0.40</td>
</tr>
<tr>
<td></td>
<td>Time</td>
<td>0.15</td>
<td>0.11</td>
<td>1.42</td>
</tr>
<tr>
<td></td>
<td>Treatment</td>
<td>0.34</td>
<td>0.43</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td>Time:Treatment</td>
<td>-0.16</td>
<td>0.09</td>
<td>-1.73</td>
</tr>
<tr>
<td>Emergent deaths/month</td>
<td>(Intercept)</td>
<td>2.00</td>
<td>0.42</td>
<td>4.73***</td>
</tr>
<tr>
<td></td>
<td>Time</td>
<td>0.07</td>
<td>0.25</td>
<td>1.53</td>
</tr>
<tr>
<td></td>
<td>Treatment</td>
<td>0.02</td>
<td>0.25</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Time:Treatment</td>
<td>-0.03</td>
<td>0.06</td>
<td>-0.52</td>
</tr>
<tr>
<td>Total emergents present/month</td>
<td>(Intercept)</td>
<td>2.00</td>
<td>0.42</td>
<td>4.73***</td>
</tr>
<tr>
<td></td>
<td>Time</td>
<td>0.07</td>
<td>0.25</td>
<td>1.53</td>
</tr>
<tr>
<td></td>
<td>Treatment</td>
<td>0.02</td>
<td>0.25</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Time:Treatment</td>
<td>-0.03</td>
<td>0.06</td>
<td>-0.52</td>
</tr>
</tbody>
</table>

Seedling recruitment models also contain a ‘random observation’ included as a random effect to correct for overdispersion (**P < 0.001).
there are no reports in the literature of yellow crazy ants preying on other land snail species. However, simply the presence of these formicine ants in high density (up to 1000 ant m$^{-2}$; Abbott 2006) may be disruptive for *A. fulica*, causing individuals to spend more time in their shells and less time feeding than they would otherwise. At the time of our study, no rainforest sites where both yellow crazy ants and red crabs were absent supported a high-density population of *A. fulica*. Future research could focus on

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The location and activity of observed *Achatina fulica*. Percentage of individuals found inside (In) or outside (Out) of their shell either on the ground (Ground) or on vegetation (Veg) during the day (a) or night (b). (c,d) Percentage of active individuals (Out) involved in a particular action (feeding, moving, mating or nothing) during the day (c) or night (b).

**Table 3.** Sample description and isotopic values (mean ± 1 SE; δ^{15}N and δ^{13}C) for *Achatina fulica* and samples from other trophic positions

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Tissue used</th>
<th>n</th>
<th>δ^{15}N (%)</th>
<th>δ^{13}C (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baseline</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fresh plant</td>
<td>Leaf</td>
<td>20</td>
<td>5.18 ± 0.56</td>
<td>-28.50 ± 1.74</td>
</tr>
<tr>
<td>Detritus plant</td>
<td>Leaf</td>
<td>5</td>
<td>6.29 ± 0.77</td>
<td>-30.89 ± 0.70</td>
</tr>
<tr>
<td>Herbivore</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stick insect</td>
<td>Leg</td>
<td>5</td>
<td>5.08 ± 0.22</td>
<td>-29.14 ± 0.28</td>
</tr>
<tr>
<td>Detritivore</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Millipede</td>
<td>Whole body</td>
<td>5</td>
<td>5.77 ± 0.89</td>
<td>-24.79 ± 0.61</td>
</tr>
<tr>
<td>Carnivore</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spider</td>
<td>Leg</td>
<td>4</td>
<td>12.12 ± 0.98</td>
<td>-25.93 ± 0.40</td>
</tr>
<tr>
<td><em>Achatina fulica</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Field</td>
<td>Foot muscle</td>
<td>10</td>
<td>7.27 ± 0.16</td>
<td>-25.76 ± 0.21</td>
</tr>
<tr>
<td>Fresh diet</td>
<td>Foot muscle</td>
<td>8</td>
<td>8.01 ± 0.17</td>
<td>-24.06 ± 0.19</td>
</tr>
<tr>
<td>Detritus diet</td>
<td>Foot muscle</td>
<td>16</td>
<td>7.61 ± 0.08</td>
<td>-25.11 ± 0.21</td>
</tr>
</tbody>
</table>

Values denoted with the same superscript letter do not differ significantly (ANOVA with Bonferroni post hoc tests).
areas with those conditions, and low-density *A. fulica* populations, to determine whether snail activity is higher in the absence of yellow crazy ants.

It is unlikely that the lack of a treatment effect on leaf litter cover and biomass was the result of compensation by other detritivores increasing their abundance and influence on exclusion plots. Other species of land snail are also found in high numbers with *A. fulica* following the impacts of yellow crazy ant invasion (O’Loughlin & Green 2015), suggesting very little competition exists between these species (Barker & Mayhill 1999). Furthermore, we found no examples in the literature of *A. fulica* or other land snail species exhibiting competitive dominance over leaf litter processing, meaning it was likely that control and exclusion plots contained similar numbers of other ground-dwelling invertebrates. Similarly, plots were paired and arranged in such a way that it was unlikely that litter input differed between treatments, thereby masking an effect of *A. fulica*. Research that directly considered the role of other detritivores in the system, the rate of litter accumulation and seasonal variation would complement our study by providing further insight into the true impact of *A. fulica* on standing leaf litter.

Exclusion of *A. fulica* had no effect on seedling recruitment or mortality. *Achatina fulica* is described as a generalist and opportunistic herbivore/detritivore (Mead 1961; Raut & Barker 2002), yet we did not observe herbivory on any new seedling germinants during our study. The lack of an impact on seedling recruitment dynamics is not surprising if *A. fulica* is predominantly detritivorous. The literature on *A. fulica* notably lacks quantitative data on feeding preferences, particularly in natural communities (Raut & Barker 2002). However, anecdotal accounts have suggested their dietary preference may change across life stages with the youngest *A. fulica* feeding on decaying matter, juveniles preferring the fresh leaves of younger plants and adults behaving primarily as detritivores while not completely ignoring fresh material (van Weel 1948/49; Dun 1967; Olson 1973). The potential for this kind of ontogenetic dietary shift has been demonstrated by Ciomperlik et al. (2013) who found that pellet formulations of molluscicides were most effective at killing juvenile *A. fulica* because they are predominantly herbivorous, compared to liquid and granular formulations that were more effective on other, predominantly detritivorous, life stages. Our study was focussed on assessing the impacts of a high-density population of *A. fulica* (>10 mm in size) that were observed to be almost exclusively detritivorous. It is clear from these examples and others (i.e. Meyer et al. 2008) that the dietary preference of *A. fulica* remains under-researched and poorly understood.

Our conclusion that *A. fulica* is highly detritivorous is based entirely on behavioural observations. Investigation into trophic position using stable isotopes was inconclusive, failing to confidently differentiate field-collected *A. fulica* from either known herbivores and detritivores, or from *A. fulica* individuals with known fresh plant or detrital diets. This method has been used successfully by others to determine trophic position (nitrogen ratios $\delta^{15}N$; Post 2002) and dietary source (carbon ratios $\delta^{13}C$; Ostrom et al. 1997) for a number of land snail species within a tropical community (Meyer & Yeung 2011). Our samples may have been affected by the time spent in ethanol, although many studies have concluded ethanol preservation has little affect on both $\delta^{15}N$ and $\delta^{13}C$ values (Sarakinos et al. 2002; Barrow et al. 2008). The *A. fulica* individuals of known diets may not have had sufficient time to assimilate the isotopic signature of their diet, yet the high mortality in the group fed an exclusively fresh diet meant the experiment could not run for longer. That result alone may suggest that *A. fulica* is highly detritivorous and performs poorly on an exclusively fresh diet of Christmas Island plant species.

*Achatina fulica* is widely documented to consume live plant material (Mead 1961; Corlett & Rungoria 1983; Raut & Barker 2002; Albuquerque et al. 2008), and was observed at our study site and elsewhere on Christmas Island up to several metres high in the foliage consuming fresh leaves (L.S. O’Loughlin & P.T. Green, pers. obs., 2013). However, that none of the snails observed in the transect surveys were found consuming fresh leaf material suggests this must be a comparatively rare behaviour. One reason for this could be that the vegetation of Christmas Island rainforest may be relatively unpalatable to *A. fulica* compared to where they have been observed to be highly herbivorous (Albuquerque et al. 2008). Around one-quarter of *A. fulica* individuals observed were on the trunks and stems of seedlings during the day and the few individuals on vegetation during the night were almost exclusively observed moving toward the ground. We suggest that most arboreal behaviour of *A. fulica* on Christmas Island is for something other than using arboreal resources for food, such as ingrained predator avoidance (Mead 1961).

Any impact of *A. fulica* on Christmas Island may be on something other than the key ecological processes investigated here. Elsewhere, these snails are thought to impact the abundance of other land snail species either by direct competition or indirectly by fouling the habitat with excessive faeces and mucus (Giveyrel & Simberloff 1996; Raut & Barker 2002; Thiengo et al. 2007). However, high-density populations of other land snail species are present in rainforest void of red crabs on Christmas Island that may also contain abundant *A. fulica* (O’Loughlin & Green...
2015). *Achatina fulica* may have a negative impact on human health, as it is a known intermediate host for the nematode responsible for eosinophilic meningoencephalitis (Cheng & Alicata 1965), yet so are many other species (Kim et al. 2014). Civeyrel and Simberloff (1996) suggested that this potential impact has been exaggerated and in fact *A. fulica* are not a serious hazard to human health. *Achatina fulica* has been noted as a road hazard, causing cars to skid when driving over large numbers (Mead 1961), which may be applicable to Christmas Island where mass breeding concentrations of snails are commonly observed on the crushed-limestone roads (Authors pers. obs.).

**CONCLUSIONS**

We found little evidence to support the assumption that highly abundant *A. fulica* cause impact in an invaded natural rainforest. On Christmas Island, *A. fulica* appear to be eating a relatively small quantity of dead leaves and doing little else. This benign introduction would be easily managed by restoring the ecosystem’s natural biotic resistance, through the recovery of red crab populations (Green et al. 2011). Although a challenge, past management actions have resulted in many areas being re-colonized by red crabs following the removal of yellow crazy ant supercolonies (Green et al. 2011). In this context, managing the mechanism which facilitates the entry and spread of *A. fulica* — yellow crazy ant invasion — should continue to be prioritized (Neumann et al. 2016) in preference to direct control of this secondary invader.

Our study represents an important first step in quantifying the impacts of *A. fulica* and assessing the assumption that abundance always precipitates impact. Ecosystem-level impacts of invasive species can be subtle and remain unnoticed even when dedicated research is undertaken (Simberloff 2011; Vilà et al. 2011). Any impact may also not become apparent until long after the species has invaded (Yokomizo & Possingham 2009), such that significant higher management costs are incurred if no initial action was undertaken (Pyšek & Richardson 2010). Further research that continues our approach beyond a single season is required to understand the longer-term dynamics of *A. fulica* invasion. A cautious approach is still recommended when aiming to minimize both the impacts of invasive species and the effort and cost of management actions. On Christmas Island, *A. fulica* should be considered an invader with minimal impact (Blackburn et al. 2014) and therefore a targeted approach to their management is unnecessary.

**ACKNOWLEDGMENTS**

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

**Appendix S1.** *Achatina fulica* density (4 m$^{-2}$) to experimental treatments (*A. fulica* exclusion and control) and time (week) as calculated by generalized linear mixed models (GLMMs).