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Endemic predators, invasive prey and native diversity

Thomas C. Wanger[1,2,*], **Arno C. Wielgoss**[2], **Iris Motzke**[2],
Yann Clough[2], **Barry W. Brook**[1], **Navjot S. Sodhi**[3]
and Teja Tscharntke[2]

[1]*Environment Institute and School of Earth and Environmental Sciences, University of Adelaide, Adelaide, Australia*
[2]*Agroecology, University of Göttingen, Göttingen, Germany*
[3]*Department of Biological Sciences, National University of Singapore, Singapore*

Interactions between native diversity and invasive species can be more complex than is currently understood. Invasive ant species often substantially reduce diversity in the native ants diversity that act as natural control agents for pest insects. In Indonesia (on the island of Sulawesi), the third largest cacao producer worldwide, we show that a predatory endemic toad (*Ingerophrynus celebensis*) controls invasive ant (*Anoplolepis gracilipes*) abundance, and positively affects native ant diversity. We call this the invasive-naivety effect (an opposite of enemy release), whereby alien species may not harbour anti-predatory defences against a novel native predator. A positive effect of the toads on native ants may facilitate their predation on insect vectors of cacao diseases. Hence, toads may increase crop yield, but further research is needed on this aspect. Ironically, amphibians are globally the most threatened vertebrate class and are strongly impacted by the conversion of rainforest to cacao plantations in Sulawesi. It is, therefore, crucial to manage cacao plantations to maintain these endemic toads, as they may provide critical ecosystem services, such as invasion resistance and preservation of native insect diversity.

Keywords: amphibians; ants; biocontrol; ecosystem services; invasive-naivety effect

1. INTRODUCTION

Cacao is the largest international trade commodity after petroleum and coffee, and currently covers 8 million ha in the tropics [1]. Cacao plantations, despite their structural similarities to natural tropical forests, harbour reduced biodiversity, especially when shade trees are removed to maximize crop yields [2,3]. The effects of land-use change can be further intensified when these agricultural areas are subsequently colonized by invasive species, particularly on remote islands with high endemism [4,5]. Structural simplification in plantations can also compromise the ecosystem services provided by native biodiversity. Natural ant diversity, for example, has been shown to regulate insect vectors of cacao pests and decrease the risk of disease outbreaks [6]. Introductions of the yellow crazy ant (*Anoplolepis gracilipes*) are known to affect native biodiversity and ecosystem processes on islands [7,8]. As a result, *A. gracilipes* is ranked among the top 100 invasive species worldwide [9].

A ubiquitous (yet expensive and often unsuccessful) approach to controlling invasive ant species in poor developing countries is the heavy application of pesticides, which can also damage native biodiversity and human health [10]. Theoretically, native diversity could provide free services by controlling invasive ants and mitigating pesticide use [11]. This requires that native predators become effective predators of invasive ants (figure 1). Further, the native predator should be abundant, ground-living and, ideally, an ant specialist. The common celebes toad (*Ingerophrynus celebensis*) and a skink (*Eutropis grandis*) are the most abundant ground-living vertebrates in the cacao plantations of Sulawesi [12]. To assess their roles as invasive ant control agents, we first determined dietary preferences of these two species and then experimentally excluded ant-predating specialists (the toads) from cacao plantations. We tested the hypothesis that an endemic amphibian species can control an invasive ant and thereby alleviate its impact on natural ant diversity.

2. MATERIAL AND METHODS

(a) *Amphibian, reptile and ant sampling*

To predict toad and lizard abundances by different ant species abundances and richness, we collected data from 43 cacao plots (40×40 m; 21 cacao agroforest and 22 cacao monoculture plantations) around the Lore Lindu National Park in Central Sulawesi (Indonesia). Amphibians and reptiles were sampled three times during day and night with visual and acoustic encounter surveys [12]. Ants were sampled with observation plates (10 on the ground and 10 in the trees) on each plantation, baited with tuna and sugar solution. For ant recruitment rates (hereafter we refer to 'ant abundance' for clarity) and species richness, we counted the number of ant individuals and species on each plate every 15 min for 1 h. We used the mean maximum number of all plates as a measure of ant abundances per plot. For ant diversity, we used the total number of species encountered in the plot [13].
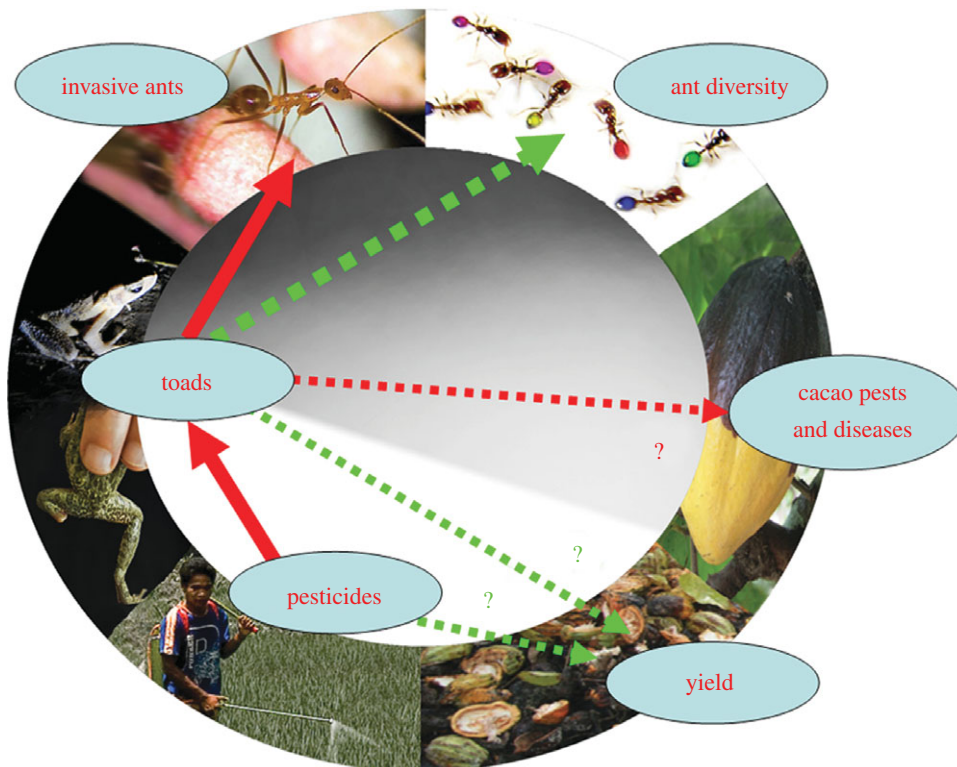
Figure 1. Toad abundance reduces invasive ant abundance and thereby positively affects native ant diversity (red and green dashed arrow, respectively, in dark grey area). The literature suggests that a decline in native ant diversity increases disease outbreak frequency (light grey area), which probably affects crop yield. However, excessive pesticide application may hamper toad ecosystem services (red arrow). Effects of the toads on cacao disease and yield are not yet confirmed (question marks). Thickness of arrows indicates strength of an effect; dashed arrows resemble an indirect effect. Red arrows mean a negative and green a positive relationship between two groups.

(b) *Biomass analysis: faeces and reference data from the cacao plantations*

We collected faeces samples of amphibians and reptiles between December 2007 and August 2009, and analysed arthropod species composition. All individuals captured in the 43 plots were kept in plastic containers for 12 h and faeces were collected. We identified the prey items found in faeces samples to taxonomic order whenever identifiable species parts were available, and where possible we quantified individual numbers (e.g. counting the number of heads, thoraxes etc.). We equated hymenopterans with ants, because we mainly identified ant remnants in the faeces; thus, we assume that bees and wasps are less likely prey items for these lizard and toad species. We used five Barber traps randomly placed within a plot equipped with a 1 : 1 ethylene : glycol solution. The traps were emptied twice (once every four weeks) over a period of two months. We identified the samples to taxonomic order and measured dry weight. The summed biomass of all traps within a plot was used for standardization of the faeces biomass.

(c) *Toad exclosure*

The toads migrate through the plantations to form calling choruses in the rice fields roughly every three months. They stay in the plantations for an average of one week, where their abundance can reach up to 300 toads per hectare (T. C. Wanger & I. Motzke 2008, personal observation). In contrast to the control plots, we expected that by excluding the toads from treatment plots, *Anoplolepis* abundance would increase owing to a lack of toad predation. If this is a long-lasting effect, the removal of the exclosure would not change ant abundance patterns when few or no toads are present in the plantations. Therefore, exclosures were removed.

For the fence exclosure experiment, 14 plots (10×10 m; for environmental details, see electronic supplementary material, table S1 and figures S1 and S2) with *Anoplolepis* present were sampled four times in cacao agroforests. Ant abundances were determined once in the evening and morning over 7 days; on the first day before an exclosure fence had been established, the third and fifth day after the fence had been established and on the seventh day after the fence had been removed. Seven plots were randomly assigned to treatment and control groups. While the control plots were only disturbed on the edges for all sampling sessions, we built 50-cm-tall exclosures of 3 mm-wide plastic mesh on the treatment plots. Fences and exclosures were maintained every day and checked every night for toads inside the fence. In all plots and sampling sessions, ant diversity and *Anoplolepis* abundance—as the only invasive species present—were determined with four sampling plates per plot, baited with tuna and sugar solution [13]. We only used four plates because increasing the number of plates may have resulted in unrealistic abundances owing to overabundant food sources. Time frames were chosen so that the evening sample was conducted before the toads moved through the experimental area and the morning sampling was after the toads had finished feeding in the area. For the analysis, we pooled abundance data from morning and evening sampling sessions for higher robustness of samples

(e.g. climatic variation between morning and evening sessions may potentially lead to changes in ant abundances).

We sampled the plots for one week to minimize confounding climatic effects in the field rather than accounting for it in the models with limited sample size. Only 14 sites were sampled because each site had to fulfil a strict set of requirements for a robust sampling design: (i) toads had not moved through the cacao plot prior the first sampling session (all candidate sites were checked every night over a three-month period), (ii) toads were moving through the plots until the third sampling session was completed, and (iii) climatic conditions were suitable and similar for the ants (i.e. no rain or wet soil) to minimize confounding climatic effects on the results.

(d) Analysis
We used Bayesian linear modelling with multi-model inference to determine whether individual ant species abundances and general fossorial ant diversity were drivers for toad and lizard abundance. We defined three *a priori* main hypotheses that were challenged in a Bayesian multi-model inference approach: (i) cumulative abundance of large ants (i.e. *A. gracilipes*, *Paratrechina longicornis*, *Pheidologeton* sp., *Philidris* sp.), (ii) individual large ant abundances or (iii) ground-dwelling ant species richness drive abundance patterns in the most common amphibian and reptile species. For an introduction of Bayesian model evaluation, see [14] and the supplementary material of [12].

The exclosure experiment and its impact on ant diversity were analysed with a Bayesian repeated-measures ANOVA, where the first sampling session was specified as the reference level, and site was coded as a random effect to account for spatial differences not accounted for in the fixed effects. The treatment effect was modelled as an interaction with the sampling session, because we were interested in the exclosure effects over time and not a treatment effect *per se*. To reduce the predictors in the model, we used the relative abundance and relative native ant species richness (i.e. difference between treatment and control plots) as response variables.

3. RESULTS
Dietary analyses revealed that ants dominated arthropod biomass (74%; standardized by plantation arthropod biomass) in the faeces samples of the toad. In the skink faeces, ants played a minor role and prey items were evenly distributed between arthropod orders (electronic supplementary material, figure S3). A comparison of arthropod biomass removal between cacao agroforest and monoculture plantations revealed that *I. celebensis* had the highest impact on ant biomass (i.e. 45%) in both habitats. *Eutropis grandis* had the greatest impact on orthopterans and dermapterans (i.e. 26 and 65% in cacao agroforest and monocultures, respectively; electronic supplementary material, figure S4). Based on behavioural observations of toads feeding on ants (see also [15]), we are confident that results from the faecal analysis are not strongly biased (i.e. soft-bodied prey items are unlikely to be fully digested and thus overlooked).

Bayesian regression modelling showed that abundance of *Anoplolepis* ants was the strongest predictor of toad abundance; the model explained 19.4 per cent of the deviance in the data and was greater than 1 000 000
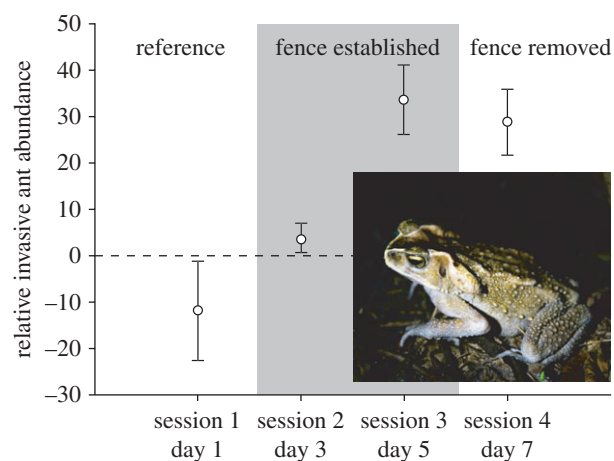

Figure 2. Effects of native toad exclosure on invasive yellow crazy ant (*A. gracilipes*) abundance. Shown is the treatment effect of the exclosure fence (sessions 2 and 3, grey) relative to the reference (session 1). Fence removal (session 4) served to show persistence of ant abundance changes over time. The photo shows a female common celebes toad (*I. celebensis*). The means (black dots $\pm$95% credibility intervals) represent the relationship of ant abundance between treatment and control plots as derived from a Bayesian linear mixed-effects model.

more likely than the null relationship (electronic supplementary material, table S2). Skink abundance was predicted by abundance of large ant species in general, but the relationship was weaker, with 7.7 per cent deviance explained. These results suggest that—as an *Anoplolepis* predator—the toads choose plantations with higher *Anoplolepis* abundance, and are abundant in cacao plantations during regular migration to their breeding grounds in rice fields at night.

A Bayesian repeated-measures ANOVA revealed a treatment (i.e. toad exclosure) effect over time relative to the reference sample (i.e. the first sampling session (session 1) before the exclosure fence was built; figure 2). We found measurable effects at all four sample sessions; the credibility intervals do not overlap with zero. While the relationship between treatment and control plots at the reference sample is negative (session 1: -11.9 (-22.5 to -1.2)), this relationship inverts over time (session 2: 3.5 (0.6–6.9)) and remains positive even after the fence is removed in the last sampling session (as suggested by the overlapping credibility intervals in the last two sessions, sessions 3 and 4: 33.6 (26.2–41.1)) and 28.7 (21.7–35.9), respectively). These effects were not confounded by the presence of the skink, because it is diurnal and not specialized on ants. In contrast, toads forage most actively at midnight, because their calling period has ended and their energy requirements are at their highest (T. C. Wanger & I. Motzke 2008, personal observation; [16]). *Anoplolepis* activity also peaked around midnight, but was constant throughout the day (electronic supplementary material, figure S5).

We found that overall mean ant diversity did not measurably differ between treatment and control plots in the reference sampling session, but decreased over time (0.8 (-1.8 to 3.2); -1.5 (-4.7 to 1.8); -2.1 (-5.1 to 1.1); -2.9 (-6.0 to 0.45); figure 3). As the credibility intervals
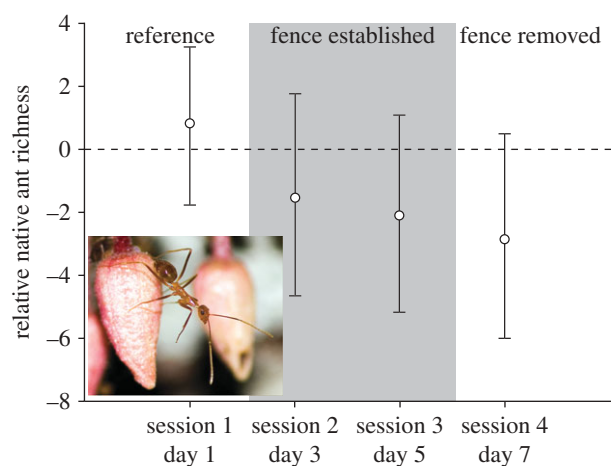
Figure 3. Effects of toad exclosure on native ant diversity. Shown is the treatment effect of the exclosure fence (sessions 2 and 3, grey) relative to the reference (session 1). As in figure 2, fence removal (session 4) served to show persistence of ant abundance changes over time. The photo shows *A. gracilipes* on a cacao flower, where this species is tending Homoptera (T. C. Wanger 2009, personal observation). The means (black dots $\pm$95% credibility intervals) represent the relationship of native ant species richness between treatment and control plots as derived from a Bayesian linear mixed-effects model.

of all sampling sessions overlap with zero, we found a strong trend but no effect of the manipulation (and, hence, *Anoplolepis* abundance) on ant diversity over time.

4. DISCUSSION

Island endemics are often claimed to be inferior competitors to invasive species, because they have been released from selective pressures [17]. We show that an island endemic toad (*I. celebensis*), as a predator, negatively affects the noxious invasive ant *A. gracilipes*, and this, in turn, mitigates the impact of *A. gracilipes* on natural ant diversity. Thus, in contrast to an enemy-release effect, this is an invasive-naivety effect: the alien prey species may not harbour anti-predatory defence against the novel endemic predator. This effect may be widespread and so offer resistance to biotic invasions.

For an invasive-naivety effect to occur, the native species must possess certain defensive and dietary traits. The invasive success of the ant *A. gracilipes* is grounded in its tendency to aggregate in high densities, aggressiveness and chemicals used for attack [18,19]. Bufonids have a tough skin capable of producing potent toxins [20], and amphibian skin can be distasteful for ants [21]. In addition, toads are sit-and-wait predators, sometimes exclusively feeding on ants [15]. As endemic toads probably have been ant specialists *before* the invasion occurred, their prey search image may be 'pre-set' for an *Anoplolepis* type of prey. Density-dependent predation of the toads on the abundant invasive ants may be a likely explanation of the reduction of *A. gracilipes* abundance. In addition, there may be nutritious preferences for the invasive to the native ants such as essential amino acid composition. A preference for *A. gracilipes* may lead to reduction in their abundance owing to toad predation.

Based on skin defences and potential predefined feeding preference of many toads, there may be a general potential for bufonids as biocontrol agents; this is an area in need of further research.

Intuitively, toads can only provide useful ecosystem services if they are abundant; yet (endemic) amphibians are the most threatened vertebrates on the planet [22]. If toad populations are reduced as a result of land-use change and pesticide use [23,24], our results suggest that *A. gracilipes* can flourish as an 'ecosystem transformer' (figure 1). In Sulawesi, rapid expansion of these ants drastically depletes natural ant diversity [25]. This may have a real economic impact because native ants in Southeast Asia have been shown to provide various ecosystem functions, including biocontrol of insect-mediated cacao pests (see table 1 in [6]). On other islands, *A. gracilipes* affects litter decomposition and nutrient cycling [26], trophic cascades [7] and even the tourism industry (via displacement of a bird species [27]). These negative impacts may, however, take several decades to unfold fully; on Christmas Island, yellow crazy ant populations exploded 60 years after its introduction [28].

The economic magnitude of the toad's biocontrol service in cacao agroforestry systems is, however, conditional on parameters affecting cacao yield and *Anoplolepis*'s effectiveness as a predator of cacao pest insect vectors. In Sulawesi, both pest and disease occurrence are important determinants of cacao yield [29]. Thus, the less effective *Anoplolepis* is as a predator on disease vectors relative to the native ant species, intuitively more economical it is to have the toads in cacao plantations. It is possible that the time period to detect an effect of invasive ants on the native ant species in our study may be too short. However, it has previously been shown that *A. gracilipes* depletes native ant diversity in Sulawesi's cacao plantations [25]; thus, we believe that our results indicate effects that will be evident over the long term.

Clearly, then, it is important to maintain toads and other amphibian populations in cacao plantations to sustain ecosystem services in the future. Plantation management for leaf litter cover and maintenance of intact canopy structure to buffer against temperature fluctuations will benefit amphibian diversity [12]. This will also facilitate toad abundance in cacao agroforest and, hence, translate into ant biomass removal. In contrast, *A. gracilipes* invasions are facilitated by thinned canopy, which alters microclimatic conditions in cacao plantations and enhances the frequency of cacao disease outbreaks [25]. It is through the beneficial effect for the toads in cacao agroforest that biomass removal of ants will increase. Managed sensibly, native biodiversity offers great potential to provide invasion resistance [30] and probably contributes to sustainable, pesticide-reduced crop production.

REFERENCES

1 FAOSTAT. 2009 FAO statistical databases. See http://faostat.fao.org/site/567/default.aspx#ancor.

2 Schroth, G. & Harvey, C. 2007 Biodiversity conservation in cocoa production landscapes: an overview. *Biodivers. Conserv.* **16**, 2237–2244. (doi:10.1007/s10531-007-9195-1)

3 Clough, Y. *et al.* 2009 Biodiversity patterns and trophic interactions in human-dominated tropical landscapes in Sulawesi (Indonesia): plants, arthropods and vertebrates. In *Tropical rainforests and agroforests under global change* (eds T. Tscharntke, C. Leuschner, E. Veldkamp, H. Faust, E. Guhardja & A. Bidin), pp. 15–71. Berlin, Germany: Springer Verlag.

4 Roemer, G. W., Donlan, C. J. & Courchamp, F. 2002 Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. *Proc. Natl Acad. Sci. USA* **99**, 791–796. (doi:10.1073/pnas.012422499)

5 Wagner, D. L. & Van Driesche, R. G. 2010 Threats posed to rare or endangered insects by invasions of nonnative species. *Ann. Rev. Entomol.* **55**, 547–568. (doi:10.1146/annurev-ento-112408-085516)

6 Philpott, S. M. & Armbrecht, I. 2006 Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecol. Entomol.* **31**, 369–377. (doi:10.1111/j.1365-2311.2006.00793.x)

7 O'Dowd, D. J., Green, P. T. & Lake, P. S. 2003 Invasional 'meltdown' on an oceanic island. *Ecol. Lett.* **6**, 812–817. (doi:10.1046/j.1461-0248.2003.00512.x)

8 McNatty, A., Abbott, K. & Lester, P. 2009 Invasive ants compete with and modify the trophic ecology of hermit crabs on tropical islands. *Oecologia* **160**, 187–194. (doi:10.1007/s00442-009-1279-z)

9 GISD. 2007 Global Invasive Species Database. See http://www.issg.org/database/species/search.asp?st=100ss.

10 Wanger, T. C., Rauf, A. & Schwarze, S. 2010 Pesticides and tropical biodiversity. *Front. Ecol. Environ.* **8**, 178–179. (doi:10.1890/10.WB.015)

11 Chivian, E. & Bernstein, A. 2008 *Sustaining life: how human health depends on biodiversity* New York, NY: Oxford University Press.

12 Wanger, T. C., Saro, A., Iskandar, D. T., Brook, B. W., Sodhi, N. S., Clough, Y. & Tscharntke, T. 2009 Conservation value of cacao agroforestry for amphibians and reptiles in South-East Asia: combining correlative models with follow-up field experiments. *J. Appl. Ecol.* **46**, 823–832. (doi:10.1111/j.1365-2664.2009.01663.x)

13 Wielgoss, A., Tscharntke, T., Buchori, D., Fiala, B. & Clough, Y. 2010 Temperature and a dominant dolichoderine ant species affect ant diversity in Indonesian cacao plantations. *Agr. Ecosyst. Environ.* **135**, 253–259. (doi:10.1016/j.agee.2009.10.003)

14 McCarthy, M. 2007 *Bayesian methods for ecology.* Cambridge, UK: Cambridge University Press.

15 Clarke, R. D. 1974 Food habits of toads, genus *Bufo* (Amphibia, Bufonidae). *Am. Midl. Nat.* **91**, 140–147.

16 Wells, K. D. 2001 The energetics of calling in frogs. In *Anuran communication* (ed. M. J. Ryan), pp. 45–60. Washington, DC: Smithsonian Institute Press.

17 Simberloff, D. 2010 Invasive species. *Conservation biology for all* (eds N. S. Sodhi & P. R. Ehrlich), pp. 131–152. Oxford, UK: Oxford University Press.

18 Holway, D. A., Lach, L., Suarez, A. V., Tsutsui, N. D. & Case, T. J. 2002 The causes and consequences of ant invasions. *Ann. Rev. Ecol. Syst.* **33**, 181–233. (doi:10.1146/annurev.ecolsys.33.010802.150444)

19 Kenis, M., Auger-Rozenberg, M.-A., Roques, A., Timms, L., Pere, C., Cock, M. J. W., Settele, J., Augustin, S. & Lopez Vaamonde, C. 2009 Ecological effects of invasive alien insects. *Biol. Invasions* **11**, 21–45. (doi:10.1007/s10530-008-9318-y)

20 Zug, G. R., Vitt, L. J. & Caldwell, J. P. 2001 *Herpetology: an introductory biology of amphibians and reptiles,* 2nd edn. San Fransisco, CA: Academic Press.

21 Fritz, G., Rand, A. S. & Depamphilis, C. W. 1981 The aposematically colored frog, *Dendrobates pumilio,* is distasteful to the large, predatory ant, *Paraponera clavata. Biotropica* **13**, 158–159.

22 Rowley, J. *et al.* 2009 Impending conservation crisis for southeast Asian amphibians. *Biol. Lett.* **6**, 336–338. (doi:10.1098/rsbl.2009.0793)

23 Relyea, R. A. 2005 The impact of insecticides and herbicides on the biodiversity and productivity of aquatic communities. *Ecol. Appl.* **15**, 618–627. (doi:10.1890/03-5342)

24 Wanger, T. C., Iskandar, D. T, Motzke, I., Brook, B. W., Sodhi, N. S., Clough, Y. & Tscharntke, T. 2010 Land-use change affects community composition of tropical amphibians and reptiles in Sulawesi (Indonesia). *Conserv. Biol.* **24**, 795–802. (doi:10.1111/j.1523-1739.2009.01434.x)

25 Bos, M. M., Tylianakis, J. M., Steffan-Dewenter, I. & Tscharntke, T. 2008 The invasive Yellow Crazy Ant and the decline of forest ant diversity in Indonesian cacao agroforests. *Biol. Invasions* **10**, 1399–1409. (doi:10.1007/s10530-008-9215-4)

26 Dunham, A. E. & Mikheyev, A. S. 2010 Influence of an invasive ant on grazing and detrital communities and nutrient fluxes in a tropical forest. *Divers. Distrib.* **16**, 33–42. (doi:10.1111/j.1472-4642.2009.00620.x)

27 Feare, C. 1999 Ants take over from rats on Bird Island, Seychelles. *Bird Conserv. Int.* **9**, 94–95.

28 Abbott, K. L. 2005 Supercolonies of the invasive yellow crazy ant, *Anoplolepis gracilipes,* on an oceanic island: forager activity patterns, density and biomass. *Insectes Soc.* **52**, 266–273. (doi:10.1007/s00040-005-0800-6)

29 Juhrbandt, J., Duwe, T., Barkmann, J., Gerold, G. & Marggraf, R. 2010 Structure and management of cocoa agroforestry systems in Central Sulawesi across an intensification gradient. In *Tropical rainforests and agroforests under global change* (eds T. Tscharntke, C. Leuschner, E. Veldkamp, H. Faust, E. Guhardja & A. Bidin), pp. 115–140. Berlin, Germany: Springer Verlag.

30 Carlsson, N. O. L., Sarnelle, O. & Strayer, D. L. 2009 Native predators and exotic prey: an acquired taste? *Front. Ecol. Environ.* **7**, 525–532. (doi:10.1890/080093)